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Words in the brain's language

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Abstract: If the cortex is an associative memory, strongly connected cell assemblies will form when neurons in different cortical areas are frequently active at the same time. The cortical distributions of these assemblies must be a consequence of where in the cortex correlated neuronal activity occurred during learning. An assembly can be considered a functional unit exhibiting activity states such as full activation ("ignition") after appropriate sensory stimulation (possibly related to perception) and continuous reverberation of excitation within the assembly (a putative memory process). This has implications for cortical topographies and activity dynamics of cell assemblies forming during language acquisition, in particular for those representing words. Cortical topographies of assemblies should be related to aspects of the meaning of the words they represent, and physiological signs of cell assembly ignition should be followed by possible indicators of reverberation. The following postulates are discussed in detail: (1) assemblies representing phonological word forms are strongly lateralized and distributed over perisylvian cortices; (2) assemblies representing highly abstract words such as grammatical function words are also strongly lateralized and restricted to these perisylvian regions; (3) assemblies representing concrete content words include additional neurons in both hemispheres; (4) assemblies representing words referring to visual stimuli include neurons in visual cortices; and (5) assemblies representing words referring to actions include neurons in motor cortices. Two main sources of evidence are used to evaluate these proposals: (a) imaging studies focusing on localizing word processing in the brain, based on stimulus-triggered event-related potentials (ERPs), positron emission tomography (PET), and functional magnetic resonance imaging (fMRI), and (b) studies of the temporal dynamics of fast activity changes in the brain, as revealed by high-frequency responses recorded in the electroencephalogram (EEG) and magnetoencephalogram (MEG). These data provide evidence for processing differences between words and matched meaningless pseudowords, and between word classes, such as concrete content and abstract function words, and words evoking visual or motor associations. There is evidence for early word class-specific spreading of neuronal activity and for equally specific high-frequency responses occurring later. These results support a neurobiological model of language in the Hebbian tradition. Competing large-scale neuronal theories of language are discussed in light of the data summarized. Neurobiological perspectives on the problem of serial order of words in syntactic strings are considered in closing.

Keywords: associative learning; cell assembly; cognition; cortex; ERP; EEG; fMRI; language; lexicon; MEG; PET; word category

1. Words in the brain: Where? Why? How?

Human language production is caused by neuronal activity and any speech signal necessarily activates neurons in the brains of listeners when being perceived. It is the purpose of language science to specify these processes and their underlying mechanisms. However, owing to the enormous complexity of language and the sparsity of our knowledge about brain functioning, neuroscientists, psychologists, and linguists have not attacked this goal directly. Indeed, biological knowledge currently available is still far from making it possible to spell out the great variety of language phenomena in terms of neurons. Nevertheless, it is possible to choose paradigmatic questions about language and to try to find answers for them based on biological principles. I will use this strategy here to approach the problem of language and the brain.

The issue I would like to address is that of different vocabulary classes. At school, one learns to categorize words into fifty or so lexical categories, such as noun or verb, and one may also be asked to categorize words on the basis of their meaning, according to semantic criteria. Of course it is useful, for didactic purposes, to make a large number of distinctions between classes of words, not only based on their meaning and their function in syntactic structures, but also based on criteria such as their intonation, syllable complexity, number of letters or speech sounds, or the frequency with which they are used in ordinary language. However, one may wonder whether some of these distinctions reflect differences that are biologically real. This would mean that the members of word classes A and B, which can be distinguished on the basis of linguistic or didactic criteria, would also be represented differently in the human brain. In psycholinguistics, much effort has been expended to demonstrate processing differences between word classes, for example between the major lexical classes

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called *content words* (or open-class words, including nouns, verbs, and adjectives) and *function words* (or closed-class words, including articles, pronouns, auxiliary verbs, conjunctions, and so on. Some of these studies will be discussed in sect. 5.). It is good to know that two word groups are different; however, it is better to know (or to have an idea about) what the actual differences are. A biological approach aims at specifying the difference in terms of neurons and neuronal connections.

In recent years, more and more neuropsychological studies have been devoted to the investigation of cortical mechanisms necessary for word processing, and psychophysiological studies have been investigating the brain areas that "light up" when words are being produced or comprehended. Such studies are most welcome because they may contribute to an answer of the "where" question, that is, the question of where representations are housed and processes take place. However, even when questions such as "Which word classes will be selectively impaired after focal brain lesion in cortical area X?" or "Which brain areas will become active when words of class A are being produced or comprehended?" have been definitely answered, the question of why this is so may still be open. Why are words of class A processed in area X? An explanation of language mechanisms in the brain is only possible if such "why" questions can be answered from known biological principles. But even definite and exhaustive answers to "where" and "why" questions may still not be a satisfactory end point of cognitive neuroscientific research: If it is clear where in the brain particular language units are represented and processed, and if it is clear why this is so, one can still ask how language representations are laid down, and how they are activated when language units are being processed.

This target article will certainly not provide complete answers to "where," "why," and "how" questions related to language. It will provide preliminary answers to the "where" question as far as words of certain classes are concerned; it hopes to convince the reader that the "why" question can be answered in a few clear cases; and it tries to specify some very basic features of cortical representations and the way they become active and maintain their activity. All this is done on the basis of a brain model rooted in Hebb's concept of cell assemblies. In fact, the purpose of this article is not only to discuss the issue of words in the brain, but to make it evident that the Hebbian approach is a powerful tool for cognitive neuroscience that may lead to a biological explanation of our language capacity and of other higher cognitive capacities as well.

2. The Hebbian model, recent modifications and evidence

In the late 1940s, Donald Hebb (1949) proposed a neuropsychological theory of cortical functioning that can be considered an alternative to both localizationist and holistic approaches. Localizationists would assume that small cortical areas are fully capable of performing complex cognitive operations. A localizationist would, for example, propose that an area of a few square centimeters of cortical surface is the locus of word comprehension (Broca 1861; Lichtheim 1885; Wernicke 1874). According to this view, the psychological process (word comprehension) is restricted to one area – that is, no other areas are assumed to contribute to this specific process. Only under pathological conditions or during development may there be a shift of the process to another equally narrow area (Luria 1970; 1973). In contrast, a holistic approach would imply that the entire cortex exhibits equipotentiality with regard to all cognitive operations and that all cortical areas (or even brain parts) can contribute to sufficiently complex processes, such as those involved in language (for discussion, see Freud 1891, Lashley 1950, and, for an overview, Deacon 1989).

The Hebbian proposal is in sharp contrast to both of these views. Cell assemblies with defined cortical topographies are assumed to form the neurobiological representations of cognitive elements such as gestalt-like figures or words. This position is radically different from a localizationist approach, because it assumes that neurons in different cortical areas may be part of the same distributed functional unit. The Hebbian viewpoint is also different from the holistic view that "everything is equally distributed," because it implies that the representation of, for example, an image may involve cortical areas entirely different from those contributing to the representation of, say, an odor. Accordingly, the representation of a word would not be restricted to a small cortical locus, but would be distributed over well-defined areas, for example over Broca's, Wernicke's, and some other areas.

The Hebbian model is based on three fundamental assumptions about cortical functioning, which can be summarized as follows:

1. Coactivated neurons become associated.
2. Associations can occur between adjacent or distant neurons; that is, the entire cortex is an associative memory.
3. If neurons become associated, they will develop into a functional unit, a cell assembly.

Hebb was frequently criticized, because his assumptions were considered too speculative and because some of his colleagues believed that his ideas would not be testable. Therefore, it is necessary to discuss his assumptions in light of evidence presently available.

Electrophysiological studies have demonstrated that having cortical neurons frequently active at the same time strengthens their connections. If a neuron, call it L, sends one connection to a second neuron, M, their synapse will strengthen when both are repeatedly active together, so that L will later have a stronger influence on M. Because this effect may last for many hours or days, or even longer, it has been termed *long-term potentiation* (LTP) (Ahissar et al. 1992; Gustafsson et al. 1987). After this kind of associative learning, connection strength will be a function of the frequency of coincident activity. Table 1 describes this kind of coincidence learning (Palm 1982).

One may object to this and similar learning rules that coincidence learning is only one form of associative learning known to take place between neocortical neurons. If only one of the two neurons is active while the other one remains silent, this could also have an effect on the strength of their connection. In fact, it was shown by electrophysiological experiments that activation of presynaptic neuron L alone, while the membrane potential of postsynaptic neuron M is stable (or only slightly depolarizes), leads to a weakening of their synaptic connection (Artola et al. 1990; Artola & Singer 1987; 1993; Rauschecker & Singer 1979). Because this reduction (or depression) of the influence of one neuron on the other is long-lasting, the phenomenon has been called *long-term depression* (LTD). There is also evidence for

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Table 1. *Associative synaptic learning according to a Hebbian coincidence rule*

		neuron L	
		active	inactive
neuron M	active	+w*	--
	inactive	--	--

*+w indicates an increase in connection strength between neurons L and M; hyphens indicate no change in connection strength.

LTD occurring when presynaptic neurons are silent while postsynaptic neurons fire frequently (Tsumoto 1992; Tsumoto & Suda 1979). Therefore, the original idea proposed by Hebb needs a slight but important modification: Connection strength is not only modified by coincident activity, it also changes if only one of two connected neurons is active while the other one is inactive. Table 2 describes this kind of learning, which will be called *correlation learning*, because after this kind of synaptic modification, the strength of the synaptic connection will include information not only about the frequency of coincident firing of neurons, but also about how strong the correlation was between their activations.

This formulation is very general. It does not make distinctions implied by more precise formulations of synaptic learning rules (Artola & Singer 1993; Bienenstock et al. 1982; Tsumoto 1992), in which, for example, the states called "active" and "inactive" above, have been replaced by gradual activity levels (quantified in terms of the frequency of action potentials or the membrane potential of the postsynaptic neuron). In addition, the above formulations leave open the questions of how the w-values should actually be chosen. Whereas w_1 may be assumed to be larger than w_2 and w_3, the exact values of the variables are unknown. These questions will not be addressed here, because they have been discussed in great detail based on what is known about synaptic dynamics in the neocortex (Tsumoto 1992) and in light of storage properties of artificial associative networks (Palm 1982; Palm & Sommer 1995; Willshaw & Dayan 1990). In the present context, it is most important to keep in mind that a correlation rule, rather than a coincidence rule, is a fundamental principle of synaptic learning in the cortex.

It appears uncontroversial that excitatory cortical neurons located close to each other are likely to have a synaptic contact. Although this is not a 100% probability – it is actually far below (Braitenberg 1978a; Braitenberg & Schüz 1991) – it is evident that adjacent neurons are much more likely to be connected than neurons located far apart, that is, in distant cortical areas (Young et al. 1995). It is clear from neuroanatomical studies, however, that most cortical pyramidal cells have long axons reaching distant areas or subcortical structures, and that connections from one area project to several other areas. In the Macaca, for example, what may be considered the homologues of Broca's and Wernicke's areas are not only intensely connected to each other; they also exhibit connections to additional premotor, higher visual, and association cortices (Deacon 1992a; 1992b; Pandya & Vignolo 1971; Pandya & Yeterian 1985). Therefore, if correlated neuronal activity is present in a large number of neurons in different cortical areas, some of these neurons will exhibit direct connections to each other. These neurons will become more strongly associated even if they are located far apart. Thus, although the cortex is not a fully connected associative memory in which every processing unit is connected to every other one, it still appears to be an associative network well suited to allow for both local and between-area associative learning (Braitenberg & Schüz 1991; 1998; Fuster 1994; Palm 1982).

Table 2. *Associative synaptic learning according to a correlation rule*

		neuron L	
		active	inactive
neuron M	active	$+w_1$*	$-w_2$
	inactive	$-w_3$	--

*$+w_1$, $-w_2$, and $-w_3$ indicate positive or negative changes in connection strength.

If neurons in an associative network exhibit correlated activity, they will be a stronger influence on each other. This implies that these neurons will be more likely to act together as a group. Hebb (1949) calls such anatomically and functionally connected neuron groups "cell assemblies." The strong within-assembly connections are likely to have two important functional consequences: (1) If a sufficiently large number of the assembly neurons are stimulated by external input (either through sensory fibers or through cortico-cortical fibers), activity will spread to additional assembly members and, finally, the entire assembly will be active. This explosion-like process has been called ignition of the assembly (Braitenberg 1978b). (2) After an assembly has ignited, activity will not stop immediately (because of fatigue or regulation processes), but the strong connections within the assembly will allow activity for some time. Cell assemblies are sometimes conceptualized as packs of neurons without an ordered inner structure. However, according to Hebb's (1949) proposal, assembly neurons are connected so that ordered spreading and reverberation of neuronal activity can occur.

The latter point needs further elaboration: Figure 1 is taken from Hebb's 1949 book and depicts what the author believed to be a possible inner structure of an assembly. In this diagram, arrows represent subgroups of neurons included in the assembly. These subgroups would each become active at exactly the same point in time. Arrowheads indicate the other subgroups to which a given subgroup would project, and numbers denote a possible activity sequence. After synchronous activity of the neurons represented by the arrow labeled "1," a wave of excitation will run through the assembly as indicated by the numbers, and activity will finally cease. Thus, it is evident that in Hebb's early proposal, a cell assembly was already conceptualized as a highly structured entity. Whereas ignition of the assembly may simultaneously involve all assembly neurons, it is also possible to have a wave of excitation circulating and reverberating in the many loops of the assembly. The wave can be described as a *spatiotemporal pattern* of activity in which many cortical neurons participate.

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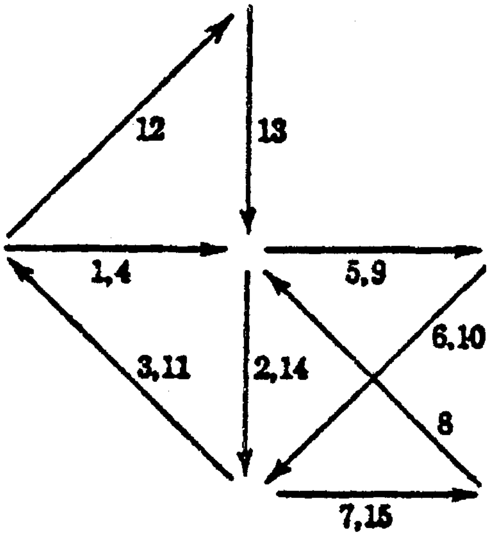

Figure 1. Hebb's (1949) illustration of the inner structure of a cell assembly consisting of several subgroups of neurons. Arrows represent subgroups of neurons that become active at exactly the same time. Numbers indicate the activation sequence following activity of the subgroup labelled 1. An ordered spatiotemporal pattern of activity is produced whenever a wave of excitation runs through the assembly.

The question of whether cell assemblies that represent stimuli and cognitive entities exist in the cortex has long been thought impossible to test by empirical research. As mentioned earlier, this belief was probably one of the main reasons why Hebb's theory was not generally accepted in the 1940s and 1950s. However, more recent experimental work has provided strong evidence for the Hebbian ideas. Neurophysiological work by Abeles, Aertsen, Gerstein, and their colleagues (Abeles 1982; 1991; Abeles et al. 1993; 1994; Aertsen et al. 1989; Gerstein et al. 1989) revealed exactly timed spatiotemporal firing patterns in cortical neurons. The specific neuronal connections these patterns are probably related to were labeled *synfire chains* by Abeles, because a subpopulation of neurons must synchronously activate the next subpopulation to keep the chain going. It is important to note that spatiotemporal activity patterns actually detected in cortical neurons frequently involve the repeated activation of a given neuron, thus suggesting reverberations caused by loops in the chain (Abeles et al. 1993). Evidently, the concept of a reverberating synfire chain emerging from recent neurophysiological data comes very close to Hebb's original proposal summarized in Figure 1. In contrast to the original proposal, it appears more realistic to postulate connections not only between consecutive subpopulations of neurons, but also connections that skip subgroups and directly link, for example, subgroups 1 and 3 in the example illustration (Fig. 1). Such bypass connections may be realized by relatively slowly-conducting cortico-cortical fibers (Miller 1996). Furthermore, Abeles's findings suggest that the neuron subgroups represented by arrows in Hebb's diagram overlap, so that a given neuron can be part of, say, subgroups 1 and 7.

In summary, after its full activation (ignition), neuronal activity may reverberate in the loops of an assembly. Ignition and reverberation may represent important functional states of Hebbian cell assemblies. On the cognitive level, ignition may correspond to perception of a meaningful stimulus and to activation of its representation. The fact that an object partially hidden behind another one can frequently be identified can be explained by full ignition of a cell assembly after stimulation of only some of its neurons (Hebb 1949). Sustained activity of the assembly and reverberation of activity therein may represent an elementary process underlying short-term or active memory (Fuster 1989; 1995; Fuster & Jervey 1981). The latter view arises from studies that evidence a systematic relationship between the occurrence of defined spatio-temporal activity patterns in cortex and particular engrams an experimental animal has to keep in active memory (Fuster 1995; Villa & Fuster 1992).

Recent neurophysiological work not only revealed well-timed spatiotemporal activity patterns in cortical neurons related to memory processes but another line of research uncovered stimulus-specific synchronization of activity in cortical neurons related to perceptual processes. If an elementary visual stimulus, for example a bar moving in a particular direction, is presented to an experimental animal, numerous neurons in various visual cortices in both hemispheres start to synchronize their firing and, in many cases, exhibit coherent rhythmic activity in a relatively high frequency range, that is, above 20 Hz (Eckhorn et al. 1988; Engel et al. 1990; 1991b; Gray et al. 1989; Kreiter & Singer 1992).[1] This provides further evidence that neurons in different areas are strongly coupled and can act as a unit. Although synchronization phenomena have been observed in subcortical structures and even in the retina (Kirschfeld 1996; Neuenschwander & Singer 1996; Sillito et al. 1994; Steriade et al. 1993), cortico-cortical connections are apparently necessary for synchronization of neuron responses in cortex (Engel et al. 1991a; Gray et al. 1989; Singer & Gray 1995). Because synchronized responses change with stimulus features, for example the direction in which a bar moves (Eckhorn et al. 1988; Gray et al. 1989; Gray & Singer 1989), the idea receives support that there are stimulus-specific distributed neuron groups. It appears that these neurophysiological data can only be explained if cell assemblies are assumed that are (a) activated by specific external stimuli, (b) distributed over different cortical areas, and (c) connected through cortico-cortical fibers (and possibly additional subcortical connections).

These results can be interpreted as evidence for a version of Hebb's theory according to which cell assemblies must synchronously oscillate at high frequencies when active. However, synchronous oscillations are a special case of well-timed activity (Abeles et al. 1993; Aertsen & Arndt 1993). Therefore, these data are also consistent with the weaker position made explicit by Hebb that cell assemblies generate well-timed activity patterns in their many neurons. The latter position would imply that at least a fraction of the activated neurons (e.g., those forming one subgroup represented by an arrow in Fig. 1) exhibit synchronized activity when the assembly reverberates (see Pulvermüller et al. 1997 for further discussion).

If it is taken into account that most cortico-cortical fibers conduct action potentials with velocities around 5–10 m/s or faster (Aboitiz et al. 1992; Patton 1982), it becomes clear that a wave of activity running through and reverberating within an assembly will lead to rather fast activity changes. Suppose a large-scale physiological recording device (e.g., an electrode recording the local field potential, or even an EEG electrode or an MEG coil) is placed close to a frac-

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tion of the neurons of the assembly sketched in Figure 1. In this case, a reverberating wave of activity in the assembly will cause rather fast activity changes at the recording device. If the neuronal subpopulations represented by arrows are assumed to be located in different cortical areas separated, say, by a few centimeters, it will take some hundredths of a second for neuronal activity to travel the loop labelled 1-2-3 and for the neurons denoted by the first arrow (the first and the fourth in the sequence) to become synchronously active for the second time. It follows that synchronous and fast reverberating activity in the assembly is most likely to lead to spectral dynamics in the high frequency range (>20 Hz) recorded by the large-scale devices.[2]

If specific dynamics in high-frequency cortical activity are taken as an indicator of reverberating activity in Hebbian cell assemblies, the question of whether particular cognitive processes are related to high-frequency dynamics becomes particularly relevant for further testing the Hebbian ideas. It is known from animal experiments that if the receptive fields of two neurons in visual cortices are each stimulated by a moving bar and both stimuli are aligned and move together in the same direction, neuron responses can synchronize their fast rhythmic activity. However, if one neuron is stimulated by a bar moving in a particular direction, while the other is stimulated by a bar moving in the opposite direction, synchrony of rhythmic responses vanishes (Engel et al. 1991a). This result and similar findings indicate that synchrony of high-frequency neuronal activity reflects gestalt criteria, for example the fact that two objects move together (Singer 1995; Singer & Gray 1995). Consistent with this finding in animals, patterns of regularly moving bars have been found to evoke stronger high-frequency electrocortical responses recorded in the EEG compared to irregular bar patterns (Lutzenberger et al. 1995). Further support for the role of high-frequency cortical activity in cognitive processing comes from studies of electrocortical responses to attended and unattended stimuli (Tiitinen et al. 1993). Most important, gestalt-like figures such as Kanizsa's triangle have led to stronger high-frequency EEG responses around 30 Hz compared to physically similar stimuli that are not perceived as a coherent gestalt (Tallon et al. 1995; Tallon-Baudry et al. 1996). Thus, dynamics of high-frequency responses appear to be an indicator of the cognitive process of gestalt perception. These results are consistent with the idea that gestalts, such as a coherent bar pattern or a triangle, activate cortical cell assemblies that generate coherent high-frequency responses, while physically similar stimuli that are not perceived as coherent gestalts lack cortical representations and, therefore, evoke desynchronized electrocortical responses. Therefore, the idea that cell assemblies are relevant for cognitive processing not only receives support from recordings in animals' brains, but is consistent with noninvasive recordings of human brain activity using large-scale recording techniques such as EEG.

In summary, recent theoretical and empirical research provides support for the existence of Hebbian cell assemblies and for their importance for cognitive brain processes. It must be noted, however, that, based on experimental and theoretical work, the Hebbian concept and the assumptions connected with it have changed slightly. Some of these modifications are summarized in the following postulates (which are closely related to points (1) to (3) in sect. 2):

1′. Simultaneous pre- and postsynaptic activity of cortical neurons leads to synaptic strengthening. However, pre- or postsynaptic activity alone leads to synaptic weakening.

2′. Associations can occur between adjacent neurons and between cortical neurons located far apart, provided there is a synapse connecting them. The cortex is an associative memory although it is not fully connected.

3′. If synaptic strengthening occurs among many neurons, they will develop into an assembly that can ignite and exhibit well-timed reverberatory activity.

Future empirical testing of the modified Hebbian framework is, of course, necessary, and neuroimaging techniques make it possible to perform such testing, although techniques available at present do not allow for localizing each member of a widely distributed neuron set in different cortical areas. If an assembly ignites and stays active, signs of activity should be visible in single-cell and multiple-unit responses, local field potentials, and more global electrocortical activity, and possibly in metabolic changes in the brain as well. The cortical topography of these activity signs may allow for conclusions concerning assembly topographies. In addition to general signs of activity enhancement – enhanced blood flow, larger event-related potentials, more powerful single-cell responses – changes in well-timed high-frequency cortical responses may include information about reverberatory neuronal activity in cell assemblies.

It may be appropriate at this point to mention possible theoretical problems of the Hebbian approach, some of which have been summarized in a recent article by Milner (1996). If an ignition takes place, there is danger that activity will spread to additional assemblies and finally to the entire cortex or even brain, resulting in overactivity such as that seen during seizures. To avoid this, it is necessary to have a control device regulating the cortical equilibrium of activity. This device has been called "threshold control mechanism" (Braitenberg 1978b) and its neuroanatomical substrate has been proposed to be located in the basal ganglia (Miller & Wickens 1991; Wickens 1993) or, as an alternative, in the hippocampus (Fuster 1995). Furthermore, if a large number of cell assemblies are built up in the cortex, this may lead to an increase in average connection strength, and, in the worst case, to a clumping together of all assemblies. This would make it impossible to activate representations individually. However, this problem primarily occurs if a coincidence learning rule is assumed (Table 1). If LTD rules are added (e.g., in the case of correlation-based learning as sketched in Table 2), simultaneous activity of a set of cortical neurons will not only lead to synaptic strengthening between them, but also to a weakening of connections to neurons outside the set (Hetherington & Shapiro 1993; Palm 1990; Willshaw & Dayan 1990). In this case, the problem will occur only if w-parameters (see Table 2) are chosen inappropriately. It has also been argued that the cell assembly framework is not flexible enough to allow for a representation of complex objects. If a house includes a door and a window, how would the respective representations relate to each other? Here, it is necessary to allow for hierarchical organizations of cell assemblies: One assembly may be a subset of another one. This is also important for the semantic representations of words with similar meanings, for example, for hyponyms and hyperonyms. Adjustment of the global activation threshold may account for whether the set or its subset is being activated (Braitenberg 1978b). Furthermore, concepts that have features in com-

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mon may be represented in cell assemblies that share some of their neurons. These assemblies will, therefore, not be entirely different neuron sets, but they will overlap. The relations of inclusion and overlap can be realized quite naturally within a cell-assembly theory built on the Hebbian notion (Braitenberg 1978b; Palm 1982). Therefore, a modified version of the original Hebbian proposal appears to be well suited to provide neurobiological answers to important questions in cognitive science.

3. Cortical distribution of cell assemblies

In recent years, the Hebbian idea of distributed assemblies with defined cortical topographies has been incorporated into large-scale neuronal theories of language and other cognitive functions (Abeles 1991; Braitenberg & Schüz 1991; Damasio 1989a; Edelman 1992; Elbert & Rockstroh 1987; Fuster 1995; Gerstein et al. 1989; Mesulam 1990; Miller & Wickens 1991; Palm 1982; Posner & Raichle 1994; Pulvermüller 1992; Singer 1995; Wickens et al. 1994). At this point, there appears to be a consensus that neurons in distant cortical areas can work together as functional units. However, the Hebbian framework would not only postulate that there are large-scale neuronal networks, it also provides clear-cut criteria for the formation of cell assemblies and, therefore, straightforward predictions on assembly topographies.

For assembly formation, Hebb (1949) outlines the following scenario (pp. 235f): If a particular object is frequently being visually perceived, a set of neurons in visual cortices will repeatedly become active at the same time. Therefore, a cell assembly will form representing the shape of the object. This assembly is distributed over cortical regions where simultaneous neuronal activity is evoked by visual stimulation, that is, in primary and higher-order visual cortices in the occipital lobes, for example in Brodmann's (1909) areas 17, 18, 19, and 20. For convenience, Figure 2 displays a lateral view of the left cortical hemisphere on which the approximate locations of Brodmann's areas are indicated. If correlated neuronal activity is caused by input through other sensory modalities, or if it is related to motor output, the cortical distribution of the coactivated set of neurons will be different. For example, if motor behavior co-occurs with sensory stimulation, cell assemblies may form including neurons in motor and sensory cortices. To put it in a more general way, the cortical localization of a representation is a function of where in the cortex simultaneous activity occurred when the representation was acquired or learned.

Whereas correlated neuronal activity of a connected cortical neuron set is a sufficient condition for cell assembly formation, correlated occurrence of sensory stimuli is not. In the most extreme case, when an individual is asleep, correlated stimuli (e.g., in the somatosensory and acoustic modality) may not cause enough cortical activity to lead to synaptic strengthening. The same may be true in an individual exhibiting very low arousal. Furthermore, the amount of cortical activation caused by a stimulus depends on whether it is being attended (Heinze et al. 1994; Mangun 1995). Therefore, to make it possible for correlated stimuli to induce synaptic learning, sufficient arousal and attention to these stimuli appear necessary, and synaptic learning may depend on how much attention is being directed to relevant stimuli. In the following considerations it will be tacitly assumed that correlated stimuli receive a sufficient amount of attention from the learning individual to allow long-lasting changes of synaptic connections to occur.

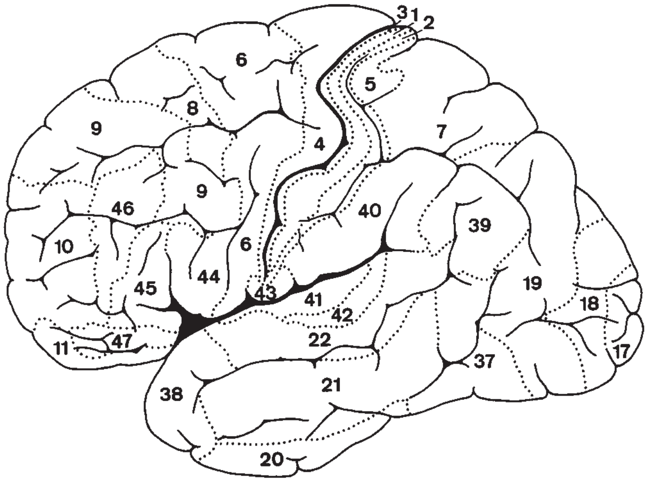

Figure 2. Lateral view of the left cortical hemisphere. Brodmann's (1909) areas are indicated. (Adopted from Pulvermüller & Preissl 1991.)

3.1. Assemblies representing word forms

Turning to language, it appears relevant to ask where in the cortex correlated neuronal activity occurs during verbal activities at early ontogenetic stages, when language learning takes place (Pulvermüller 1992; Pulvermüller & Schumann 1994). The infant's repeated articulations of syllables during the babbling phase are controlled by neuronal activity in inferior motor, premotor, and prefrontal cortices (Brodmann areas 4, 6, 44, 45). One may well envisage that one specific synfire chain controls the articulation of a given syllable and thus represents its articulatory program (Braitenberg & Pulvermüller 1992). In addition to and simultaneous with cortical activity related to motor programs, specific neurons in the auditory system are stimulated by the sounds produced during articulation (Braitenberg & Schüz 1992; Fry 1966). These neurons are localized in primary and higher-order auditory cortices (superior temporal lobe; Brodmann areas 41, 42, and 22). Furthermore, somatosensory self-stimulation during articulatory movements evokes activity in somatosensory cortices (inferior parietal lobe; areas 1–3 and 40). Therefore, neuronal activity can be assumed to be present almost simultaneously in defined primary and higher-order motor and sensory (auditory and somatosensory) cortices. All of these areas are within the first gyrus surrounding the sylvian fissure, the so-called perisylvian cortex (Bogen & Bogen 1976). Neuroanatomical evidence from monkeys suggests that the perisylvian areas are strongly and reciprocally connected, whereby long-distance connections between areas anterior to motor, adjacent to primary auditory, and posterior to primary somatosensory cortex are particularly relevant (Deacon 1992a; Pandya & Yeterian 1985; Young et al. 1995). Given that necessary long-distance connections are available, it follows by learning rule 1′ (see also Table 2) that the coactivated neurons in the perisylvian areas develop into cell assemblies (Braitenberg 1980; Braitenberg & Pulvermüller

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1992; Braitenberg & Schüz 1992; Pulvermüller 1992). Figure 3 represents an attempt to sketch such a perisylvian assembly. The individual circles in this diagram are thought to represent local clusters of strongly connected neurons. On the psychological level, the network may be considered the organic counterpart of a syllable frequently produced during babbling, or as the embodiment of the phonological form of a word acquired later during language acquisition.

The Hebbian framework implies that different gestalts and word forms have distinct cortical assemblies, because perception of these entities will activate different but possibly overlapping populations of neurons. If a language is not learned through the vocal and auditory modalities, but through the manual and visual modalities (sign languages), cortical localization of cell assemblies representing meaningful elements should be different. Because gestures are performed with both head and hands and perceived through the eyes, they are related to neuronal activity farther away from the sylvian fissure (more superior motor cortices and occipital visual cortices). Thus, it must be assumed that meaningful gestures included in sign languages involve these extra-perisylvian visual, motor, and association cortices (see Pulvermüller 1992 for futher discussion).

In assuming cell assemblies distributed over perisylvian cortices, the Hebbian perspective is in apparent contrast to older localizationist models according to which motor and acoustic representations of words are stored separately in Broca's (areas 44 and 45) and Wernicke's regions (posterior part of area 22), respectively (Geschwind 1970; Lichtheim 1885; Wernicke 1874). The Hebbian view implies that the motor and acoustic representations of a word form are not separate, but that they are strongly connected so that they form a distributed functional unit. For this unit to function properly, both motor and acoustic parts need to be intact. This is important for the explanation of aphasias, in particular of the fact that in the majority of cases these organic language disturbances affect all modalities through which language is being transmitted. Whereas localizationist models have great difficulty explaining this (see, e.g., Lichtheim 1885 for discussion), a cell assembly model can account for the multimodality of most aphasias.[3] Furthermore, the assumption that word form representations are distributed over inferior frontal and superior temporal areas receives support from imaging studies revealing simultaneous activation of both language areas when words or word-like elements are being perceived (Fiez et al. 1996; Mazoyer et al. 1993; Zatorre et al. 1992).

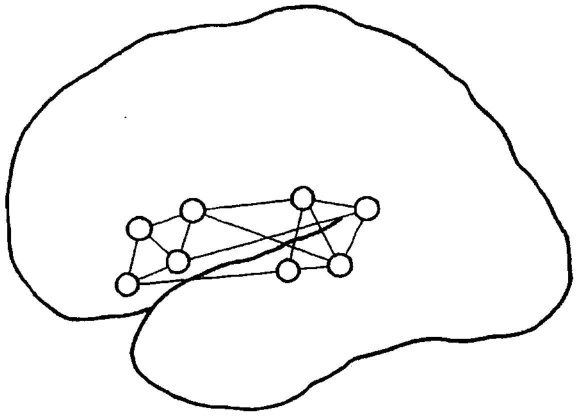

Figure 3. The cell assembly representing a phonological word form may be distributed over perisylvian areas. Circles represent local neuron clusters and lines represent reciprocal connections between such clusters. The connections are assumed to have strengthened because of correlated activity of neurons during articulation of the word form.

3.2. Cortical lateralization

From the Hebbian viewpoint, localization of language mechanisms is determined by associative learning and by the neuroanatomical and neurophysiological properties of the learning device (the cortex). The cortical loci where simultaneous activity occurs during motor performance and sensory stimulation follow from the wiring of efferent and afferent cortical connections, which are genetically determined. Genetic factors are also important for the formation of cortico-cortical fiber bundles, which are a necessary condition for long-distance association of coactivated neurons located in different areas. Furthermore, a pure associationist approach may have difficulty explaining why, in most right-handers, the left hemisphere – but not the right – is necessary for many aspects of language processing. Left hemispheric "language dominance" is evident from lesion studies in adults and in infants (Woods 1983) and from psychophysiological experiments in young children, demonstrating that stronger language-specific electrocortical activity can be recorded from the left hemisphere than from the right (Dehaene-Lambertz & Dehaene 1994; Molfese & Betz 1988). Neuroanatomical correlates of language laterality have been found in the size of perisylvian areas (Galaburda et al. 1978; 1991; Geschwind & Levitsky 1968; Steinmetz et al. 1990) and in size (Hayes & Lewis 1993), ordering (Seldon 1985), and dendritic arborization (Jacobs et al. 1993; Jacobs & Scheibel 1993; Scheibel et al. 1985) of pyramidal cells in the language areas. For differences in size of particular areas, epigenetic processes appear to be very important (Steinmetz et al. 1995). It is well known that differences in cell size and dendritic arborization may be influenced by sensory stimulation and motor output (Diamond 1990; Diamond et al. 1967) and, consistent with this view, language laterality has been proposed to be caused by environmental factors, such as lateralized auditory stimulation before birth (Previc 1991). Such stimulation may well underlie some of the morphological asymmetries mentioned. However, there are also arguments for a contribution of genetic factors to language lateralization (Annett 1979). At this point, it therefore appears safer not to dismiss a possible role of genetics here. For the Hebbian framework to operate, an anatomical substrate is necessary and this substrate is determined by genetic factors. Nevertheless, given the brain with its preprogrammed input and output pathways, its specific cortico-cortical projections, and its probably genetically determined left-hemispheric preference for language, the Hebbian approach leads to highly specific hypotheses about cortical distribution of language-related processing units.

One of these hypotheses concerns the cortical realization of laterality of language. According to localizationists, language processes take place in only one hemisphere. In contrast, the Hebbian framework suggests a different view. Although genetic and/or environmental factors lead to stronger language-related activation of left perisylvian cortex when language is being produced or perceived, articu-

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lation of a word form is probably controlled by bi-hemispheric activity in motor regions, and acoustic perception of the word certainly leads to activation of bilateral auditory cortices. Because neurons in both hemispheres are coactivated when a word form is being produced or perceived, the cell assembly representing the word form should be distributed over bilateral perisylvian cortices (Mohr et al. 1994b; Pulvermüller & Mohr 1996; Pulvermüller & Schönle 1993). However, if the left hemisphere's neurons are more likely to respond to language stimuli and to control precisely timed articulations, cell assemblies representing word forms would be gradually lateralized to the left in the following sense: They include a large number of neurons in the left hemisphere and a smaller number of neurons in the right. According to this view, a lateralized cell assembly is not restricted to one hemisphere, but a greater percentage of its neurons would be in the "dominant" hemisphere and a smaller percentage in the "nondominant" hemisphere (Pulvermüller & Mohr 1996).

What would be the cause of this lateralization? Given that genetically programmed differences in the hemispheres' anatomical and physiological properties are the cause of lateralization of cognitive functions, it becomes important to develop ideas about how left/right differences in the "hardware" could influence the "software." Based on an extensive and profound review of neuroanatomical and neurophysiological asymmetries, Robert Miller (1987; 1996) recently proposed that axonal conduction times in the left hemisphere are slightly slower, on average, than those in the right hemisphere. According to Miller, this may lead to a bias in favor of the left hemisphere for storing short time delays, such as are important for distinguishing between certain phonemes (Liberman et al. 1967). For example, the probability of finding a neuron that responds specifically to a [p], but does not respond to a [b], may be greater in the left hemisphere than in the right, because neurons with slowly conducting axons that could be used as delay lines for hardwiring the long (>50 msec) voice onset time of the voiceless stop consonant would be more common in the left hemisphere. The availability of axons with particular conduction times may also be relevant for attributing additional distinctive features to acoustic input (Sussman 1988; 1989). If neurons sensitive to certain phonetic features have a higher probability of being housed in the left hemisphere, the neuron ensemble representing a phonological word form should finally be lateralized to the left. Although Miller's theory of cortical lateralization needs further support by empirical data, it clearly illustrates how hemispheric specialization at the cognitive and functional levels may arise from basic neuroanatomical and physiological differences between the hemispheres.

3.3. Word categories

Associative learning may not only be relevant for the cortical representation of word forms, it may also play an important role in the acquisition of word meanings. When the meaning of a concrete content word is being acquired, the learner may be exposed to stimuli of various modalities related to the word's meaning, or the learner may perform actions to which the word refers. Although such stimulus and response contingencies are certainly not sufficient for full acquisition of word meanings (Gleitman & Wanner 1982; Landau & Gleitman 1985) – they would not, for example, allow the learner to distinguish between the morning and the evening star (Frege 1980) – they may nevertheless have important brain-internal consequences. From the Hebbian viewpoint, it is relevant that neurons related to a word form become active together with neurons related to perceptions and actions reflecting aspects of its meaning. If this coactivation happens frequently, it will change the assembly representing the word. Coactivated neurons in motor, visual, and other cortices and the perisylvian assembly representing the word form will develop into a higher-order assembly. A content word may thus be laid down in the cortex as an assembly including a phonological (perisylvian) and a semantic (mainly extra-perisylvian) part (Pulvermüller 1992).

After such an assembly has formed, the phonological signal will be sufficient for igniting the entire ensemble, including the semantic representation and, vice versa, the assembly may also become ignited by input only to its semantic part.[4] Thus, frequent co-occurrence and correlation of word form and meaning-related stimuli is only necessary at some point during the acquisition process. Later on, the strong connections within the higher-order assembly guarantee ignition of the entire assembly when part of it is being activated and, thus, they guarantee a high correlation of activity of all assembly parts, and, consequently, the endurance of the assembly.

When phonological word forms become meaningful, quite different cortical processes may take place, depending on what kind of information is being laid down in the associative network. Hebbian associationist logic suggests that cortical representations differ radically between words of different vocabulary types. In the following paragraphs, a few such differences will be discussed.

3.3.1. Content and function words. Neurons activated by stimuli related to the meaning of most concrete content words (nouns, adjectives, and verbs) are likely to be housed in both hemispheres. For example, the visual perceptions of objects that can be referred to as "mouse" will probably activate equal numbers of left- and right-hemispheric neurons because a corresponding visual stimulus is equally likely to be perceived in the right and left visual half-fields, and, in many cases, will be at fixation so that half of it is projected to the left visual field (right hemisphere) and the other half to the right visual field (left hemisphere). Therefore, if word form representations are strongly lateralized to the left, the assemblies representing content words (word form plus meaning) will be less strongly lateralized. Assemblies with different degrees of laterality are sketched in Figure 4.

In contrast to content words with concrete and well-imaginable meaning, function words such as pronouns, auxiliary verbs, conjunctions, and articles serve primarily a grammatical purpose. Many of them contribute significantly to the meaning of sentences, for example, "and," "or," "not," and "if." However, their meanings cannot be explained based on objects or actions to which the words refer. Rather, their meaning appears to be a more complex function of their use (Wittgenstein 1967) and can only be learned in highly variable linguistic and nonlinguistic contexts. Evidently, the correlation between the occurrence of a particular function word and certain stimuli or actions is low. Therefore, there is no reason why the perisylvian assembly representing the word form should incorporate additional neurons. If this is correct, assemblies representing

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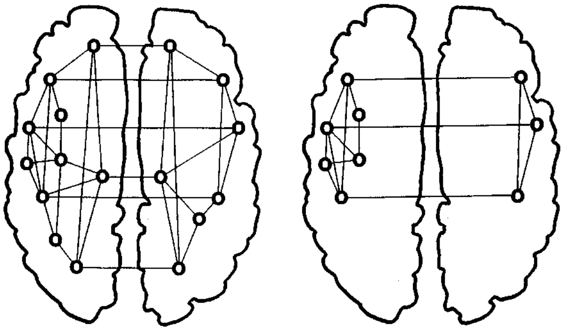

Figure 4. Cell assemblies relevant for cognitive processing may be distributed over both hemispheres and may be lateralized to different degrees. Whereas for cell assemblies representing phonological word forms and grammatical function words a high degree of laterality appears likely (right), an assembly representing a concrete content word may exhibit a reduced degree of laterality (left). (Adopted from Pulvermüller & Mohr 1996.)

function words remain limited to the perisylvian cortex and strongly left-lateralized in typical right-handers.

Note that this argument depends on the formulation of the cortical learning rule. If coincidence of neuronal activity was the factor causing synaptic modification, function words should have widely distributed cell assemblies because these words occur in a multitude of stimulus constellations and, in addition, they occur much more frequently than most content words (Francis & Kucera 1982; Ortmann 1975). When a function word (e.g., the article "the") is being learned, it may be used with various content words ("the cat," "the dog," "the horse") and, if there is a systematic relationship between the use of the content words and the occurrence of nonlinguistic stimuli (e.g., animal pictures), there will be a strong coincidence between the occurrences of each of these nonlinguistic stimuli and the word form. If only coincidence learning took place, cell assemblies representing function words should include even more neurons in visual cortices than most content word assemblies, because the assembly representing the function word would incorporate all neurons related to coincident visual nonlinguistic stimuli. However, because connections weaken if only pre- or only postsynaptic neurons fire (Table 2), the relatively infrequent co-occurrence of the function word with each of the visual stimuli will guarantee that its assembly does not become associated with representations of either visual stimulus. Correlation of neuronal activity is important for synaptic strengthening in the cortex, and this implies that function words are represented in cell assemblies restricted to perisylvian areas, or, at least, that they do not include large numbers of neurons outside.

3.3.2. Abstract content words. One may argue that the postulated difference in semantic meaning between content and function words does not apply for all members of these vocabulary classes. Rather, it appears that there is a continuum of meaning complexity between the "simple" concrete content words that have clearly defined entities they can refer to (so-called referents), more abstract items that may or may not be used to refer to objects and actions, and function words that cannot be used to refer to objects. It is therefore inappropriate to make a binary distinction between vocabulary classes based on semantic criteria. If semantic criteria are crucial for intracortical representation, the suggested gradual differences in the correlation between word form and meaning-related stimuli or actions should be reflected in gradual differences in cortical lateralization and how assemblies are distributed. An abstract content word, such as "philosophy," may therefore have an assembly somewhat in-between typical content and function word assemblies: It may exhibit an intermediate degree of laterality consisting mainly of perisylvian neurons, but including a few neuron clusters outside perisylvian areas.

Among the abstract content words are words referring to emotional states, for example "anger" and "joy." For these words, it is not difficult to find characteristic visual stimuli related to their meaning – for example, angry or joyful faces. In addition, there are characteristic meaning-related patterns of muscle activity – namely, the contraction of the respective facial muscles – and autonomic nervous system activity (Ekman et al. 1983; Levenson et al. 1990). It should therefore be noted that, although these words do not refer to objects and actions in the sense in which the word "house" refers to an object, the likely co-occurrence of patterns of muscle contractions with the word forms may nevertheless lead to the formation of widely distributed cortical cell assemblies representing these words. In addition to cortical neurons added to the word form representations during learning, it has been proposed that these assemblies acquire additional links to subcortical neurons in structures of the limbic system related to emotional states (Pulvermüller & Schumann 1994). "Emotion words" may therefore be represented by a cortical assembly plus a limbic assembly-tail. The amygdala and the frontal septum may be the most important structures for linking the cortical assembly to its subcortical tail (Schumann 1990; 1997).

These considerations should make it clear that the degree of abstractness of an item is not the only factor influencing assembly topographies. According to the present proposal, the important criterion is the strength of the correlation between the occurrences of a given word form and a class of nonlinguistic stimuli or actions. In the clear cases, this likelihood is related to abstractness, but there are exceptions.

3.3.3. Action words, perception words, and other word classes. Content words are used to refer to odors, tastes, somatic sensations, sounds, visual perceptions, and motor activities. During language learning, word forms are frequently produced when stimuli to which the words refer are perceived or actions to which they refer are carried out by the infant. If the cortex is an associative memory, the modalities and processing channels through which meaning-related information is being transmitted must be important for formation of cortical assemblies. This has inspired models of word processing in the brain postulating distinct corical representations for word classes that can be distinguished based on semantic criteria (Warrington & McCarthy 1987; Warrington & Shallice 1984).

If the modality through which meaning-related information is transmitted determines the cortical distribution of cell assemblies, a fundamental distinction between action and perception words can be made. Action words would refer to movements of one's own body and would thus be used frequently when such actions are being performed. In this case, a perisylvian assembly representing the word form would become linked to neurons in motor, premotor, and

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prefrontal cortices related to motor programs. Perception words, whose meaning can best be explained using prototypical stimuli, would consist of a perisylvian assembly plus neurons in posterior cortex. In many cases, visual stimuli are involved and the respective word category may therefore be labelled vision words. Assemblies representing words of this category would be distributed over perisylvian and visual cortices in parietal, temporal, and/or occipital lobes. Figure 5 presents sketches of the assembly types postulated for action and vision words. Examples of words whose meanings are related to the visual modality are concrete nouns with well-imaginable referents, such as animal names. The best examples of action words are in the category of action verbs.

This model draws too simple a picture of the relation between word forms and their meanings, because it does not explain homonymy (Bierwisch 1982; Miller 1991). If a phonological word form has two exclusive meanings – if it can, for example, be used as a noun with one meaning or as a verb with another meaning (the/to beat) – a mechanism must be assumed that realizes the exclusive-or relationship between the two meanings. As suggested earlier, homonyms could be represented by overlapping cell assemblies, that is, by two content word assemblies sharing one perisylvian phonological part. Inhibition between the semantic assembly parts is unlikely to be wired in cortex, because the percentage of cortical inhibitory neurons is low and these neurons are usually small (Braitenberg & Schüz 1991). Intracortical inhibitors would therefore be unlikely candidates for mediating inhibition between cortical areas – for example, between assembly parts in frontal and occipital lobes. However, such mutual inhibition between overlapping assemblies could be realized by striatal connections (Miller & Wickens 1991). Accordingly, homonymic content words may be realized as widely distributed assemblies sharing their perisylvian part while inhibiting each other through striatal connections. This wiring would allow the perisylvian word form representation to become active together with only one of its "semantic" assembly parts (see Pulvermüller 1992 for further discussion).[5]

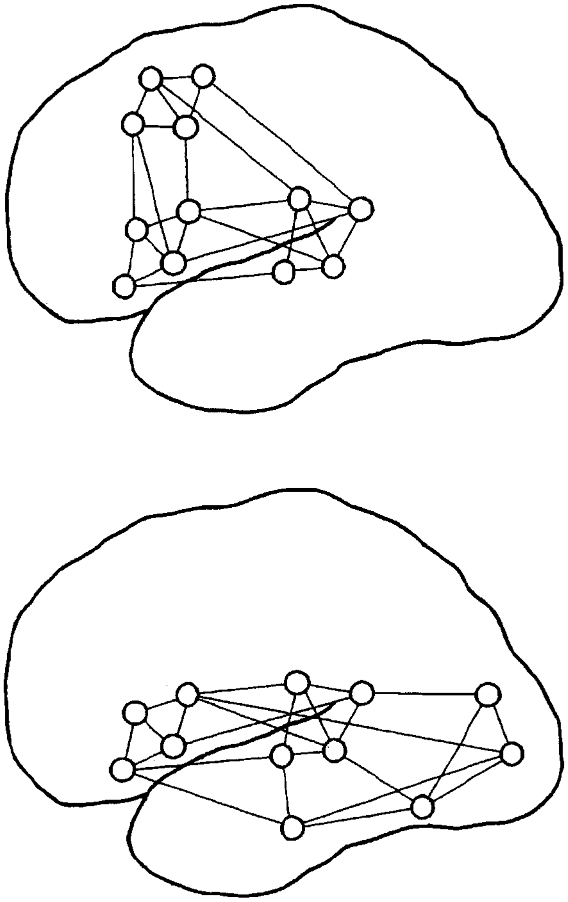

Figure 5. Whereas words eliciting strong visual associations ("vision words") may be organized in assemblies distributed over perisylvian and additional visual cortices, words that remind one of movements of one's own body ("action words") may be organized in assemblies distributed over perisylvian and additional motor cortices. Many (but not all) concrete nouns are vision words and many verbs are action words.

The argument made above for action and visually-related words can be extended to words referring to stimuli perceived through other modalities. For those, additional word categories – odor, taste, pain, touch, and sound words – can be postulated. Members of these word classes should be represented in assemblies with specific cortical topographies. For example, whereas an assembly representing a pain or touch word may include substantial numbers of neurons in somatosensory cortices, sound words may have exceptionally high numbers of neurons in bilateral auditory cortices included in their assemblies. Again, it must be stressed that neurons responding to stimuli of various modalities and neurons controlling body movements and actions are located in both hemispheres. It is for this reason that cell assemblies representing these words are assumed to be distributed over both hemispheres and to be less strongly lateralized compared to assemblies representing function words (Pulvermüller & Mohr 1996).

The definition of action words is particularly delicate because not all action-related associations involve the motor modality. Here it is important to distinguish movements that are performed by the subject's own body from movements that are only perceived visually. "To fly" or "the plane," for example, are words that are frequently heard by children when they perceive certain moving visual stimuli. Although a relation of visual stimuli to the motor modality can hardly be denied – because perception of visual stimuli is usually accompanied by eye movements related to neuronal activity in frontal eye fields – this eye movement-related neuronal activity is probably not very stimulus-specific (similar saccades are made when different objects are looked at). Therefore, the correlation between visual input patterns and the occurrence of the word forms "fly" or "plane" may be highest and these words may thus be organized in assemblies including a significant number of neurons in visual cortices responding to specific moving contours. These words should therefore be classified not as action words but as visually-related words of a certain kind (as words referring to visually perceived movements). On the other hand, action words as defined above, that is, words usually referring to movements of one's own body, may include movement detectors in visual cortices in their assemblies. Many body movements are visually perceived when they are performed, suggesting that sensory-motor assemblies are established for representing these actions – an idea for which there is ample support from recent studies (Fadiga et al. 1995; Gallese et al. 1996; Rizzolatti et al.

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1996). These considerations indicate that Figure 5 draws too crude a picture of cell assemblies representing action words. Such assemblies can include additional neurons in visual cortices primarily processing movement information – many of which are probably located in the posterior part of the middle temporal gyrus (Watson et al 1993; Zeki et al. 1991). A similar point can be made for somatosensory stimulations caused by body movements, suggesting that neurons in parietal cortices may be added to the assembly representing an action word, as well.

Further word class-distinctions can be made based on the cortical areas active during meaning-related motor activity. Different kinds of action words can be distinguished considering the muscles most relevant for performing the actions (to chew, to write, to kick), the complexity of the movement (to knock, to write), and the number of muscles involved (to nod, to embrace). These factors may "shift" the neurons in frontal lobes added to the perisylvian assembly in the inferior/posterior (mouth/hand/foot representation) or anterior/posterior direction (complex/simple movements), or enlarge/reduce their cortical distribution (many/a few muscles involved in movement).

Similar, more fine-grained distinctions are desirable for visually-related words. Some vision words refer to static objects (house), others to moving objects (train), some refer to colors or colored objects (iguana), others to objects lacking colors (penguin). Furthermore, some visual stimuli are very simple (line), others are more complex (square, cube, house, town, megalopolis). This suggests that different sets of neurons are being added to the assembly when contingencies between words and different kinds of visual stimuli are being learned. The assembly of a word used to refer to colors or colored objects may include neurons maximally responding to color, and, as discussed above, neurons sensitive to moving visual stimuli may be included in the assemblies representing words referring to such stimuli. Recently, cortical processing streams have been discovered in temporal lobes that are primarily concerned with movement or color information from the visual input (Corbetta et al. 1990; Watson et al. 1993; Zeki et al. 1991). If movement-detecting cells are more frequent in one area, for example in the posterior middle temporal gyrus, and neurons in primary and secondary visual cortex that respond to color preferentially project to other areas, for example in the inferior temporal lobe, this would suggest that words referring to colors or colored objects are realized as assemblies including additional neurons in color areas (e.g., in the inferior temporal gyrus), and that words referring to visually perceived movements have assemblies that comprise additional neurons in visual movement areas (in the middle temporal gyrus).

It is important to stress that (1) word types defined in this way[6] do not necessarily have a congruent lexical category; most – but not all – verbs are action words, and there may be action words from other lexical categories; and (2) it is not always clear from theoretical consideration to which category a particular word should be assigned. Most concrete content words probably exhibit a high correlation with stimuli of more than one modality, and their presentation may therefore remind subjects of multimodal stimuli. Whereas verbs referring to body movements are probably action words, and concrete nouns (such as animal names) are almost certainly related to vision, other word groups – for example, nouns referring to tools – probably lead to both visual and motor associations. Therefore, when evaluating the present ideas about word class-differences related to word meaning in neuroscientific experiments, it is most important to assess quantitatively semantic associations elicited by word stimuli.

4. Cortical activation during word processing: Predictions and methodological remarks

Cognitive brain theories lead to empirical predictions in psychophysiological studies. Testing such predictions is not trivial, however. In the case of language, it is particularly difficult to design experiments and interpret their results because there are so many possible confounds to which, for example, a physiological processing difference between two stimulus words could be attributed. Furthermore, the subtraction logic used in many imaging studies of cognitive processes has frequently been criticized, and one may prefer designs that could prove more useful in testing precise predictions on cognitive processes of comparable complexities.

After summarizing selected predictions derived from the Hebbian model (sect. 4.1), the subtraction logic underlying many imaging studies will be contrasted to what will be called the double dissociation approach to neuroimaging (sect. 4.2), and, finally, methodological issues specific to the investigation of word processing will be addressed (sect. 4.3).

4.1. Predictions about where and how

Hebbian logic suggests that content and function words, and words referring to actions and perceptions, have different neurobiological counterparts. The cell assemblies representing these lexical elements may differ with regard to their laterality and cortical topography. Whereas all assemblies representing words are assumed to include a strongly lateralized perisylvian part, neurons outside perisylvian language areas (and in both hemispheres) would only be added to the assembly if words refer to actions and perceivable objects. If assembly topographies are a function of semantic word properties, signs of cortical activity should differ when these different assemblies are being activated.[7] Based on these ideas, one would expect:

1. function words to evoke strongly left-lateralized signs of cortical activity restricted to perisylvian cortices,
2. content words to evoke less lateralized signs of cortical activity in perisylvian areas and outside,
3. action words to evoke additional activity signs in motor cortices of frontal lobes,[8] and
4. visually-related words to evoke additional activity signs in visual cortices of occipital and inferior temporal lobes.

These are some of the predictions obvious from the above considerations (sect. 3) that relate to the *where* question. When the assumptions leading to these predictions were discussed in section 3, the *why* question was traced back, in each case, to a Hebbian learning rule postulating that correlated neuronal activity is the driving force of assembly formation. With regard to the *how* question, it is important to recall that cell assemblies were assumed to exhibit two functional states, namely, ignition (or full activation) and reverberation (or sustained partial activity). When outlining

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empirical tests of the cell assembly framework and its application to language, one may not only be interested in testing predictions about assembly topographies, but one may also want to think about how to distinguish and detect possible physiological signs of ignition and reverberation. As detailed in section 2, ignition may be reflected in a sudden spreading of neuronal activity shortly after stimulation, and reverberation would follow ignition and could become visible in high-frequency brain responses. Therefore, the following additional predictions are possible:

5. shortly after stimulation, signs of cell assembly ignition are simultaneously present at the cortical loci where the assembly is located, and
6. after a longer delay, signs of reverberation emerge in the same areas.

It is not possible to deduce the exact point in time when these putative physiological processes take place. However, because words are recognized rather quickly – for example, lexical decisions, that is, judgments on letter strings according to whether they are real words or not, can be made as early as $\frac{1}{2}$ second after the onset of written stimuli – it is clear that the postulated physiological process of cell assembly activation must take place during the first few hundreds of milliseconds after the stimulus has been presented.

Although numerous additional predictions can be derived from the discussion in section 3, sections 5 and 6 will focus on hypotheses 1–6. These hypotheses will be discussed based on the results of psychophysiological and neuroimaging experiments.

4.2. Subtractions versus double dissociations in psychophysiology

In psychophysiology, numerous neuroimaging techniques are available for investigating higher cognitive processes. Activity of large neuron ensembles can be visualized using electrophysiological recording techniques, such as electroencephalography (EEG) and magnetoencephalography (MEG). These techniques provide exact information about temporal dynamics of electrophysiological activation and deactivation processes that occur in the millisecond range. They also allow for localization of sources, although such localization is usually much less precise than imaging of brain metabolism. Metabolic imaging techniques with high spatial resolution, such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), are extremely valuable for localizing brain structures that maximally become active, thereby increasing their metabolic rates during cognitive tasks. However, the metabolic methods give only a rough picture of temporal dynamics of brain processes, and it is therefore important to use both electrophysiological and metabolic imaging techniques when investigating brain processes of cognitive functions.

It is necessary to recall that important information about where, why, and how cognitive processes take place in the human brain was obtained before modern imaging techniques were available. Most of these studies used the individuals' behavior as the dependent measure. In addition, studies of neurological patients with focal lesions can answer the question of which brain structures are necessary for particular cognitive operations (Jackson 1878; 1879). Studies of healthy individuals in whom stimulus information reaches only one hemisphere – for example, using the technique of lateralized tachistoscopic presentation of visual stimuli – can provide important insights into the hemispheres' roles in language processing (Hellige 1993; Pulvermüller & Mohr 1996). Together with such neuropsychological evidence, modern neuroimaging and psychophysiological data can provide even stronger conclusions about language mechanisms in the human brain (Posner & Raichle 1994).

In recent years, a large number of imaging studies of word processing have been carried out, many of which are relevant for evaluating the Hebbian model outlined above. When interpreting these results, it is necessary to consider basic methodological issues. Giving an overview of all possible methodological problems that may become relevant is outside the scope of the present article (see, e.g., Posner & Raichle 1995 and comments therein). Rather, two important points will be mentioned briefly, the so-called subtraction logic and the question of stimulus matching, which are both crucial for investigating word class-differences.

Various dependent measures recorded by large-scale imaging techniques are usually interpreted as signs of cortical activity. However, the exact mechanisms by which an increase in cortical activation (i.e., the frequency of excitatory postsynaptic potentials in a set of neurons) may lead to an increase in the CO_2 concentration in numerous blood vessels, to an increase in intracellular glucose levels, to an enhancement of biomagnetic signals, or to a more positive or negative event-related brain potential are not sufficiently understood to make quantitative predictions possible. For example, one may predict that higher glucose metabolism or event-related potential amplitudes are present in or close to the inferior prefrontal cortex during processing of a given word class, but quantification of the expected difference, in terms of microvolts, for example, would not be possible. Ultimately, even the rationale underlying the more/less logic may be flawed, because an increase in biomagnetic activity or enhancement of cortical metabolism may be caused by the activation of inhibitory neurons (Mitzdorf 1985; Posner & Raichle 1995). Nevertheless, at least in the cortex, excitatory neurons represent the majority (>85% of cortical neurons are excitatory), and they are, on average, much larger than inhibitory neurons (Braitenberg & Schüz 1998). Furthermore, their function is probably to control excitatory activity in cortex, rather than to process more specific information. It is therefore possible, but not likely, that an enhancement of large-scale measures of cortical activity exclusively reflects inhibitory processes on the neuronal level. (This may be more likely for structures with high percentages of inhibitory neurons, such as the striatum.) Therefore, in the majority of cases, it appears reasonable to use large-scale neuroimaging measures to draw conclusions on activity changes in large numbers of excitatory neurons in the cortex.

The logic underlying all imaging work is that a dependent measure indicates a difference in brain activity between two conditions. In most cases, a critical condition is compared to a baseline or control condition. In the simplest case, looking at an empty computer screen or at a fixation cross may be compared to reading words or to making lexical decisions on these stimuli. Using a more complex design, the task of silently reading a word may be compared to the generation of a verb that somehow relates to the meaning of a displayed word. If an area of cortex is found to "light up" in such an experiment, one can conclude that

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the perceptual, cognitive, or motor operations induced by the two conditions differ with regard to neuronal activity in this particular area.

Unfortunately, however, in many experiments there are several differences between critical and control conditions. For example, the tasks of looking at an empty screen and of making lexical decisions about words appearing on the screen differ with regard to several aspects: (1) perceptions – either a word or nothing is being perceived; (2) higher cognitive processes – the stimulus has to be classified as a real word or as a meaningless element, or nothing has to be done; and (3) motor activities – a button press is either required or not. In addition, silently reading a noun (e.g., cow) and silently generating a word that refers to an activity related to the object to which the noun refers (e.g., to milk, to buy) involve quite different cognitive processes. Although identical words may be displayed in the two conditions and no overt response may be required, the two conditions differ because only one of them requires strong attention and involves search processes, semantic inferences, repeated lexical access, and so on (see also the discussion in Posner & Raichle 1995). Finally, another difference between the reading and the generation tasks is that only in the latter are verbs involved (but nouns are being read in both conditions). Given that an area is found to "light up" in the generation condition if compared to the reading condition, it is not clear which of the many different cognitive processes relates to the difference in brain activity. The difference may even be used to evaluate prediction 3 (sect. 4.1) because action verbs are relevant in only one of the conditions, but, of course, if the prediction is met, the experimental result would not provide strong support for it because of the many confounds.

A solution to the problem may lie in a more careful selection of the conditions and stimuli that are being compared. If, for example, silently reading words is compared to reading random letter strings made up of the same letters, one may argue that in this case the critical and control conditions differ only with regard to well-defined linguistic processes, such as word form identification and processing of semantic information. However, the objection can be raised that processing of words is not even necessary under such conditions because random letter strings can frequently be distinguished from real words merely by looking at the first three letters of the items and deciding whether these letters can be combined according to the phonological or orthographic rules of the language from which the real words are taken. Thus, word processing could be avoided by experiment participants in these conditions. To allow conclusions on processes specific for words, even more similarity between the stimulus classes should be required. For example, only letter strings that are in accord with the phonological rules of the language could be allowed as pseudowords, and lexical decisions could be required so that experiment participants would be forced to attend to and process the stimuli. In this case, a neuroimaging difference between conditions could be attributed to the difference between word and pseudoword processing, although from a psycholinguistic perspective these processes may differ under various aspects (including word form identification, semantic processes, and the use of a "time out" strategy for rejecting pseudowords; Grainger & Jacobs 1996; Jacobs & Grainger 1994; Mohr et al. 1994b). Nevertheless, a difference in brain activity between these conditions would allow stronger conclusions on the cortical processes induced by the words.

In many cases, two conditions are being compared in which condition 1 is considered to induce a subset of the processes induced in condition 2. The subtraction of the brain responses would then be interpreted as reflecting the psychological processes that condition 2 exhibits but condition 1 lacks. Subtractions can be performed repeatedly, so that a hierarchy of conditions corresponds to a set of subtractions (Posner & Raichle 1995). However, the principal problems remain, namely, (I) that a difference in more than one psychological process may be attributed to each pair of conditions, making it difficult to attribute a physiological contrast to one of them, and (II) that statistical criteria for the comparison of two conditions are difficult to choose if multiple pairs of physiological data are compared. If many comparisons are being made (when data from tens of channels or thousands of voxels are contrasted), the likelihood of a difference occurring by chance is high. On the other hand, if critical significance levels are adjusted to reduce the likelihood of significant results (e.g., by following Bonferoni logic), an actual difference between brain responses in two conditions may be masked because the too rigid statistical criterion is almost impossible to reach (Wise et al. 1991).

The only way to avoid problem (I) appears to be to choose maximally similar experimental conditions. To investigate word class-specific processes, a good option appears to be a comparison of two psycholinguistically similar stimulus classes while the experimental task is kept constant in conditions 1 and 2. To reduce the risk of obtaining by-chance results with standard significance criteria (II), more risky predictions can be derived and tested. One way to do this is to predict interactions between topographical variables and stimulus classes, rather than only more or less activity at a not-yet-specified locus. In the best case, condition 1 and condition 2 would induce quite similar cognitive processes, but condition 1 would induce a process not induced by 2, and, conversely, condition 2 would induce a specific process not induced by 1. Based on theoretical predictions, processing of stimuli of class 1 in the task chosen may then be assumed to activate a set A of cortical loci not activated by class 2, whereas stimuli of class 2 processed in the same task would be assumed to activate a different set B of areas not activated by 1. (Of course there may be additional areas C activated by both classes.) The brain areas activated by the two conditions or stimulus types would be distinct, and each set of areas would include loci not included in the other. This can be called a *physiological double dissociation*. The prediction to be tested by analysis of variance would be that direct comparison of the two activity patterns leads to a significant interaction of the task variable with the topography variable. It is unlikely that such a prediction is being verified by chance in a neuroimaging experiment, in particular if the loci where differences are actually found have been specified before the experiment based on theoretical considerations. The rationale underlying this is very similar to the logic used in neuropsychology, where double dissociations are taken as strong evidence for processing differences (Shallice 1988; 1989), although the dependent measure is behavioral in neuropsychology, but physiological in psychophysiology.

In summary, one perspective on overcoming some of the problems of a simple subtraction logic in neuroimaging ex-

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periments is offered by a double dissociation approach to psychophysiology. In this approach, physiological signs induced by maximally similar tasks – or even patterns of brain activation caused by matched stimuli in the same task – are being compared, and the prediction would be that class 1 of stimuli activates cortical loci A more strongly than class 2, whereas class 2 induces stronger activity signs than class 1 at distinct loci B. With regard to the present discussion, classes 1 and 2 may represent different word categories – for example, action and visually-related words – and loci A and B would then be large sets of cortical areas – for example, motor versus visual cortices.

4.3. Word properties affecting brain processes

Given that comparable stimulus materials are used in an imaging experiment on processing differences between word classes, the expectation would be that defined cortical areas "light up" when members of a given word class are being processed (see predictions 1–4). But what would "comparable" mean in this case? Behavioral studies in which response times and accuracies of responses were measured precisely have clearly shown that various properties of stimuli influence information processing in the brain, and many of the results from behavioral studies could be confirmed by psychophysiological experiments. Imaging techniques with good spatial resolution have only been used for a few years and, therefore, many methodological studies on the influence of stimulus properties have not yet been performed using these techniques. When evaluating imaging studies of word processing, it is essential to keep in mind the stimulus properties for which behavioral and earlier psychophysiological studies have demonstrated strong effects on brain processes.

Words can vary on various scales. The naive observation that long words are more difficult to read than short ones is paralleled in the observation that words of different length elicit different electrocortical responses measured in the EEG. This appears to be the case regardless of whether the items are presented acoustically (Woodward et al. 1990) or visually (Kaufman 1994). A second important factor influencing behavioral and physiological responses to words is whether they are common or exceptional. In contrast to pictures or real objects for which it is difficult to estimate whether they are frequently or rarely being perceived, the frequency of words can be exactly determined based on the evaluation of large corpora of spoken or written text. Word frequency is well known to have a strong influence on response times and accuracies of word processing (see, e.g., Bradley 1978; Mohr et al. 1996). In addition, word frequency has a strong influence on cortical potentials evoked by word presentation (Polich & Donchin 1988; Rugg 1990; Rugg & Doyle 1992). Because certain word classes exhibit enormous differences in word frequencies, this variable may affect the outcome of studies of word class-differences. For example, whereas most function words are in the highest frequency range, only a small percentage of the content words can be found in this high range, and most content words are used only rarely. Thus, word frequency is a likely confounding factor of experimental results about differences between word classes.

Additional possible confounds of word category differences are related to psychological processes induced by the stimuli. Some words are more arousing than others: The word "spider" may lead to much more pronounced brain activity in an arachnophobic patient compared to "beetle," and normal individuals may exhibit similar differences in brain responses. That event-related potentials reliably differ between more or less arousing words has been shown by numerous studies (Chapman et al. 1980; Johnston et al. 1986; Naumann et al. 1992; Williamson et al. 1991), and there is also evidence that a variable called "valence," that is, the degree to which the stimulus is evaluated as positive or negative, can have an effect on event-related potentials. Therefore, there is some reason to believe that what has been called the "affective meaning" of words (Osgood et al. 1975) can influence the brain processes these stimuli induce. Stimulus matching for the variables' valence and arousal therefore appears desirable – except, of course, if the role of these variables in word processing is the subject of the experiment.

Another variable strongly affecting behavioral and physiological responses to word stimuli is the context in which they are being presented. There are different types of context effects. They can be elicited not only if words are presented in well-formed or ill-formed sentences, but also when words are presented one by one. If a word occurs twice in the same experiment, event-related potentials are usually more positive-going for the second occurrence (see, e.g., Rugg 1985; Smith & Halgren 1987). The repetition effect appears to be quite complex and can interact with other variables, for example word frequency (Rugg 1990). Therefore, if a physiological difference is observed between words of different frequencies that are repeatedly presented in the same experiment, it cannot be decided to which variable the difference should be attributed.

Context effects can also occur between different words that are semantically related (semantic priming). Presentation of a prime word changes electrocortical signs of activity elicited by a subsequently presented target that is semantically related to the prime (Holcomb & Neville 1990; Nobre & McCarthy 1994; Rugg 1985). Similar priming effects may also occur when a word is being presented in sentence context. A pronounced negative deflection is seen when meaningful words appear at the end of a sentence where they are highly uncommon (Kutas & Hillyard 1980a), and different brain waves have been identified that may indicate different forms of syntactic or semantic violations (Neville et al. 1991; Osterhout & Holcomb 1992). Although there are several different effects of sentence context on word-evoked potentials, at least one of these effects appears to be quite similar to the effect induced by semantic priming (Van Petten 1993). Most importantly, context effects are not necessarily the same for all word classes (Besson et al. 1992). As mentioned above for the effects of word frequency and word repetition, sentence context effects may vary between word classes as well. Event-related potentials elicited by content words are attenuated by a sentence context, provided that semantic and syntactic restrictions are met by the sentence. In contrast, function words also show attenuation of event-related potentials when presented in semantically deviant strings that still preserve some basic sentence-like structure (Van Petten & Kutas 1991). If words are presented in sentences or in sentence-like word strings, it may well be that not only the effect of a stimulus word is seen in the neurophysiological response, but a complex blend of the effects of the critical word, its preceding words, and their semantic and syntactic rela-

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tions. The various context effects may therefore either artificially produce word class-difference, or they may mask real processing differences between word classes.

When brain processes distinguishing between word classes are investigated, it appears necessary to keep in mind these effects of word length, word frequency, emotional (arousal and valence) properties of the stimuli, as well as those of word repetition, priming, and syntactic and semantic sentence context. These properties of word stimuli and strings may confound results of any imaging study investigating differences in brain activity evoked by two word groups. Only if such confounds are excluded can a strong conclusion on differences between lexical or semantic word categories be drawn.[9]

5. Brain activity during word processing: Where?

In this section, studies on the cortical areas activated during word processing will be discussed. The main question will be whether there is evidence for or against predictions 1–4. Studies on differences between content and function words will be dealt with in section 5.1, and section 5.2 will be concerned with action and visually-related words and related categories.

5.1. Content and function words

Neuropsychological work clearly indicates that different brain areas are necessary for processing content and function words. Whereas aphasic patients with anomia have difficulty finding content words (Benson 1979), for patients with agrammatic aphasia function words are more difficult to produce (Caramazza & Berndt 1985; Pick 1913). In addition, aspects of agrammatics' deficit in language comprehension can be explained based on the assumption that they have a selective deficit in processing these lexical items (Pulvermüller 1995a). Lesions within the entirety of the perisylvian region can be the cause of the agrammatic language disturbance (Vanier & Caplan 1990). In contrast, lesions at various cortical sites outside left-hemispheric perisylvian cortices can lead to selective impairment in using or comprehending word categories included in the content word vocabulary (see the discussion in sect. 5.2). If function word representations are assumed to be restricted to perisylvian cortices (see Fig. 3), and content word representations are assumed to be more widely distributed (see examples in Fig. 5), a perisylvian lesion will destroy a large percentage of neurons included in function word representations, but will only remove a smaller part of the representations of content words. In contrast, lesions outside the perisylvian region will only affect representations of content words. Thus, different cortical distributions of cell assemblies representing content and function words can account for the double dissociation in processing content and function words in specific aphasic impairments such as agrammatism and anomia (Pulvermüller 1995a; Pulvermüller & Preissl 1991).

In addition, evidence from behavioral experiments in healthy individuals using lateralized tachistoscopic presentation have provided further support for processing differences between content and function words. It is well known that words presented either in the left visual hemifield (and, thus, to the right hemisphere) or in the right visual hemifield (to the left hemisphere) of right-handed individuals exhibit a processing advantage after presentation in the right visual field ("right visual field advantage"; see, e.g., Bradley 1978). In behavioral experiments, these effects can be quantified exactly in terms of response times and accuracies. A frequently applied paradigm is lexical decision, where words and matched meaningless pseudowords are presented in random order and study participants have to indicate whether an item is a legal word or not. In lexical decision experiments, the "right visual field advantage" has been found to be stronger for function words compared to content words matched for word frequency and length (Chiarello & Nuding 1987; Mohr et al. 1994b). For function words, direct stimulation of the left hemisphere leads to faster or more accurate responses compared to stimulation of the right hemisphere. This is consistent with the idea that cell assemblies representing function words are strongly lateralized to the left (sect. 3.3.1). The weaker or even absent right visual field advantage for content words supports the idea that cell assemblies underlying content word processing are less lateralized (Mohr et al. 1994b).

Several studies investigating event-related potentials (ERPs) have been conducted in search of differential brain activity induced by content and function words. Garnsey's (1985) early experiment revealed a fine-grained word class-difference in event-related potentials uncovered by principal component analysis. Neville et al. (1992) presented content and function words in sentence context and had subjects indicate whether the sentences made sense or not. Words of the two classes were not matched for word length or frequency. These authors reported a left-lateralized component evoked by function words which peaked at 280 msec after stimulus onset, whereas a peak more symmetrical over the hemispheres was evoked by content words at 350 msec. A similar result was obtained by Nobre and McCarthy (1994), who used stimuli matched for word length but not for word frequency. These authors presented words one by one and their subjects studied the sequence while trying to detect words of a particular semantic class. Again, a left-lateralized negative peak followed function word presentation (latency: 288 msec), whereas content words led to an enhanced negativity (latency: 364 msec) that was more symmetrical over the hemispheres. Gevins et al. (1995) used a cued two-stimulus paradigm and asked subjects to indicate whether two stimuli were similar according to phonological, syntactic, or semantic criteria. These authors reported a lateralized positivity (latency: 445 msec) elicited by function words which was most pronounced over left frontal regions, whereas content words failed to elicit a late lateralized component. These authors did not report stimulus lengths or frequencies, however, and it is therefore not possible to exclude the most likely confounds. In an experiment comparing brain responses to content and function words matched for word frequency and word length (Pulvermüller et al. 1995a) while study participants had to make speeded lexical decisions, a negative-going wave that peaked around 160 msec after the onset of visual stimuli revealed a significant interaction of the word class and hemisphere factors. The peak in the event-related potential was equally visible over both hemispheres after presentation of content words, but it was pronounced over the left hemisphere and reduced over the right when function words were processed. Mean event-related potentials obtained between 150 and 300 msec after stimulus onset also re-

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vealed a significant interaction of the factors hemisphere and word class (left/right difference strong for function words, but minimal or absent for content words).

It is important to point out some of the differences between these studies. For example, the tasks to be performed by participants differed (lexical decision, sentence judgment, etc.). In spite of these differences, all of these experiments revealed differences in electrocortical responses between the major vocabulary types. Results were very similar in the studies by Neville et al. and by Nobre and McCarthy. In both cases an early left-lateralized component was found after function words and a component symmetrical over the hemispheres followed content words after a longer delay. In Gevins et al.'s results, function words led to a left-lateralized component that occurred much later compared to both earlier studies, and, again, no such lateralized component was present for content words. In our study, we found no word class-difference in latencies of event-related potentials, but this study again confirmed the observation of a left-lateralized component evoked by function words and a component symmetrical over the hemispheres evoked by content words. Thus, all of these studies agreed on the finding of left-lateralized electrocortical responses to function word presentation and less or even absent lateralization of potentials evoked by content words.

Checking these studies against possible confounds reveals the following: Words were presented in sentence context only in Neville's experiment, whereas context effects are likely to play a minor role in the remaining studies. Matching of stimuli for word length was performed for Nobre and McCarthy's and for Pulvermüller et al.'s experiment. Only the latter study used content and function words matched for word frequency. As already pointed out in section 4.3, the issue of frequency matching is of particular relevance for electrocortical content/function word differences, because there are data (reported by King & Kutas 1995) indicating that latency differences may be the result of different word frequencies of the stimuli chosen from the two vocabulary classes. After frequency-matching of stimuli, word class-differences in latencies of event-related potentials indeed vanished. However, the differences in laterality of electrocortical responses to content and function words were still present with frequency-matched stimuli (Pulvermüller et al. 1995a). Therefore, the difference in laterality – rather than the difference in latency – appears to be characteristic of the major word classes.[10]

These studies are consistent with predictions 1 and 2 proposed in section 4.1. A possible explanation for the differences in cortical laterality of brain responses to content and function words is that specific cortical representations of these stimuli have different degrees of laterality. At present, there is no strong evidence from neuroimaging that content and function word representations are differently distributed within each hemisphere, although neuropsychological data support this view (Pulvermüller et al. 1996c; Vanier & Caplan 1990). However, recent preliminary PET data indicate that this prediction may also be correct (Nobre et al. 1997).

The Hebbian viewpoint suggests that differences in cortical loci involved in representing and processing words depend on semantic word properties. However, the summarized studies do not include information about which of the many properties distinguishing content and function words are crucial for differential brain activation induced by these stimuli. Content and function words not only differ with regard to semantic criteria (e.g., only the former can be used to refer to objects and actions), they also belong to different lexical categories, and even their phonological structure may be different. To find out whether semantic factors are indeed crucial, it is necessary to compare words that share phonological and lexical properties and differ only in their meaning. In a study comparing nouns with concrete and abstract meaning, electrocortical responses were also found to be different over the hemispheres (Kounios & Holcomb 1994). Abstract nouns led to an interhemispheric difference in electrocortical activity, whereas concrete nouns evoked similar responses over both hemispheres. This is consistent with the assumption that semantic differences underlie differential laterality of event-related potentials to concrete and abstract nouns. One may argue that this result makes it plausible that the same is true for the difference between content and function words, although this suggestion cannot be proven to be correct at present. Consistent with this view, however, the high degree of abstractness of function words is paralleled by a strong interhemispheric difference in event-related potentials, and the smaller degree of abstractness of abstract nouns is paralleled by a weaker interhemispheric difference evoked in a lexical decision task.[11] This pattern of results is in agreement with the assumption of strongly lateralized cell assemblies representing function words, weakly lateralized assemblies representing concrete content words, and a moderate degree of laterality for assemblies representing abstract content words (see sect. 3.3.2). Therefore, the view that the degree of laterality of brain responses to words reflects semantic stimulus properties receives support from the summarized psychophysiological studies.

5.2. Words related to action and vision

If the cortical distribution of word representations is determined by the cortical pathways through which meaning-related information is being transmitted, differences in cortical localization should not only distinguish representations of content and function words, but, in addition, words that differ in their motor and visual associations, such as nouns and verbs or animal and tool names, should have cell assemblies with different cortical topographies. The Hebbian model, and probably any associationist approach, suggests that semantic word class-differences determine differences in cortical representations. Most importantly, however, based on a Hebbian associationist model the semantic differences between word categories can be used to generate predictions on cortical areas that are involved in processing words of such categories. As discussed in section 3.3.3, we can expect words eliciting strong visual associations to be represented and processed in perisylvian and additional visual cortices in inferior temporal and occipital areas, whereas words with strong motor associations would be expected to involve additional motor areas in the frontal lobe. Concrete nouns referring to animals or large man-made objects appear to be examples of typical vision words, verbs referring to actions usually performed by humans are probably typical action words, and words referring to tools may evoke both strong motor and visual associations.

Neuropsychological data clearly indicate that focal brain lesions can affect these word categories to different degrees. Whereas lesions in temporal and/or occipital regions

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sometimes selectively impair processing of nouns, lesions in frontal areas have been reported to be associated with deficits in processing verbs (Damasio & Tranel 1993; Daniele et al. 1994; Goodglass et al. 1966; Miceli et al. 1984). There is also evidence for more fine-grained disturbances primarily affecting, for example, words referring to small man-made objects, such as tools, or words referring to living entities, such as animals (Damasio et al. 1996; Warrington & McCarthy 1983; 1987; Warrington & Shallice 1984). The relationship between anatomical lesion site and category-specific deficit has not yet been investigated systematically for all cortical lobes. However, studies of lesions in the left temporal lobe indicate that damage to the middle part of the inferior temporal gyrus most strongly impairs naming of animals whereas more posterior lesions involving inferior and middle temporal gyri result in a more pronounced deficit in naming tools (Damasio et al. 1996). The idea that cell assemblies representing words of different semantic and lexical categories have different cortical distributions therefore receives support from neuropsychological research, although it is not yet clear whether all of the more exact predictions on the cortical loci involved can be verified.

Imaging work that might reveal clues about processing differences between nouns and verbs was frequently carried out after Petersen et al. (1989) and Wise et al. (1991) reported that verb generation involved cortical areas less activated during noun reading. These authors and several more recent investigations used PET to measure brain activity while experiment participants either read visually presented nouns (reading task) or tried to generate verbs that "go with" the nouns (verb generation task).[12] If "car" is being presented, generation of "drive" or "race" may be expected. For evaluation, brain activity maps from the reading task were subtracted from those from the verb generation task. Significantly enhanced brain metabolism in a particular area during the generation task was attributed to cognitive processes necessary for verb generation and not necessary for reading nouns.

Although not all of the studies agree on the cortical loci of activity enhancement during verb generation, it appears that increased blood flow in prefrontal and temporal cortices can be observed.[13] Activity enhancement in the left frontal lobe has been reported in Broca's area and anterior and superior to it (McCarthy et al. 1993; Petersen et al. 1989). Also Wernicke's region (posterior area 22; Wise et al. 1991) and the middle temporal gyrus (Fiez et al. 1996) showed increased blood flow. Thus, during verb generation stronger activity in perisylvian language cortices and in additional premotor, prefrontal, and temporal areas was found. Figure 6 presents results from one study revealing both prefrontal and middle temporal activation during verb generation relative to the reading condition.

When interpreting these results to draw conclusions on cognitive processes, such as processing of a particular class of words, the following should be noted. As the above example clearly demonstrates ("car" leading to generation of "drive" or "race"), the generated words are not necessarily verbs, in particular if the experimental language is English where many verbs can also be used as nouns and vice versa. From this point of view, it does not seem appropriate to call it a "verb generation task," but rather a task to generate action words. However, even this may not be correct, because subjects may have been instructed to describe "what the nouns might be used for or what they might do" (Fiez et al. 1996, p. 1), thus allowing for the generation of both action words and vision words related to perceived movements. In addition, arguments raised in section 4.2 become relevant here, namely, that it is difficult to interpret these results in psychological terms because comparison of word generation to the reading task reveals several differences on the cognitive level. Recall that the generation of action words makes not only semantic processes necessary, it also requires, for example, lexical search and stronger attention compared to the highly automatized process of reading common words. Furthermore, in most cases no information about stimulus or response properties is given that would allow for evaluation of possible confounds as pointed out in section 4.3. Based on these PET results alone, it is therefore not possible to attribute blood-flow changes to verb or action word processing. Nevertheless, assuming that action words were frequently produced by experiment participants, these results appear consistent with the following view. During the generation of action words, an additional cell assembly was activated (compared to the reading task) that included neurons not only in perisylvian cortices but also in prefrontal, premotor, and middle temporal areas. This is probably not too far from what could be expected based on the associationist framework discussed in section 3 (see also prediction 3 above). However, from a methodological more rigorous point of view it appears necessary to compare brain activity when action and vision words are being processed in the same task (see sect. 4).

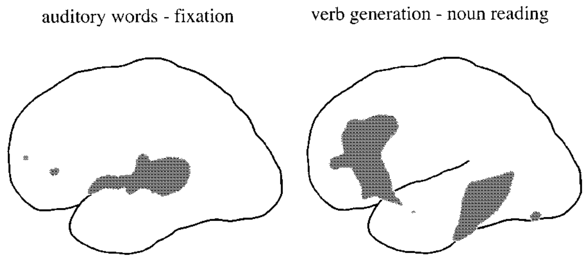

Figure 6. Presentation of spoken words leads to increased blood flow in perisylvian areas relative to looking at a fixation point (left diagram). In contrast, verb generation can activate additional prefrontal areas and the middle temporal gyrus (right diagram). (Modified from Fiez et al. 1996.)

In a recent PET study, Martin et al. (1995) presented achromatic line drawings of objects and had subjects generate action names and color words associated with the objects. Direct comparison of activity patterns evoked during generation of these word categories revealed increased metabolic rates in the ventral temporal lobe when color words were generated. In contrast, generation of action words led to stronger activity in more superior temporal areas on the middle temporal gyrus, and in inferior frontal areas, but not in additional motor cortices. This failure may reflect the fact that, as these authors emphasize (footnote 26, p. 105), many of the words actually generated by experimental subjects did not refer to movements the subjects would perform themselves, but rather to movements of objects that are perceived visually. Examples of responses listed by these authors include the verbs "fly," "see," and "sleep," for which visual associations are plausible, but a classification as action words may appear inappropriate. If many verbs without motor associations were produced, this

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may be the reason why visual areas were activated instead of additional motor areas relevant for controlling hand or foot movements. This point further evidences the necessity to control both stimulus and response properties carefully. It is important to note, however, that part of the left middle temporal gyrus was active during verb generation in the study by Martin et al. and that either the same or a closely adjacent area has been found to be active during verb generation from visually presented nouns (Fiez et al. 1996; Petersen et al. 1989).

Differences between action and vision words were also investigated using event-related potentials calculated from EEG recordings. Most of these studies compared electrocortical responses to nouns and verbs. Whereas an early study (Samar & Berent 1986) reported generally more positive potentials following verbs (compared to nouns), more recent work using larger electrode arrays (32 or 64 channels) and more sophisticated analysis techniques (e.g., current source density analysis) suggest word class-differences in cortical topographies of event-related potentials. In a study investigating potentials evoked by several word classes, Dehaene (1995) presented numerals, nouns (animals' and persons' names), and verbs matched for word length.[14] Whereas word-evoked potentials were generally larger over the left hemisphere, word class-differences were discovered over both hemispheres around 300 msec after stimulus onset (see p. 2155). Verbs elicited a left-lateralized positive component maximal over inferior frontal cortical sites which was not found for nouns. Both nouns referring to animals and verbs led to almost identical left-temporal negativities. These results are consistent with the assumption of additional left-frontal activity during processing of verbs, but do not indicate any noun/verb processing differences in more posterior cortical loci. With regard to the methods, however, it should be noted that no matching for word frequency or arousal and valence values was performed for nouns and verbs, one third of the verb stimuli had homophonous common nouns, and stimuli were repeated in the experiment. The first point makes a replication with matched stimulus materials desirable.

Presenting nouns and verbs matched for word frequency, length, arousal, and valence in a lexical decision task, Preissl and colleagues (Preissl et al. 1995; Pulvermüller 1996a) found electrocortical differences as early as 200 msec after the onset of visual stimuli. When average noun- and verb-evoked potentials (between 200 and 230 msec) were compared, significant differences were seen only over the frontal cortex. After submission of data to current source density analysis in order to maximize the contribution of local generators to the signal (Hjorth 1975; Perrin et al. 1989), stronger electrocortical signs of activity were found after verb presentation over bilateral motor cortices, but more pronounced event-related potentials over visual cortices in the occipital lobes were seen after nouns. It is significant that stimuli were carefully evaluated for motor and visual associations. Ratings of experiment participants confirmed differences in associations of body movements and visual scenes elicited by stimulus words. Verbs were judged to elicit significantly stronger motor associations than nouns, and nouns were judged to elicit stronger visual associations than verbs.[15] The electrocortical differences seen over motor and visual cortices paralleled these differences in conscious motor and visual associations. The left diagram in Figure 9 presents these differences in event-related potential topographies elicited by well-matched nouns and verbs. These data are in agreement with predictions 3 and 4 listed in section 4.1. They can be explained by the assumption that action words activate additional neuronal generators close to motor cortices, whereas vision words spark additional neuron populations in or close to primary visual areas in the occipital lobes.

It could be argued that although an influence of the confounding factors discussed in section 4.3 appears unlikely in this case, it is not clear whether the electrocortical word class-differences are related to semantic associations elicited by the stimuli, or to the fact that stimuli belong to different lexical categories (noun and verb). However, because the assumption that semantic differences are crucial can explain the topographical differences found in electrocortical responses, this view should probably be preferred. Differential involvement of motor and visual cortices could be predicted based on associationist principles. In contrast, there is no a priori reason why members of different lexical categories should involve different cortical lobes. However, to further confirm the idea that semantic properties of words, not their lexical categories, are crucial for differences in the topography of cortical activation, it is appropriate to look at stimuli from the same lexical category (nouns) that nevertheless evoke either primarily visual associations (e.g., animal names) or associations of body movements (e.g., tool names).[16]

Recently, Damasio and colleagues (1996) examined differences in brain activity during naming of animals and tools. In a PET study investigating activity changes in the temporal lobes, they found strong activation of the middle part of the left inferior temporal gyrus during animal naming (compared to a baseline condition), whereas enhancement of activity in more posterior cortices in the inferior and middle temporal gyri were found when naming of tools was compared to the baseline. These results suggest that different neuronal populations and cortical areas in the left temporal lobe contribute to processing of action words compared to words with additional visual associations.

Differences in brain activation during naming of tools and animals were also investigated in a PET study by Martin and colleagues (1996). In this case, subjects had to silently name objects depicted either in line drawing or in silhouette (to eliminate differences in internal detail of drawings).[17] The names of these objects were matched for word frequency. Direct statistical comparison of activity patterns elicited by animal and tool naming revealed the following. Animal naming led to relatively enhanced blood flow in primary and higher visual cortices in the calcarine sulcus in the left hemisphere (and to small activity foci in the prefrontal lobe). In contrast, tool naming was accompanied by activity enhancement in left premotor areas, plus an activity increase in the middle temporal gyrus. These data provide additional evidence that areas outside the perisylvian cortices contribute to processing of animal and tool names. Consistent with earlier studies using the verb generation task, a cortical locus in the left middle temporal gyrus was activated when words with strong motor associations (tool names, action verbs) were generated. In contrast to the results of the Damasio study, activity enhancement during animal naming involved occipital visual cortices rather than inferior temporal sites (which is consistent with prediction 4). Most importantly, however, naming of tools led to an additional activity focus in the premotor area con-

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trolling hand movements (Fig. 7). This is consistent with the assumption that processing of words with motor associations activates motor cortices involved in programming such movements.

Although this study has several methodological advantages over other PET studies (e.g., matching of stimuli, of responses, calculation of significant differences between critical conditions rather than only between critical condition and baseline), it should be kept in mind that a naming study was carried out and differences between naming conditions may be related to several cognitive processes. Looking at the list of methodological desiderata from section 4, it is relevant that for most PET studies it is not clear whether and to what degree complexity, frequency, arousal or valence values, and repetition of stimuli or responses influenced the results.[18] Furthermore, when naming of depicted animals and tools is being compared, it must be noted that whereas animal pictures include many curved lines, are usually rather complex, and can include various colors or shadings, tools can be drawn with a few straight lines and usually lack extensive coloring or shading. If matching of visual stimuli for visual complexity has not been performed, physical differences of stimuli may account for differential activation of visual pathways specialized for processing of particular aspects of stimuli.

The possible merit of exact investigation of psychological properties of stimuli and responses can be further illustrated based on results from the Damasio study mentioned above (Damasio et al. 1996). In that investigation, highest activation values during naming of famous persons' faces were observed in the temporal poles of both hemispheres. It is unclear to which psychological variable this activity enhancement relates. However, it is clear from psychophysiological investigations that faces are among the most arousing stimuli (Lang 1979; Lang et al. 1990), and words referring to such stimuli are very likely to exhibit comparatively high arousal values, as well. It has been proposed that high-arousal words (i.e., words evoking strong emotional associations) are represented in cell assemblies that include additional neurons in the amygdala and subcortical structures (e.g., midbrain dopamine system; Pulvermüller & Schumann 1994; Schumann 1990).[19] This provides a tentative explanation why Damasio and colleagues found enhanced activity in temporal poles during naming of famous persons. When persons' names were retrieved, it may be that cell assemblies including large numbers of amygdala neurons became active, and, therefore, blood flow increases were found in adjacent cortical areas strongly connected to the amygdalae (see Amaral et al. 1992), that is, in temporal poles. Thus, differential arousal values of words and/or pictorial stimuli may explain differential involvement of temporal poles during naming of pictures of famous persons.[20]

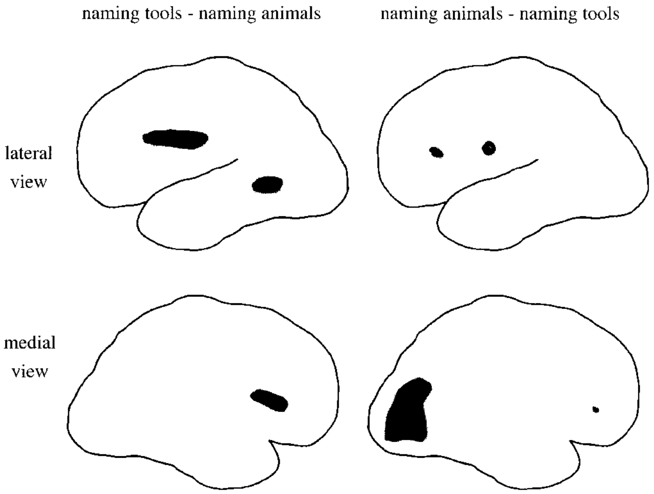

Figure 7. Naming of tools and animals can activate quite different cortical regions. Diagrams indicate significant differences in brain metabolism between animal and tool naming. In the left occipital cortex, enhanced metabolism is seen during animal naming. In the left premotor cortex close to the hand representation and in the middle temporal gyrus activation is stronger when tools are being named. (Modified from Martin et al. 1996.)

In summary, these studies include the following results relevant to the idea of different cortical representation and processing of action and vision words:

1. PET and fMRI studies using the verb generation task revealed enhanced activity in perisylvian language areas and adjacent temporal and prefrontal cortices in the left hemisphere. Perisylvian activity enhancement may be accounted for by assuming that an additional word form representation is being activated in the generation task (relative to the baseline, usually noun reading). Activation of additional cortical areas outside the perisylvian region may indicate psychological processes coupled to word form processing. Whereas prefrontal activity increases dorsal to Broca's area may relate to body movements to which the words refer, activity enhancement in middle temporal gyrus may be related to visual imagination of movements.

2. ERP studies indicate that nouns with strong visual associations and verbs with strong motor associations activate different cortical generators in both hemispheres. Whereas stronger signs of electrocortical activity following action verbs have been recorded from anterior and central regions, nouns led to more pronounced activity signs over occipital visual cortices. These differences appear to be related to neuronal activity in or close to primary motor or visual cortices underlying movement and visual associations, respectively.

3. PET studies of animal and tool naming provide additional evidence for processing differences between action and vision words. Tool naming with nouns that probably elicit motor associations activated premotor cortices and additional sites in the middle temporal gyrus, and naming animals using visual nouns led to activity enhancement in inferior temporal cortices and in occipital cortices close to the primary visual area.

Although these studies are subject to methodological problems to different degrees (as pointed out in great detail above), a coherent picture can nevertheless be drawn on their basis. Both ERP and PET studies support a contribution of occipital areas close to primary visual cortices to the processing of vision words. There is also PET evidence for a specific contribution of inferior temporal cortices to the processing of vision words. Thus, the processing of words that evoke visual associations appears to be related to neuronal activity in visual cortices (see postulate 3).

In contrast, processing words eliciting motor associations such as certain action verbs and tool names activates areas in the frontal lobe close to motor cortices, as revealed by ERP, PET, and fMRI studies (see postulate 4). PET studies revealed an additional area of activation in the middle

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temporal gyrus which may be related to visual imagination of movements induced by action words. This focus may be localized in such a way that its activity is difficult to record in the EEG, or that even higher spatial resolution and, therefore, larger numbers of electrodes are necessary to monitor it. Thus, the data are consistent with the view that the processing of words that remind experiment participants of movements of their own bodies and the visual perceptions associated with these movements activate cortical loci in frontal lobes and temporal lobes related to the perception and imagination of such movements.

From a methodological point of view, it appears particularly important to stress that, in some cases, not only were significant differences in the activation of critical areas found when word processing was compared to a resting condition, but physiological double dissociations (see sect. 4.2) between the processing of action and vision words were discovered and substantiated by interactions of the factors topography and vocabulary type. These interactions could even be obtained for action and vision words well matched for various psychological variables specified in section 4.3.

Although there is considerable agreement between electrophysiological and metabolic studies of action and vision words, there is one major incompatibility that calls for brief discussion. Whereas, in most cases, PET studies revealed processing differences between word class-differences only in the left hemisphere,[21] ERP studies also indicated word class-differences in the right hemisphere. This was not only so in ERP studies of noun and verb processing, it was also true for most of the studies revealing electrocortical differences between content and function words (see sect. 4.2). It is possible that some of the differences recorded over the right hemisphere were actually caused by generators in the left hemisphere. For example, larger, right-sided, event-related potentials over the occipital cortex related to noun processing (Pulvermüller 1996a) may be caused by left-hemispheric neuronal generators within the interhemispheric sulcus (which can be activated during processing of visual nouns, as suggested by the study of Martin et al. 1996; see Fig. 7). However, at this point it appears unlikely that all electrocortical differences seen at recording sites over the right hemispheres are caused by left-hemispheric generators (see discussion in sect. 5.1). Lack of right-hemispheric word class-differences reported in PET studies does not prove that the null hypothesis of equal activity patterns is correct. Fine-grained differences may be ruled out by too rigid a criterion of significance (Wise et al. 1991). Furthermore, some metabolic imaging studies provided direct support for processing differences between word classes in the right hemisphere (footnote 21). Thus, a final decision regarding the right hemisphere's role in word class-specific processes must be left for future investigation.

These results are consistent with the Hebbian postulate of different cortical distributions of widespread cortical assemblies related to cognitive processing. In addition to neurons in the perisylvian language areas of Broca and Wernicke, assemblies representing action words may comprise neurons in motor, premotor, and prefrontal cortices and in middle temporal gyrus.[22] Vision words may be organized as assemblies distributed over perisylvian and additional higher-order cortices in temporal and occipital lobes, and even over primary visual cortices. Thus, postulates 3 and 4 formulated above receive support from the data discussed. However, the Hebbian model implies that physiological word class-differences should be present in both hemispheres – a postulate that can, at present, be supported only by some of the studies.

6. Word processing in the brain: How?

The question of *where* in the brain cognitive processes take place is only one of the interesting issues to be addressed in cognitive neuroscience. Perhaps equally relevant are the questions of *how* the building blocks of cognitive operations – for example, meaningful words and gestalt-like figures[23] – are represented in the brain and in which way these representations are activated during processing of meaningful information. As discussed in section 2, the Hebbian framework provides tentative answers to both of these questions: The elements of representation are strongly connected but distributed populations of several thousand nerve cells. If such an assembly is being activated, an ignition takes place and, subsequently, neuronal activity will be retained in the assembly, leading to fast and coherent reverberation of activity in many of its neurons. As already mentioned, these ideas have received empirical support from investigations of high-frequency coherent brain activity and precisely timed spatiotemporal patterns of neuronal firing in cats, nonhuman primates, and humans. Stimulus-specific coherent and rhythmic activity in distant cortical neurons is usually seen in the high frequency range above 20 Hz. Spatiotemporal patterns are precisely timed with millisecond precision and reverberations may occur after short time lags of a few hundredths of a second. Reverberation of a cortical cell assembly may therefore lead to dynamics in high-frequency responses. If signals are large enough, they may well be picked up using large-scale neuroimaging techniques. It is clear that only EEG and MEG have a temporal resolution fine-grained enough to reveal spectral dynamics in high frequencies.

Starting from the working hypothesis that cell assemblies produce well-timed fast activity changes in many neurons, it appears most crucial to investigate high-frequency cortical responses in the EEG and MEG to further test the Hebbian model of word processing summarized above. Words – but not meaningless pseudowords – are assumed to be cortically represented as Hebbian cell assemblies. If high-frequency cortical activity reflects reverberation of neuronal activity in assemblies, such high-frequency responses during word processing should be stronger compared to processing of pseudowords. In addition, differences in topographies of high-frequency responses can be predicted for words with different meanings. Furthermore, because reverberatory activity can be assumed to occur only after ignition of cell assemblies, stimulus-related differences in high-frequency activity should occur only after differences observed using other measures of electrocortical activity, such as event-related potentials (predictions 5 and 6 in sect. 4.2).

Several experiments were carried out to test these hypotheses. In the earliest study, the EEG was recorded while subjects performed lexical decisions on German words and matched pronounceable and orthographically regular pseudowords displayed on a monitor. EEG data were submitted to a technique called Current Source Density Analysis to minimize the contribution of distant sources to the

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signals and to maximize the contribution of generators close to the recording electrodes (Law et al. 1993; Perrin et al. 1989).[24] Spectral responses were obtained by filtering in various frequency bands. These spectral responses were rectified and averaged over trials. Results revealed a stimulus-specific difference in high-frequency responses around 30 Hz. Words evoked stronger responses in the band between 25 and 35 Hz compared to matched pseudowords. The difference was not only specific to this frequency band, it also showed topographic specificity in that it was visible only at recording sites over left perisylvian cortices, and it was only significant in the time interval 300–500 msec after stimulus onset (Lutzenberger et al. 1994; Pulvermüller et al. 1995b). No changes or differences between stimulus classes were visible in even higher parts of the spectrum, for example around 60 to 80 Hz where muscle activity produces most pronounced effects (Cacioppo et al. 1990).

Differences in high-frequency spectral responses between words and pseudowords were most pronounced and significant only at perisylvian recording sites. Because EEG signals were first submitted to Current Source Density Analysis (to emphasize the contribution of local generators), it appears that neuronal dynamics of large neuronal populations housed primarily in left-perisylvian cortices differed during word and pseudoword processing. The difference in spectral responses to words and pseudowords can be explained based on the assumption that additional high-frequency neuronal processes not involved after pseudoword presentation were sparked by word stimuli. Relatively strong 30 Hz activity during word processing may indicate continuous activity of large cortical assemblies producing well-timed and rapidly changing neuronal activity. Pseudowords – for which no cortical assemblies are assumed – would fail to ignite a specific neuronal representation, and, therefore, would finally cause less well-timed activity. These findings support predictions made based on the Hebbian model (Pulvermüller et al. 1994b).

It may be argued that the difference in high-frequency responses to words and pseudowords is related to the language used in the EEG experiment (German), to the EEG recording techniques, to features of the procedures used for signal analysis, to the modality of stimulus presentation (visual), or to the motor responses study participants had to perform to express their lexical decisions (yes/no button presses with the left hand; see Pulvermüller et al. 1995b). Therefore, an experiment was conducted in which all of these features of experimental setting and evaluation procedure were changed. A 74-channel biomagnetometer was used to record biomagnetic signals from both hemispheres of right-handed native speakers of English who heard English words and pseudowords spoken by a professional speaker. This time, subjects did not have to respond to the stimuli, but they were asked to memorize all stimuli in order to pass a recognition test later. For calculating spectral responses the method described by Makeig (1993) was used. For a variety of frequency bands, spectral power was determined in overlapping time windows of 0.3 seconds.

Figure 8 presents results obtained from one participant in the MEG experiment. In this subject, as well as in the group as a whole, words again evoked stronger high-frequency cortical responses than pseudowords (Pulvermüller et al. 1996a). Consistent with results from the EEG experiment, differential high-frequency responses could be observed in the 20–35 Hz range. No significant difference in spectral power was seen in any of the other bands examined. The difference was only significant for recordings from anterior channels placed over inferior frontal areas of the left hemisphere. At these channels, biomagnetic responses evoked by words and pseudowords were larger compared to all other channels, so that a maximal signal-to-noise-ratio can be assumed. The consistency of results between EEG and MEG experiments indicates that the result does not depend on the language from which stimuli are taken, on special features of the methods for analyzing spectral responses, on whether high-frequency neuronal activity is recorded in the EEG or MEG, or on the task performed by experiment participants. It should be noted, however, that in a more recent study, Eulitz et al. (1996) found left-hemispheric differences between words and nonwords in the 60–70 Hz range when experiment participants had to decide whether words included nonlinguistic signals (incomplete letters, noise). Differences in the frequency range where high-frequency dynamics occur may therefore depend on the experimental task applied (see Pulvermüller et al. 1997 for further discussion).

Although high-frequency cortical responses differed between words and pseudowords as predicted based on the Hebbian notion of a cell assembly (see Fig. 1), one may wonder why this difference was reliable only in recordings from electrodes and coils placed close to left-perisylvian cortices. In section 3, cell assemblies representing words were assumed to be distributed over wide cortical areas and over both hemispheres. One may therefore ask how the present results of word/pseudoword differences in high-frequency responses recorded only from the left hemisphere would fit the model. The answer to this question is quite straightforward: Whereas all assemblies representing word forms are assumed to include a large percentage of their neurons in left-perisylvian areas, additional neurons outside these areas would be included in the assembly only if word forms frequently co-occur with multimodal nonlinguistic stimuli. These additional areas involved are likely to

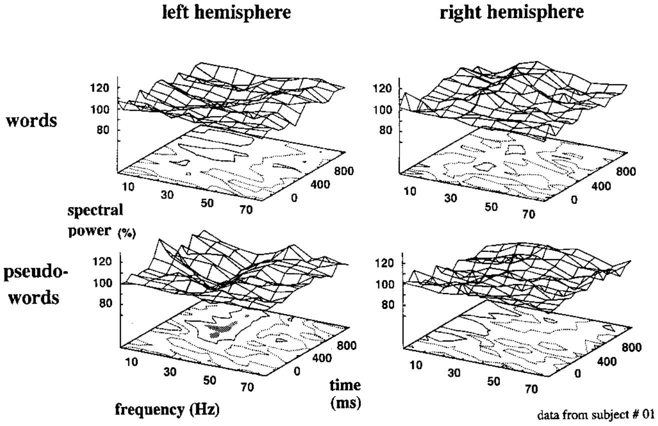

Figure 8. Spectral power calculated from biomagnetic signals elicited by words (upper diagrams) and pseudowords (lower diagrams) recorded over the left and right hemispheres. Normalized spectral power is plotted as a function of time and frequency. Word/pseudoword differences in high-frequency spectral responses are present around 30 Hz in recordings from the left hemisphere. (From Pulvermüller et al. 1996a.)

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be different for words of different types. In the studies on word/pseudoword differences discussed above, stimuli of a narrow frequency range of word frequencies were used, but no restrictions regarding semantic properties were applied. The large variety in linguistic properties of stimulus words and, hence, in the additional cortical areas possibly involved may explain why there were no consistent word/pseudoword differences outside left-perisylvian areas.[25] This view is in need of further support, however. Namely, evidence should be collected concerning differential involvement of extra-perisylvian areas during processing of word categories using high-frequency spectral responses as the dependent measure.

As emphasized earlier, the Hebbian approach not only implies that words have cell assemblies and that pseudowords lack such cortical representations, it also leads to the postulate of different cortical distributions of cell assemblies representing action and vision words (Fig. 5). This predicts that topographies of high-frequency cortical responses vary as a function of word category. Words inducing visual associations should evoke stronger high-frequency responses over visual cortices, whereas action words with strong motor associations should lead to stronger high-frequency responses over motor cortices.

Nouns inducing strong visual associations and verbs evoking strong movement associations were presented in a lexical decision task while electrocortical responses were recorded in the EEG. Stimuli were matched for word frequency, length, arousal, and valence. EEG data were submitted to current source density analysis and to analysis of spectral power. A significant word category by recording site interaction was obtained in the analysis of spectral responses in the 30 Hz range 500 msec after stimulus onset and later (Pulvermüller et al. 1996b). There was a double dissociation of word categories and loci where stronger high-frequency signals were recorded. Differences were most pronounced at central and posterior recording sites. High-frequency responses to nouns at 30 Hz were stronger over visual cortices (recording sites O1 and O2 of the international 10-20 system; Jasper 1958), whereas 30 Hz responses to verbs were stronger close to motor cortices (recording sites C3 and C4). The diagram on the right in Figure 9 displays cortical topography of the difference in 30 Hz power elicited by action and vision words. No statistically significant differences between stimulus classes were seen in any of the other frequency bands analyzed. Because the topographies of the differences between action and vision words obtained with event-related potentials and with high-frequency responses as dependent measures are very similar (although not identical; see Fig. 9), it is possible that similar cortical generators underlie these electrocortical differences between the two word classes.

If a cell assembly is conceptualized as a neuron network that generates well-timed and fast-changing neuronal activity in many neurons, the data reported in this section provide evidence:

1. that cortical assemblies in left perisylvian cortex are being activated when meaningful words are processed but fail to ignite when meaningless pseudowords are being presented, and

2. that action and vision words activate cortical assemblies with different topographies.

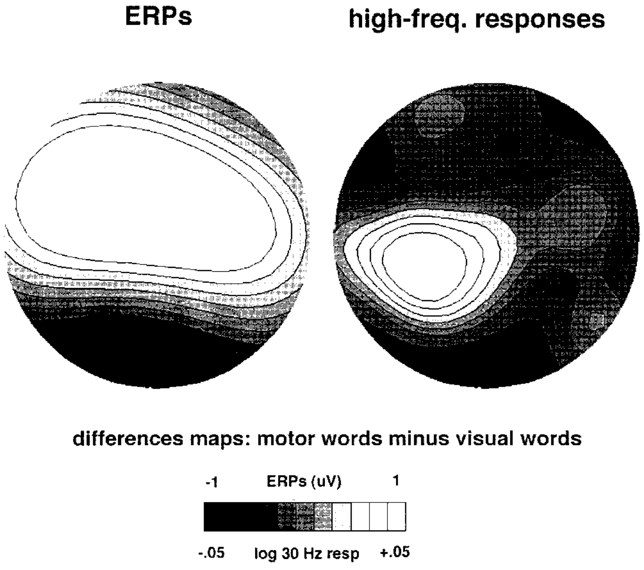

Figure 9. Processing of action verbs and nouns with strong visual associations is accompanied by significantly different electrocortical responses. Difference maps (nouns minus verbs) are shown. Large circles represent the head seen from the top (anterior is up, left is left). Differential topographies of event-related potentials (left diagram) are compared to evoked spectral responses in the frequency range 25–35 Hz. The two circles represent the head seen from above. The nose is up and left is left (right diagram). (Adapted from Pulvermüller et al. 1996b.)

Whereas most event-related potential studies summarized in section 4 indicate that word class-differences occur quite early (150–300 msec) after onset of visually presented words, high-frequency spectral dynamics related to word properties were visible only at 300 msec and later. This is consistent with predictions 5 and 6 derived in section 4.1. Two processes, one early and the other late, may be reflected in these physiological measures. The Hebbian perspective offers the view that whereas the early process is the ignition of stimulus-specific assemblies, the late process is reverberation of neuronal activity in these assemblies. The fact that the early and late physiological signs exhibit the same double dissociation with regard to their cortical topography during processing of action and vision words (and even yielded comparable difference maps) may be taken as additional evidence that similar neuronal machineries – but different activity states of these machines – underlie the differences recorded in the EEG and MEG. One possibility is that these activity states reflect the psychological processes of word perception and of active memory of particular words, respectively.

7. Summary, implications, open questions

Neuroimaging studies were used to evaluate the hypothesis that words are cortically represented in distributed cell assemblies with defined topographies that vary with semantic word properties. Electrophysiological and metabolic imaging studies provide evidence that not only the language cortices in the left hemispheres, but additional cortical areas outside the left perisylvian areas play a role in word processing. Comparison of ERP responses to content and function words indicates that both hemispheres are strongly involved in processing concrete content words, whereas predominantly left-lateralized activity in or close

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to perisylvian regions appears to be related to processing of highly abstract function words. PET, fMRI, and ERP studies revealed that cortical areas devoted to motor programming or visual perception are activated when words with strong motor or visual associations are being processed.

Based on the studies summarized, it appears likely that motor, premotor, and/or prefrontal cortices and possibly additional areas in middle temporal gyrus contribute to the processing of action words, whereas inferior temporal and/or occipital areas close to the primary visual cortex can be involved in processing words with visual associations. The observed physiological double dissociations provide additional support for the idea that semantic characteristics of words determine the loci of their cortical processing. It is not yet clear, however, to which degree primary, secondary, and higher-order association cortices, respectively, participate in word processing. The results (ERPs and PET) summarized here would suggest that both lower- and higher-order sensory and motor cortices, as well as multimodal association areas, can play a role. A further open question concerns the contribution of the right hemisphere to word class-specific processes. Most ERP and fMRI investigations advocate such right-hemispheric contributions, whereas most PET studies available at present do not.

The summarized data support a Hebbian model of word representation (cf. predictions 1–4 in sect. 4.1). Differential laterality of cortical processing of concrete content and abstract function words can be explained by bihemispheric cell assemblies with different degrees of laterality (Fig. 4). Differential involvement of motor and visual cortices in processing of action and vision words may indicate that representations of these words extend toward these extra-perisylvian areas, respectively (Fig. 5).

Although these results on differential cortical localization of word classes support the Hebbian model, they do not prove it to be correct. Obviously, the data cannot ultimately answer the question of whether there are word-specific cell assemblies. According to Hebb, each cognitive entity – each concept, word, or gestalt – has a separate assembly. An alternative appears to be that words of a particular semantic category are represented and processed by the same neurons. Processing of different words could, for example, be realized by different activity landscapes in the same neuron population, or, alternatively, by different spatiotemporal activity patterns occurring in the same neurons. Nevertheless, it may appear likely that words with similar but different meanings are organized in overlapping neuron sets, as proposed above. Some neurons of these sets may contribute to the processing of word 1 but not of word 2. If word 1 is "crocodile" and word 2 is "alligator," for example, different color-sensitive neurons in visual cortices may be included in the respective assemblies. Furthermore, there is physiological evidence indicating that neurons can be found in human cortex that respond rather specifically to acoustic presentation of particular low-frequency words or phoneme sequences (Creutzfeldt et al. 1989a; 1989b). Whereas this observation fits into the Hebbian framework, it would be difficult to explain if different activity patterns of the same neuron set were the physiological counterparts of similar words.

It must again be emphasized that recent large-scale neuronal theories and their applications to language mechanisms (Braitenberg 1980; Braitenberg & Pulvermüller 1992; Damasio 1989a; Mesulam 1990; 1994) agree on the postulate that cell assemblies with distinct topographies are the neuronal counterparts of words, and that perceptual properties of meaning-related stimuli determine cortical distributions of these assemblies. There are, however, diverging assumptions that distinguish proposals in the Hebbian tradition. For example, a contribution of the right hemisphere to language representation and processing is not assumed (or, at least, not explicitly postulated) by most of these proposals, but it is a necessary postulate according to the radical Hebbian perspective detailed in sections 2 and 3. Bihemispheric contributions to word processing are not only suggested by split-brain research (Zaidel 1976) and behavioral experiments in healthy individuals (Banich & Karol 1992; Mohr et al. 1994b), they are also consistent with recent metabolic imaging studies (Fiez et al. 1995; Mazoyer et al. 1993; Zatorre et al. 1992) and electrophysiological depth recordings (Creutzfeldt et al. 1989a; 1989b; Ojemann et al. 1988; Schwartz et al. 1996). In addition, differential laterality of electrocortical responses to words of different kinds and word-class processing-differences recorded from the right hemisphere appear to further support a radical Hebbian approach. At this point, however, one may consider it premature to reject any of the competing large-scale neuronal theories of word processing postulating that words are processed exclusively in the left hemisphere. More research is necessary to decide the controversial issue of right-hemispheric contribution to language and, in particular, to word class-specific processes.

Further open questions address the inner structure of cell assemblies. According to the proposal in section 3, most word representations consist of two parts, a perisylvian part related to the word form and a part located mainly outside the perisylvian areas representing semantic word properties. Similar proposals have earlier been formulated (Warrington & McCarthy 1987; Warrington & Shallice 1984). However, the assumption that word representations only include semantic and phonological parts may be questioned. It is evident that not only the semantic characteristics of a word and its phonological form need to be represented in the brain, but that information about its grammatical or functional properties needs to be stored as well (Garrett 1988; Levelt 1989). This information would, for example, include the knowledge about the lexical category of a word, about whether it is masculine or feminine, or transitive or intransitive, about its possible thematic roles in sentences, about whether it takes regular or irregular inflection, and, more generally, about the complements it requires. It has been argued that cortical representations of words may include a third part where such knowledge is laid down (Damasio et al. 1996). Although this is possible, it is difficult to see how formation of a separate third assembly part storing grammatical knowledge about a word can be explained by associative learning or by other biological principles. Based on Hebb's ideas it appears more likely that grammatical knowledge is represented (1) in the connections between individual cell assemblies, (2) in the connections between overlap regions of several assemblies (Pulvermüller 1995b), and (3) in the activation dynamics that cell assemblies exhibit after their ignition. For example, it can be shown that between-assembly connections and activity dynamics are a possible basis of grammatical phenomena, such as center-embedding (see sect. 8). The representation of grammatical properties of words does not, therefore, require separate cortical neurons or areas

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exclusively devoted to the storage of grammatical information (see Caramazza 1996 for further discussion). Nevertheless, the possibility that there are separate neuronal representations of grammatical features of lexical items is not ruled out by the data available at present.

The Hebbian framework has several implications regarding the loci of word representations in the brain (that is, regarding the where question). Only four of them have been evaluated here (see postulates 1–4, sect. 4.1). Additional predictions not evaluated here concern, for example, words for which meaning-related stimulus information enters the brain through channels other than the motor and visual modalities, and more fine-grained contributions of different parts of frontal or occipital cortex to processing of action and vision words (see sect. 3.3.3). With regard to action and vision words, however, at least an elementary answer to the where question appears to be possible based on the present data.

This answer may be considered preliminary, because many of the studies summarized are subject to methodological problems discussed in great detail in sections 4, 5, and 6. In some cases, tasks (such as verb generation or naming depicted objects) were chosen that may allow conclusions on word processing, but may be accounted for as well by attributing physiological changes to other cognitive processes (such as memory search or perceptual analysis). Furthermore, confounding factors related to psychological and physical properties of stimuli or responses (word length, frequency, arousal, valence, repetition, and context) may influence the results to different degrees. However, consistency of results obtained over different paradigms and with different recording methods appears to be a strong argument for their acceptability.

If the where-in-the-brain question can be answered in the case of content, function, action, and visually-related words, the Hebbian approach also provides a tentative answer to the question of why their different localizations develop and why they involve particular cortical lobes and gyri. It is unclear, however, from the localization studies dealt with in section 5 how the cortical representations are organized and how they function. To obtain information about such functional characteristics, fast changes of cortical activity need to be monitored. Cell assemblies widely distributed over distant cortical regions are probably difficult to observe through electrophysiological recordings from local neuron clusters or small areas. If large-scale neuronal theories of cognitive functions are correct, fast, large-scale recording techniques, such as EEG and MEG, are necessary to visualize activity changes in distributed assemblies, and for investigating their cortical topographies.

High-frequency spectral responses revealed processing differences between words and matched meaningless pseudowords. EEG and MEG experiments indicated that words elicit stronger high-frequency responses than pseudowords. This can be explained by assuming that although cell assemblies generating well-timed high-frequency activity are activated when words are being processed, no assembly becomes fully active when pseudowords are being perceived. A double dissociation in high-frequency responses could be observed over motor and visual cortices when action and vision words were processed. This provides additional evidence that cortical topographies of assemblies representing action and vision words differ. Furthermore, these findings suggest that the investigation of high-frequency cortical responses is a relevant tool for addressing important questions in cognitive neuroscience.

Experiments on electrocortical counterparts of words eliciting motor and visual associations showed some agreement between event-related potential and spectral response data. These measures revealed similar topographic differences between word types (see difference maps in Fig. 9). It may therefore be speculated that these measures provide information about different processes occurring in the same cell assemblies. The Hebbian framework suggests that initial activation (ignition) of cell assemblies and subsequent reverberation of neuronal activity in the assembly may be related to the two measures (see postulates 5 and 6 in sect. 4.1). After its ignition, the assembly may reverberate so that large numbers of neurons repeatedly become coherently active. Consistent with this view, peaks in the event-related potential distinguishing between word classes were seen as early as 150–200 msec after the onset of stimuli, but differences in spectral responses between words and pseudowords or between action and vision words were significant only around 300 msec or later. Early word class-specific components of the event-related potential and later dynamics in high-frequency spectral responses may therefore be related to early activation (ignition) and subsequent reverberatory activity of cell assemblies.

There is another aspect with regard to which the Hebbian approach sharply differs from many current theories of word processing. Many models assume that different aspects of a word – its phonological, grammatical, and semantic information – are processed in successive steps, for example, starting with phonology and finally arriving at semantics (see, e.g., Caplan 1992). In contrast, Hebb's view would imply that sufficiently strong partial stimulation of an assembly leads to its full ignition (Braitenberg 1978b). Ignition is assumed to be an instantaneous process, thus activating all parts of an assembly at almost the same time. According to the present proposal, phonological information is stored in perisylvian cortices, whereas at least some aspects of a word's meaning are laid down in assembly parts housed outside perisylvian space. The assumption of a one-shot activation would imply that the earliest signs of activation occur near-simultaneously in "semantic" areas and in "phonological" perisylvian cortices.

In lexical decisions tasks, electrocortical differences between words and pronounceable and orthographically regular pseudowords are usually not found before 200 msec after the onset of visual stimuli (Pulvermüller et al. 1995a), although differences between words and letter strings can occur earlier, that is, around 150 to 200 msec (Compton et al. 1991). This may be interpreted as evidence that the phonological or orthographic word form is being accessed around $\frac{1}{5}$ of a second after the stimulus is being displayed. It is important to note that word class-differences in event-related potentials summarized above were also present around 200 msec post stimulus onset, or even earlier.[26] Some of these differences were present close to visual and motor cortices and far from left-perisylvian areas. This can be explained by assuming that they relate to semantic word properties.[27] If this interpretation is correct, the summarized data would support the idea of a one-shot activation of cell assemblies in which phonological and semantic information of words are bound together and simultaneously accessed around 150–200 msec after the onset of visually

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presented word stimuli.[28] It is clear that simultaneous activation of left-perisylvian "phonological" and extra-perisylvian "semantic" areas would be inconsistent with many serial models of word processing, provided that activations of processing stages are assumed to follow each other with a measurable delay.

Although the Hebbian framework may represent an alternative to current modular theories of word processing, the two approaches are not entirely incompatible. Strictly speaking, a double dissociation in neuropsychology implies that distinct brain parts are necessary for performing two tasks. It does not prove that the processes necessary for each of the two tasks are independent of each other (although this is sometimes a convenient assumption). The Hebbian framework highlights how processes that are subject to neuropsychological double dissociation can nevertheless be tightly linked and occur simultaneously in the intact brain.[29] The double dissociation between nouns and verbs seen in certain aphasic patients does not prove that these word categories are processed in independent modules. Rather, it appears that they share most of their neuroanatomical "processing space," but that each involves neurons in additional specific areas. Likewise, lesions affecting these "additional" areas can explain category-specific impairments. The double dissociation between agrammatism and anomia with regard to the processing of content and function words (agrammatics have difficulty with function words, anomics with content words) can also be explained based on the assumption of overlapping but distinct neuroanatomical "processing spaces" (see sect. 3, and Pulvermüller 1995a for further discussion). In some cases, the neuropsychological double dissociations correspond to interactions of the stimulus and topography variables in psychophysiological data. Processing loci may be distinct, although, functionally, neurons at distant loci interact. These neuropsychological data are entirely compatible with the view that phonological and semantic information is bound together in functional units and accessed almost simultaneously when words are being processed.

8. A word on syntax

For many language scientists, the question of how words are represented and processed in the brain is only a very basic one. Even substantial improvements in our understanding of the mechanisms underlying word processing may therefore be acclaimed only if the theoretical framework they are based on can offer perspectives on the solution of more complex problems known to be crucial for language. The question of how serial order is achieved in syntactic word strings has long been considered to be at the heart of our language faculty, and, from a theoretical point of view, it appears important to make clear whether a neurobiological model of word processing can offer perspectives on the biological reality of grammar (Lashley 1951).

The claim held by many linguists that language mechanisms cannot be explained by associative learning principles[30] may be the basis for a premature rejection of an approach postulating that so much can actually be explained based on Hebbian learning. However, one is well advised not to throw out the baby with the bathwater (i.e., a perspective on the neurobiology of language with the principles of associative learning). As pointed out in much detail in section 3, even a Hebbian explanation can only function if inborn neuroanatomical and neurophysiological prerequisites are assumed to be present. More to the point, perisylvian cortices need strong intrinsic connections (Deacon 1992a; 1992b) to allow for the formation of assemblies representing word forms, and the statistics of neuroanatomical connectivity must be such that an assembly exhibiting the functional states of ignition and reverberation can form. It is possible that inborn properties of the brain have functional consequences that are crucial for processing sentences. This would be entirely compatible with a Hebbian approach: Although associative learning is an important factor for the formation of assemblies, some of their functional properties may be genetically determined and hard-wired in cortico-cortical connectivity. It would be nice to show that universal principles underlying activity dynamics of cell assemblies can be relevant for achieving serial order of words in sentences.

Looking at what is known about activity dynamics in stimulus-specific neuronal populations, Abeles's well-timed activity patterns discussed in section 3 come to mind. In addition, Fuster's (1989; 1995) finding that cells activated by specific stimulus properties can stay active for a period of several seconds after stimulus presentation may be of utmost importance here. It is certainly possible that these "memory cells" retain their activity because they are part of stimulus-specific cell assemblies in which neuronal activity reverberates. If so, these cells reveal important information about activity dynamics of the cell assemblies to which they belong (Fuster 1994).

Many memory cells exhibit well-defined activity dynamics. They do not show constantly enhanced activity after presentation of the stimulus they are specialized for, but, instead, they are strongly activated initially and lose activity almost exponentially thereafter (Fig. 10, left). What role could such neuronal units with exponential activity loss play in processing syntactic information?

Assume that several such assemblies have been primed one after the other. Due to the exponential decline of activity, the assembly activated first will later be at the lowest activity level, whereas the neuronal unit that was the last to be activated would still maintain the highest level of activity (Fig. 10, lower diagram). The information about the sequence of activations is thus stored in the hierarchy of activity levels of assemblies. Assuming a read-out mechanism that fully activates and then deactivates only the cell assembly at the highest level of activity, a set of exponentially declining assemblies can be considered equivalent to a pushdown store (Pulvermüller 1993). The unit primed first will be fully activated last, and, vice versa, the last to be primed would be the first to become fully active. If, for example, a speaker intends to say that three different persons have performed three different actions, the speaker could first talk about the actors whereby the neuronal representation of the corresponding nouns would be activated. If there is activity flow from the noun representations A, B, and C to the corresponding verb representations A*, B*, and C*, respectively, the successive activation of noun representations would lead to activity levels of the three verb representations that exhibit the hierarchy shown in Figure 10. Ignition would therefore occur first in C*, later in B*, and finally in A*, leading to a mirror image activation sequence, that is ABCC*B*A*. This mechanism could be crucial for producing center-embedded strings, such as, for

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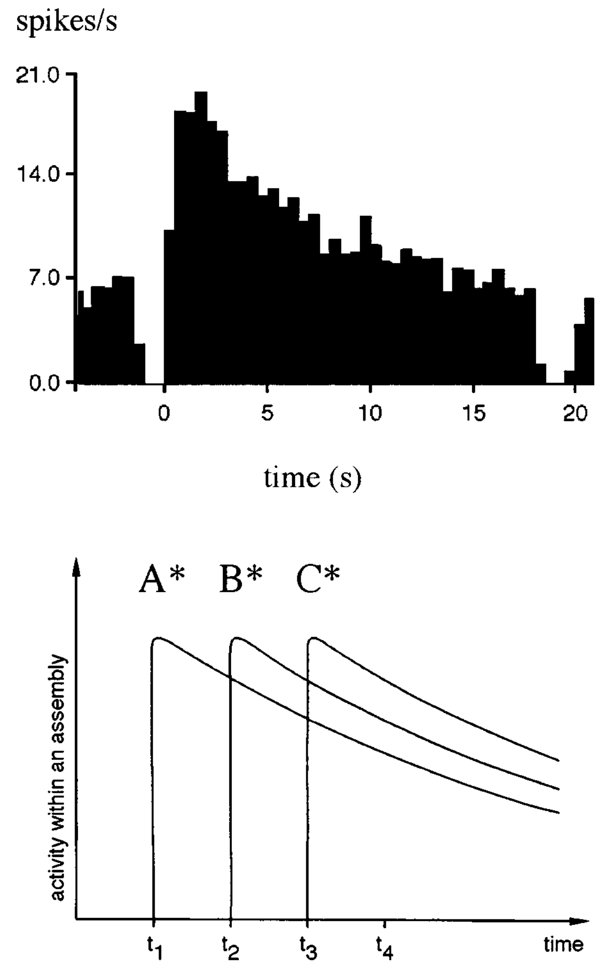

Figure 10. Top: Activity of a memory cell possibly reflecting activity dynamics in a large cell assembly to which it belongs. Note the almost exponential decrease of activity with time. (Adopted from Fuster 1995.) Bottom: If several assemblies of this kind are activated one after the other, the activation sequence is stored in the hierarchy of activity levels of assemblies. This mechanism could be used as a neuronal pushdown store. (Adapted from Pulvermüller 1993.)

example (The man [whom the girl (that the dog bit) met] came).[31] Linguists have argued that a pushdown store is quite helpful in processing such syntactic structures and, more generally, may be an integral part of our language capacity (Chomsky 1963). To derive a more powerful proposal, the assemblies making up the pushdown device may be assumed to correspond not to individual words, but to lexical or syntactic categories (for further elaboration, see Pulvermüller 1993; 1994b; 1996b).

The proposed neuronal mechanism is but one way a pushdown device could be realized in a neurobiologically plausible network consisting of cell assemblies. For it to operate properly, it must be postulated that several cell assemblies lose activity according to the same slope. It may be that it is a specific feature of the human cortex that it allows for the formation of cell assemblies with similar deactivation slopes. This could be the result of features of cortical connectivity and physiological properties of nerve cells. One possibility is that cortico-cortical links in perisylvian cortex are so numerous that very tightly connected assemblies can form therein. The deactivation slopes of these assemblies may then be determined by physiological properties common to many neurons, for example their refractory periods. Admittedly, this is speculative. However, the speculation illustrates how linguistic universals (e.g., center-embedding) can manifest themselves in brain properties, which can be revealed by neuroscientific research.

Although it is not possible to discuss syntactic issues in more detail here, these remarks on center-embedding may suffice to show that neurobiological models of language are not necessarily restricted to the single-word level. In fact, they can offer perspectives on the problem of serial order in behavior that meet linguists' claims that language mechanisms cannot be understood without considering brain mechanisms (see, e.g., Mandelbrot 1954 and Schnelle 1996a; 1996b).

What makes the results summarized in sections 5 and 6 so interesting is that many of them can be systematized and explained based on principles of associative learning evident from neuroscientific research in animals. However, this should not obscure the fact that more than associative learning is necessary to develop a neurobiological perspective on language. This target article was intended to show that biological models of word processing can produce highly specific predictions on brain processes, and that such predictions can produce experiments yielding quite unexpected results that prove the predictions correct. Furthermore, it was argued that there is at least a perspective on further developing the neurobiological approach to account for problems of serial order in behavior. It may appear evident, therefore, that biological research on language – both theoretical and empirical – is fruitful.

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NOTES

1. The frequency range >20 Hz is called the "high beta band" or the "gamma band."

2. This is based on the assumption (implicit in Hebb's diagram) that loops include only a small number of neuron subgroups. If a loop includes larger numbers of subgroups, the conclusion can only be maintained if shorter connections (and therefore shorter conduction times) are assumed.

3. For the explanation of unimodal deficits such as seen in a few cases of agrammatism (Caramazza & Berndt 1985; Kolk et al. 1985), additional assumptions are necessary. See Pulvermüller (1995a) and Pulvermüller and Preissl (1991; 1994) for discussion.

4. Assembly ignition must be possible without overt articulation of the word. Whereas infants may automatically repeat word forms and use the word form when presented with an object to which the word refers, adults have learned to think of a word with-

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out activating motor programs. This may be done by reducing the global level of activity in motor cortices controlling mouth movements. In this case, ignition of an assembly will not cause overt movements.

5. The same mechanism may underlie synonymy. Assemblies representing synonyms may share extra-perisylvian neurons but differ in their perisylvian parts (Pulvermüller 1996b).

6. I will use the term "semantic categories" although it is clear that the perceptual/motor modalities and stimulus properties involved when learning word meanings are the primary causes of different cortical distribution of representations. Thus, only one aspect of the meaning of words is assumed to play a role. Accepting Frege's (1980) distinction between "Sinn" and "Bedeutung," it would be the "Bedeutung" but not the "Sinn" that is relevant.

7. See note 6.

8. Such activity in the frontal lobe may be related to associations of body movements. As discussed in section 3.3.3, additional activity in posterior temporal and parietal areas may be related to visual perception of movements (being performed by oneself or by others) and to somatosensory self-stimulation during performance of body movements.

9. This list is probably not complete. There may be additional properties of word stimuli affecting physiological processes. For the mentioned variables, such effects are well documented.

10. Additional possible confounds are emotional properties of words, such as arousal and valence (see sect. 4.1). None of the studies checked these variables, and it appears likely that arousal values are higher for content than for function words. Therefore, it cannot be excluded that arousal differences underlie electrocortical differences between these word categories. However, it may be impossible to find high-arousal function words or content words sufficiently low in arousal to allow for stimulus matching for this variable. Differences in emotional stimulus properties – similar to those in concreteness – appear characteristic for the classes of content and function words.

11. This latter difference was enlarged when a semantic decision task was used (Kounios & Holcomb 1994).

12. It is not always clear from the publications what the exact instructions were. Subjects may have been told to say verbs that describe "what the nouns might be used for or what they might do" (Fiez et al. 1996, p. 1) or they may have been told to "say aloud a use for (. . .) nouns" (Posner et al. 1988, p. 1630). Clearly, the second instruction may bias the response toward the use of action words, whereas there is no such bias in the first instruction.

13. There were additional loci of enhanced activity including cerebellum and gyrus cinguli.

14. Only numerals and verbs were matched for frequency.

15. In fact, stimuli were chosen so that these ratings were likely. In an experiment performed before the actual EEG study, stimuli had been rated by a different set of subjects to allow for selection of action and vision words (Preissl et al. 1995).

16. In a recent study (Pulvermüller et al., submitted), we compared nouns from the action word category (tool names and other nouns rated to elicit strong motor associations) to nouns from the vision word category and found electrocortical differences between word categories quite similar to noun/verb-differences. This further supports the interpretation that semantic word properties are relevant for topographies of cortical activity.

17. The experiment was carried out twice, with essentially the same results.

18. For example, Martin et al. (1996) matched target words of the naming task for word frequency, the PET studies mentioned above did not. Furthermore, in PET studies frequency of stimulus presentation per minute and presentation time are additional factors strongly influencing amplitude and topography of brain responses (Price et al. 1994). Although the influence of these factors is at present not fully understood, it appears necessary to interpret the available data.

19. These predictions follow if an associative learning principle is assumed not only for modification of cortico-cortical synapses, but also for modification of cortico-subcortical connections such as the fibers from the cortex to amygdala and to additional nuclei of the limbic system (see Pulvermüller & Schumann 1994 for discussion).

20. It is less likely that increased activity in the temporal pole and amygdala is related to stimulus properties, because faces were also presented in the baseline condition.

21. There are exceptions: For example, Damasio et al. (1996) found bihemispheric activation at least during processing of persons' names, Martin et al. (1995) found bihemispheric differences between verb and color name processing, and McCarthy et al. (1993) obtained bihemispheric activation of inferior prefrontal areas during verb generation.

22. There is so far no evidence that processing of action words also activates parietal regions related to the processing of somatosensory self-stimulation during movements – although this appears likely based on the Hebbian approach (see sect. 3.3.3).

23. There are meaningful stimuli of other modalities – odors, tastes, nonlinguistic sounds, etc. – that can be assumed to be represented in cortical assemblies.

24. Furthermore, current source density analysis makes it possible to obtain reference-free data. Using raw EEG data would make it impossible to determine whether spectral activity was generated at the critical electrode or at the reference, and, in addition, spectral activity at the reference electrode would enter the data as noise.

25. The fact that the right perisylvian region did not evidence word/pseudoword differences in high-frequency responses may be the result of a relatively low density of assembly neurons in this areas (Fig. 4). Note that high-frequency signals in EEG and MEG recordings are small even over the left hemisphere (Lutzenberger et al. 1997).

26. The variation of these delays may be related to properties of the stimuli, for example their word frequency.

27. Further support for early access to semantic information (around 200 msec after stimulus onset) during word processing comes from recent experiments where semantic and visual discrimination tasks were used (see, e.g., Posner & Raichle 1994, p. 143).

28. For acoustic presentation, the delay must be longer because the point in time where word recognition is possible is usually several hundred milliseconds after word onset.

29. A similar possibility has earlier been discussed by Tim Shallice (1988).

30. This claim is somewhat in contrast to the fact that recent attempts to extract linguistic regularities from the language input using hidden Markov models (Charniak 1993) and perceptron-like networks including a memory component (Elman 1990) were quite successful.

31. Brackets indicate levels of embedding.

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Words in the brain are not just labelled concepts

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Abstract: Pulvermüller assumes that words are represented as associations of two cell assemblies formed according to Hebb's coincidence rule. This seems to correspond to the linguistic notion that words consist of lexemes connected to lemmas. Standard examples from theoretical linguistics, however, show that lemmas and lexemes have properties that go beyond coincidence-based assemblies. In particular, they are inherently disposed toward combinatorial operations; push-down storage, modelled by decreasing reverberation in cell assemblies, cannot capture this. Hence, even if the language capacity has an associationist characterization at some level, it cannot just be co-occurrence-based assembly formation.

1. *Orientation.* It seems an important and plausible enterprise to explore the notion that knowledge of language, like other cognitive capacities, must eventually be realized by patterns of neural connections involving specific neuronal activities. Creating associations according to Hebb's coincidence rule and its subsequent refinements might play a crucial role in the formation of such patterns. If this is the message of Pulvermüller's target article, it is an interesting attempt to determine the range and type of explanation that can be achieved along these lines. The article apparently wants to transmit a more ambitious message, however, namely, that the formation of cell assemblies according to the (extended) Hebbian principles is all that is needed for "the brain's language," or at least for the words of that language.

There seem to be at least two weaknesses with the present approach to this goal: First, Pulvermüller's discussion is rather general and abstract, looking at no concrete facts or examples of the sort that linguistics has shown to be absolutely crucial for any attempt to understand the nature of the language capacity. Second, to the extent that linguistic facts are at least hinted at, although not actually considered, they are restricted to rudimentary, and often misleading ones, mostly rather naive bits or aspects of language that fail to capture the proper characteristics of natural language. I will look at two factors that Pulvermüller apparently fails to recognize as indispensible conditions of the language capacity: the nature of words and the combinatorial character of language.

2. *Problems with words. . .* According to Pulvermüller, a word requires an assembly of neurons representing its articulatory properties associated with a second assembly representing its meaning or conceptual purport. The latter is differentiated according to various categories of words, such as function words, action words, perception words, and so forth. At first glance, the two assemblies look like a reconstruction in neuronal terms of what Levelt (1989) called the lexeme and lemma [see also Levelt: "A Theory of Lexical Access in Speech Production" *BBS* 22(1) 1999] respectively, or what is construed as phonetic form and logical form or conceptual structure in the current linguistic literature (e.g., Chomsky 1986; 1995; or Jackendoff 1990). Before showing why the two types of cell assemblies are nevertheless far from corresponding to lexemes and lemmas, I want to question Pulvermüller's use of the notion of classes or categories of words, which plays an important role in his theory of the brain's language, as he assumes different word classes to be directly related to the localization of cell assemblies in different cortical areas.

Pulvermüller's most basic distinction is between function and content words. Although it has a long history in psycholinguistics and linguistics, this distinction has never received an unequivocal and satisfactory clarification; it has instead been used in fairly different ways according to different orientations and problems. Pulvermüller's assumptions in this respect are very vague, even though crucial questions are at stake. Suppose, for example, that Pulvermüller were to consider prepositions (under one classification, a special subset of so-called closed class items) as function words, participating in the characteristic perisylvian localization. In this case, one would wonder whether and how this assumption could be reconciled with Landau and Jackendoff's (1993) tenet that locative prepositions are characteristically based on the "Where"-system of the brain, contrasting with the "What"-system, which represents spatial nouns; both spatial prepositions and nouns must clearly be considered as content words related to different cortical systems of spatial cognition. Things are even less clear with Pulvermüller's distinctions among different types of content words, notably, words of action and words of perception or vision. To be sure, he is careful to point out that there are all sorts of mixed and boundary cases, but the problem is not that mixtures and combinations are to be acknowledged (a strategy that, by the way, easily undermines the essential idea, turning it into a trivial "anything goes" type of theory). The real problem is that the very distinction between perception words, action words, and so forth as basic categories is at variance with the nature of lexical categories. Notice, for example, that one of the important contributions of Rosch et al.'s (1976) notion of prototypes was the identification of the central place to be assigned to so-called basic level categories (such as *tree* or *chair* as opposed to *oak tree* or *rocking chair* on the one hand and *plant* or *furniture* on the other). The main observation about basic level categories is the essential integration of different aspects of classification: invariant and stable perceptual, functional, and motor patterns – paired with the role of anchor points in conceptual hierarchies. On Pulvermüller's account, these facts could at best be accommodated as post hoc phenomena, the representation of which, if possible at all, is merely an incidental extension of more specific properties of classification based on cortical areas. The principled character of the conditions under consideration, their role in cognitive organization, is completely blurred. As a matter of fact, a different, or at least a further type of representation over and above coincidental activation is needed to support characteristically linguistic (and other cognitive) processes. This becomes even more obvious if we look at typical properties of lexemes and lemmas.

The main point I have in mind here is that words are inherently disposed for systematically controlled combinatorial operations, which are also the gist of their internal structure. The combinatorial structure in question is not the result of a smaller or greater number of attributes collected from different domains (and possibly different cortical areas). The essential point concerns the structured integration of subcomponents, which goes beyond coincidental activation. Consider a pair of words like *buy* and *sell* as analyzed in Jackendoff (1990). Both verbs are made up of the same ingredient parts, namely, two exchange processes involving two parties, and two objects, one of them being a sum of money (I will ignore the question of whether it makes sense to classify these processes as actions or perceptions or something else); and they differ in the way in which the parties and objects in question are involved. What is more, the components in question are necessarily activated under the same overall conditions: Every event of buying is also an event of selling, and vice versa. Hence, by definition, a mere coincidence pattern could not distinguish between the two types of events. Moreover, the different roles assigned to the parties in question are the root for the grammatical relations the verbs enter, giving rise to constructions such as those in (1) and (2), which are true in the same perceptual, intentional, or motor situations, even though they are not synonymous:

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(1) John sold the car to Bill. (2) Bill bought the car from John.

The point is that cell assemblies of the sort described by Pulvermüller cannot represent the difference between these two verbs in any revealing way other than the different phonetic patterns identifying *buy* and *sell,* respectively. An even more delicate aspect of the same phenomenon shows up in the contrast between (3) and (4), where two different representations must be associated with the same phonetic form *rent,* even though it is not a case of the type of homonymy that Pulvermüller mentions in passing and without further explanation:

(3) John did not buy the house, but he ended up renting it.

(4) John bought the house, but he ended up renting it.

In (3), John is the user, but not the owner of the house; in (4) he is the owner, but not the user. These are ubiquitous facts, for which illustrations could be piled up at will. The relation between *forget, remember,* and *think of* or the different readings of *break, melt, sink,* and all the other so-called ergative verbs are arbitrary illustrations of similar problems that are, moreover, fairly well understood linguistically. The lesson of all this is that lemmas have a much more specific structure than Pulvermüller's model of Hebbian assemblies can provide.

The issue is not one of solving methodological problems in studies that try to distinguish neuronal processes corresponding to different experimental stimuli. Pulvermüller is well aware of these problems, and they might, for the time being, turn out to be a serious obstacle to any attempt to explore experimentally the phenomena just mentioned directly in terms of neurophysiological data such as EEG or ERP. My point does not concern these difficulties. What I would like to point out is the fact that the model under consideration could not represent the differences in question, even if there were experimental techniques providing the discriminating activation data.

What has been said with respect to lemmas holds for lexemes as well. Consider for the sake of illustration a minimal pair of German verbs, differing by the position of word stress: *um*stel*len* (surround) versus um*stellen* (rearrange). The point to be noted is not the minimal phonetic difference that marks two etymologically related yet conceptually quite different types of action, but rather the formal consequences related to the phonetic distinction, as illustrated in the following constructions:

(5) Die Studenten um*stell*en das Podium. (The students surround the podium.)

(6) Die Studenten stellen das Podium *um.* (The students relocate the podium.)

Besides the characteristic syntactic behavior, separating the stressed prefix *um* from the stem *stellen* in (6), the two verbs also show different morphological properties: The respective participles are *um*stelltt versus um*gestellt.* Further properties of these constructions are discussed in Bierwisch (1987). Again, these are characteristic phenomena that could easily be multiplied by more intricate patterns from morphologically more complex languages such as Georgian or the other Caucasian languages.

To add one final point, the model proposed by Pulvermüller can hardly cope with the morpho-syntactic structure of simple idioms such as *get rid of, come up with, take advantage of,* or even phrasal verbs such as *turn out, get up,* and so on, all of which need to be associated with one integrated, noncompositional meaning, but exhibit syntactically complex behavior.

These observations do not simply amount to an amendment, adding a third, grammatical component to the association of sound and meaning, a possibility that Pulvermüller considers but is reluctant to adopt, because he feels it to be at variance with the spirit of strict associative learning. (I will turn to Pulvermüller's alternative proposal shortly.) The essential point is rather that a different type of representational organization is needed, one that might use coincidental cell assemblies recruited from different cortices, providing the basis for rather different organizational principles and structural operations, that is, operations of the sort theoretical linguistics has made explicit over the past decades.

3. . . . and their combination. The major objections about both lexemes and lemmas are directly related to the combinatorial capacity that words – as opposed to mere labelled concepts – exhibit. Pulvermüller does add "a word on syntax," which relies on the time course involved in the activation of cell assemblies to account for the way in which separate words, consisting of their respective cell assemblies, are combined. The only nontrivial conjecture added to this basic and largely implicit line of thinking is the observation that the roughly exponential decrease of reverberation in activated assemblies could be used as a kind of neural push-down store accounting for nested or self-embedding constructions. This would indeed be an interesting step toward an account of syntactic structure building in terms of an extended Hebb-model. It is not clear to me, however, from Pulvermüller's sketchy remarks, how a nested $N_1N_2N_3V_3V_2V_1$-structure (Pulvermüller's ABCC*B*A*) would originate from the verbs and nouns in question. Notice that the structure in (7), which Pulvermüller gives as an illustration, does not just combine three NPs and three verbs, but combines three nouns and verbs by means of two relative pronouns or complementizers, which is quite a different story.

(7) [The man (whom the girl [that the dog bit] met) came home]

But even if a self-embedding structure like (7) could be generated by reverberating assemblies and their decreasing activation, thereby providing the basis for an appropriate semantic interpretation – an assumption hardly any linguist would seriously defend today – a reliable account of the combinatorial properties of language would still be missing. To see the challenge, consider the minimal pair (8) and (9), where again a different stress pattern has important consequences for the way in which syntactic relations are constructed with corresponding semantic effects (no self-embedding being involved, by the way):

(8) *John* hit *Bill* and then *he* kicked *him.* (9) John *hit* Bill and then he *kicked* him.

Whereas in (8), *he* refers to *Bill* and *him* refers to *John,* the coreference pattern in (9) is the converse. I do not see how decreasing reverberation could account for these rather automatic effects. To give one more example, consider a simple German clause involving a verb with a separable prefix, which comes out as (10) if it is a subordinate clause, as (11) if it is a main clause, and as (12), if it is a yes-no question:

(10) wenn Hans seine Freundin wieder einlädt (if Hans invites his girlfriend again)

(11) Hans lädt seine Freundin wieder ein (Hans invites his girlfriend again)

(12) Lädt Hans seine Freundin wieder ein? (Does Hans invite his girlfriend again?)

Two remarks can be made here: First, ein*laden,* a verb with a stressed and hence separable prefix (like um*stellen* mentioned earlier) must be represented by a semantically integrated lexical unit, the parts of which can nevertheless show up at separate positions. Second, the conditions according to which these positions are chosen are strictly regulated; moreover, they have no characteristics of self-embedding whatsoever and depend on lexical information (Wilder 1995).

More generally, then, Pulvermüller assumes that grammatical properties of words – such as the subject and object position of verbs like *hit* and *kick,* the coreference conditions of stressed and unstressed pronouns, or the properties of separable prefixes and elements determining the position of finite verbs in German, and the combinatorial effects based on those properties – do not

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require independent representational means. Instead, according to Pulvermüller, they simply emerge from association and reverberation, which he suggests as a serious alternative to syntactic categorization and subcategorization of lexemes and lemmas. This seems inadequate to me, for absolutely principled reasons. Syntax and compositional semantics require much more specific means than uniform association, even if rather different cortical areas are involved.

4. In conclusion. I do not wish to suggest that Hebb's coincidence rule and the principles of associationism deriving from it should not be taken seriously. But just as Pulvermüller points out that it might be premature to claim that language mechanisms cannot be explained by associative learning principles, it might be equally or even more premature to claim that they can be explained (exclusively) by associative learning principles – plus neuroanatomical and neurophysiological prerequisites. What I have tried to show, hinting at some standard observations and insights well known in theoretical and descriptive linguistics, is the following: Assuming that at some level of neuronal organization the acquisition and use of language can be characterized by associationist principles, further aspects of organization are still needed to allow for characteristic properties of syntactic and semantic (and prosodic) compositionality, without which we are not likely to come to grips with human language capacity. Studying cell assemblies and their properties, to understand the brain's language, does not make sense if one does not also go beyond the properties allowed by these mechanisms.

Function and content words evoke different brain potentials

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Abstract: Word class-specific differences in brain evoked potentials (EP) are discussed for connotative meaning and for function versus content words. A well-controlled experiment found matching lexical decision times for function and content words, but clear EP differences (component with maximum near 550 msec) among function words, content words, and nonwords that depended on brain site. Another EP component, with a 480 msec maximum, differentiated words (either function or content) from nonwords.

Among the brain evoked potential research that has shown the most specific word class-specific results is the work on connotative meaning that distinguished six word classes (Chapman et al. 1980) and the work on function versus content words (Garnsey 1985; Garnsey & Chapman 1985). Here we briefly summarize the connotative meaning research and concentrate on the function/content word research.

1. Connotative meaning. Brain evoked potentials (EPs) can index the connotative meaning of words (Begleiter et al. 1979; Chapman 1974; 1979; Chapman et al. 1977; 1978; 1980). This work was based on the fact that the connotative meanings of words can be characterized by how much each of three independent factors contributes to them (Miron & Osgood 1966; Osgood 1952; Osgood et al. 1975). The factors have been labeled evaluation (E), potency (P), and activity (A) and were derived by formal multivariate procedures from subjects' judgments about many words on many semantic scales. Using normative data, which gives values for words on all three dimensions, word stimuli were selected to fall into six semantic categories, one for each polarity of each dimension. EPs were averaged across visually presented words within a semantic category so that any EP differences caused by irrelevant differences in the words (e.g., length, the particular letters composing them, etc.) could cancel out. Multiple discriminant analyses using components obtained from a principal components analysis of the EPs showed that it was possible to predict the semantic category membership of a word based on the relative contributions of the various components to its EP. So the EP reflected the aspects of word meaning captured by the multidimensional semantic differential. Subsequently, we have also shown that the semantic dimension of the scale being used by the subject to make judgments about the presented words could also be detected separately by EP components (Chapman 1979; Chapman et al. 1980). These results go considerably beyond a single-dimension notion of arousal (target article, sect. 4.3) and show the power of evoked potential techniques in studying brain processes related to word properties.

2. Content and function words and nonwords. One of the most fundamental distinctions among words is between function (closed class) and content (open class) words. In an exceptionally well controlled experiment with maximally similar experimental conditions, function and content words and nonwords evoked different brain potentials (Garnsey 1985; Garnsey & Chapman 1985).

Because word frequency itself could affect EPs, we used matched pairs of function and content words, each pair being jointly matched for frequency and length. There were 122 matched pairs, which ranged from log frequency 0.47 to 3.1 (Kucera & Francis 1967) and 3–10 letters. In addition, 2 sets of 122 nonwords were constructed to resemble words by changing 1–2 letters in real words; the nonwords were orthographically legal, pronounceable, and 3–10 letters in length. These nonword sets were compared in the data analysis with the "function" and "content" word sets, but the distinction between "function" and "content" nonwords was a pseudo-distinction that provided two control measures. In addition, mean diagram frequency was calculated for each letter string, using the Mayzner and Tresselt (1965) norms. After the stimuli had been selected, mean diagram frequency was calculated by summing the frequencies of each consecutive letter pair in the string and dividing by the number of pairs. The nonwords (mean = 464) and the content words (mean = 474) were quite similar on this measure, indicating that the nonwords were word-like. The function words (mean = 652) had higher diagram frequencies.

Each stimulus was a string of upper case letters presented briefly (20 msec) on a dark computer monitor 500 msec after a fixation asterisk. The subject pressed one of two keys to indicate whether the string was a word or not (lexical decision task). Only correct trials were analyzed further. The presentation order of stimuli was randomized separately for each subject.

The mean lexical decision times (RT) for function words (597 msec) and content words (592 msec) did not differ significantly. Nonwords were slower at 667 msec (664 and 670 msec for the two groups of nonwords). Moreover, the two RT distributions for the two word types were very similar in all respects. Thus, the behavioral RT results do NOT differentiate function and content words. The fact that the distributions for the two word types were so similar is important because it means that any differences in the brain evoked potentials cannot be explained by RT differences. Unfortunately, this was not the case in other studies; for example, the 32 German content words of Pulvermüller et al. (1995) gave a mean RT that was 28 msec faster than their 32 function words.

An EP average was obtained separately for each of the 4 stimulus types (function words, content words, nonwords matched with function and with content words) for each of the 6 electrodes for each of the 18 subjects. This produced 432 average EPs, each spanning 201 time points (4 msec), and each averaged across 122 individual trials minus the number missed by that subject for that stimulus type. The 432 EPs, each consisting of 201 time points, were submitted to a principal components analysis (PCA) using the correlation matrix of the time points (Chapman & McCrary 1995). The 10 components with eigenvalues greater than 1 were extracted (accounting for 97% of the variance in the EPs) and submitted to Varimax rotation. The waveforms of the component loadings (with metric restored by multiplying by standard devia-

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tions) are displayed as a function of time (Fig. 1 shows one of the EP components). Component scores were computed and used as quantitative measures of component contributions to each EP. Separate $2 \times 2 \times 6$ (word/nonword $\times$ function/content $\times$ electrode) repeated measures ANOVAs (18 subjects) with response hand as a between subjects factor and handedness as a covariate were done for each component with Greenhouse-Geisser adjustments ($p < .05$).

To summarize the EP results, there were clear, reliable differences between words and nonwords, and between function words and content words in the EPs (Fig. 1). These reliable results need to be emphasized to clarify the internally conflicting and mysterious statements written about this work (Pulvermüller et al. 1995a). The major word/nonword EP component, C480 (maximum at 480 msec, half-height 345–585 msec), and the major function/content component, C550 (maximum at 550 msec, half-height 500–600 msec), showed no effects of response hand. Also, the EP results were not artifacts of eye movement (EOG).

ANOVAs on these EP components' scores demonstrated that C480 differentiated words from nonwords, whereas C550 differentiated function words from content words. The relative timing of these components supports the idea that words (either content or function words) are discriminated from nonwords before content words are discriminated from function words.

EP differences between function words and content words should appear as function/content by word/nonword interactions in this design because the distinction between "function" and "content" nonwords is a pseudo-distinction. This interaction for C550 is significant ($F[1,16] = 9.22$, $p < .01$), and clearly strong enough to provide substantial evidence for the word class distinction. Furthermore, this interaction varied across electrode sites ([$F(1.66,26.59) = 4.56$, $p < .05$], using Greenhouse-Geisser adjusted df). By posthoc tests, the difference between function words and content words was significant ($p < .05$) at each of the electrodes except Broca's area (Bro-L and Bro-R for left and right hemispheres), where it does not quite reach significance.

C550 showed three distinct, reliable patterns for the function and content word types relative to the nonwords at various electrode sites (Fig. 1). Although Pulvermüller et al. (1995a) used an experimental design remarkably similar to Garnsey's (1985) with function, content, and two nonword (pseudowords) groups of stimuli, the data analyses of their EP measures did not permit comparisons of the separate word groups with the nonword groups as is reported here; this is because they used separate ANOVAs to assess function/content effects and word/nonword effects.

Our statistically significant results for C550 could be interpreted to provide partial support for the Hebbian associative learning ideas (target article, sect. 4.1 and 5.1) of left hemisphere superiority for function words, whereas content words are predicted to be more bi-laterally symmetric. C550 scores for content words were different from those for nonwords at both left and right Broca electrodes, whereas the scores for function words differed from those for nonwords only for left Broca and not right Broca electrodes.

In addition, whereas C550 over other brain areas (occipital, central-parietal) differed between content words and nonwords, function words were not different from the nonwords. This fits the interpretation that content words may involve visual and other sensory areas, as well as the classical "language" areas. However, the function word asymmetries seen at Broca electrodes were not seen at Wernicke electrodes. One possibility is that at Wernicke sites the nonwords were being processed more like content words in both hemispheres.

The major EP component in this careful study that showed differences between function and content words was C550. An earlier component, C200 (maximum near 200 msec, half-height 120–330 msec), was obtained, and its time course appears similar to an EP mean measured between 150 and 300 msec poststimulus (Pulvermüller et al. 1995a; target article, sect. 5.1). Our C200 did not have any significant effects related to function/content differences; the largest effect, the function/content main effect, was not statistically significant ($F[1,16] = 1.21$, $p = .29$), and the more important function/content by word/nonword interaction was at chance ($F[1,16] = 0.67$, $p = .43$). C200 did have a significant interaction between words/nonwords and the response hand used to perform the lexical decision task – half the subjects randomly assigned to each hand – ($F[1, 16] = 6.70$, $p < .05$).

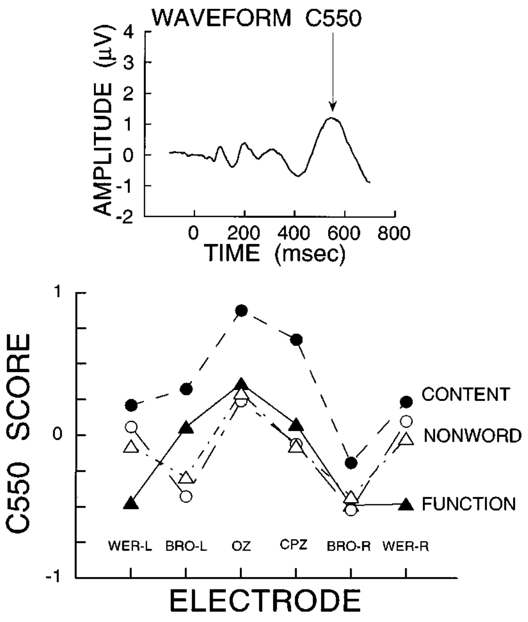

Figure 1 (Chapman). Evoked potential component C550 waveform (above) and scores for function words, content words, and two sets of nonwords as a function of electrode location (below). C550 scores are significantly different for function words and content words (main effect, as well as interactions with word/nonword and with word/nonword by electrode). The small difference between the two sets of nonwords (open symbols) at each electrode may be viewed as a graphical index of the reliability of these measures.

C550 showed three distinct, reliable patterns for the function and content word types relative to the nonwords at various electrodes sites. (1) At Broca's area (Bro-L) both function and content words are different from the nonwords. (2) At Broca's Right (Bro-R) homolog and central-parietal and occipital midline sites (CPZ, OZ) the content words are different from the nonwords, whereas the function words are not. (3) And at Wernicke's area and right homolog (Wer-L, Wer-R) the function words are different from the nonwords, but the content words are not.

C550 was one of 10 components obtained by Varimaxed PCA of 432 EPs (4 stimulus types $\times$ 6 electrodes $\times$ 18 subjects). Each stimulus type had 122 matched exemplars. The waveform values (above) were obtained for an arbitrary component score of $+1.0$ to illustrate the waveform of the component ([loadings $\times$ standard deviations $\times$ component score] as a function of time [-100 to $+700$ msec with the visual stimulus at 0 msec]). Based on Garnsey (1985) and Garnsey and Chapman (1985).

The research using German words and nonwords (target article, sect. 5.1; Pulvermüller et al. 1995a) and our research using English words and nonwords show agreement in the EP timing and polarity of "wordness" (words [function and content combined] vs. pseudowords). They report an influence of wordness around 300 msec and later, and our EP component C480 begins near 300 msec, both tending to be more negative for nonwords.

As Pulvermüller (target article, sect. 3.3.3) has reminded us, neurons responding to many sensory stimuli and neurons used in many motor acts are located in both hemispheres and tend to be widely distributed. Thus, by Hebbian associative learning, cell as-

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semblies representing many content words may be expected to be distributed over both hemispheres and not to be as strongly lateralized as assemblies representing function words (Pulvermüller & Mohr 1996).

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Re-assembling the brain: Are cell assemblies the brain's language for recovery of function?

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Abstract: Holistically ignited Hebbian models are fundamentally different from the serially organized connectionist implementations of language. This may be important for the recovery of language after injury, because connectionist models have provided useful insights into recovery of some cognitive functions. I ask whether cell assembly modelling can make an important contribution and whether the apparent incompatibility with successful connectionist modelling is a problem.

Pulvermüller shows that the connectionist implementations of language are serial and hierarchical whereas Hebbian activation is assumed to be simultaneous. Can Hebbian modelling help us seriously examine the relationship between damaged structure and impaired function and the processes underlying spontaneous recovery of aphasia? The question is important because good progress has been made recently in connectionist modelling of change in aphasic symptomatology over time.

Symptomatology can be modelled as damaged cell assemblies and cell *re*assemblies, as Pulvermüller has shown in his target article and elsewhere (Pulvermüller 1996a; Pulvermüller & Schonle 1993). However, we need to develop models of recovery with clinical utility that acknowledge cognitive (e.g., Plaut 1996) and behavioral knowledge to supplement and ultimately replace the operational psychometric models (where "recovery" is defined in terms of change in subtest scores; Code 1996). We have a confused understanding of restoration, compensation, and reorganization of function, which appear to underlie recovery, and the relationships between them.

New neural growth can occur following central nervous system damage, even in the aged brain, although it may be limited and it can have negative as well as positive effects (Kolb 1996; Le Vere 1988). Neural reorganizational mechanisms exist, allowing new connections between neurones at local and distant sites, including increased efficiency of neural transmission, dendritic branching, synaptic remodelling, and axonal sprouting (e.g., Blomert 1997; Kolb 1996).

Smaller lesions may produce restoration through neural sparing, allowing some repair to assemblies. In large lesions, however, compensation appears to occur using intact assemblies not originally concerned with the lost functions and perhaps even distant from the original assemblies (Cotman & Nieto-Sampedro 1982; Kolb 1996; Le Vere 1988). Smaller lesions allowing compensation by intact assemblies might produce some short-term behavioral gains but may suppress the only partially damaged assemblies that subserved the impaired function. Hence, neural recovery need not result in genuine restoration of cognitive and behavioral function, where neural reorganization of cell reassemblies causes maladaptive compensation.

Recent connectionist modelling of recovery suggests serial patterning to cognition. Martin et al. (1996) describe NC's deep dysphasia with impairment in naming and repeating of nonwords resulting in semantic and formal paraphasias and neologisms. NC had a dissociation between repetition and naming at the acute stage. In repetition, NC produced some formal paraphasias and neologisms, but mainly semantic paraphasias. In naming, he produced mainly formal paraphasias.

Martin et al. suggest that this pattern results from a pathologically fast rate of decay within the system. Naming something runs from semantic specification through lexical access and to phonological specification. So semantic representations will decay earlier than lexical ones, which will in turn decay earlier than phonological ones. In severe deep dysphasia naming errors will be phonologically related, formal paraphasias, because they will be more recently available.

Repetition involves auditory/acoustic analysis to a phonological output buffer, at least, and need not access semantics. So, the predominance of semantic paraphasias in repetition reflects rapidly decayed phonological specifications and a dependence on semantics, again because these are more recently available.

Martin et al. (1994) built a connectionist model to mirror NC's recovery of naming and repetition, testing their hypothesis through lesions that changed the decay rate. As the decay rate decreased, formal paraphasias decreased, with a smaller decrease in semantic paraphasias in naming, reflecting less use of phonology and easier access to semantics. In repetition, a reduction in semantic paraphasia accompanied a decreased decay rate and an increase in formal paraphasias.

This explanation depends on a serially ordered activation of semantics and phonology. What might the relationship be between this successful serial modelling of cognitive processes and a holistic Hebbian modelling of neural representation? We are told that connectionist models are biologically implausible (e.g., Harley 1993). Cell assemblies are biologically plausible. How would the neural correlate of the decrease in decay rate for NC be characterised using Hebbian modelling? Reduced reverberation? Reduced ignition? Perhaps *re*assembly or neural regrowth within or between cell assemblies results in a reduction in decay caused by increased synapses.

If cell assemblies can enhance our understanding of recovery, this will make a significant contribution to rehabilitation (Pulvermüller & Schonle 1993). The interface between serial connectionist implementations and Hebbian models would appear to be crucial, but I am not sure how or in what way.

The dynamics of language

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Abstract: To deal with syntactic structure, one needs to go beyond a simple model based on associative structures, and to adopt a dynamical systems perspective, where each phrase and sentence of a language is represented as a trajectory in a syntactic phase space. Neural assemblies could possibly be used to produce dynamics that in principle could handle syntax along these lines.

In his interesting target article, Pulvermüller presents a comprehensive view of how words are represented as neural cell assemblies in the nervous system arising out of association. These assemblies include both local and distal connections. The local connections are responsible for the creation of functional units. The distal connections are responsible for assembling different as-

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pects of the representation of a word. The theory applies Hebbian rules of learning to explain some linguistic phenomena. Moreover, it is consistent with imaging data concerning processing of linguistic material.

Pulvermüller's theory allows us to understand (or at least provides a basis for) the development of syntactic categories. He argues that words that are semantically similar are represented in a similar way in the brain. The representation of verbs, for example, contains structures in the motor cortex; the representation of concrete nouns includes structures in the visual cortex. This similarity in semantic representation may serve as a basis for the development of syntactic categories. But language is not simply a collection of words. What is critical in language is syntax: Words are arranged in a highly ordered, meaningful temporal sequence, and structure is represented in this sequence.

Pulvermüller argues in the last section of his target article that the theory of word representation he presents does not contradict what is known about syntax, and that it is possible to expand his theory to handle syntactic phenomena. According to Pulvermüller, Hebbian rules of learning do not preclude some connections being innate, so it is possible to integrate the proposed theory of word representation with the postulate of genetic origin of the language capacity. He also proposes that some aspects of syntactic structure, specifically center embedding, may be explained by a push-down store-type mechanism. Such a push-down store may be constructed by a known property of a fast decay of the potential of some nerve cells. Those cells could function to invert a temporal sequence of initial order of excitation.

The theory of word representation based on associations may provide a basis for the explanation of some lexically based syntactic phenomena. For example, similarity of the neural representation could perhaps correspond to proximity in spatial location, leading to categories. We argue, however, that to deal with syntactic structure, one needs to go beyond a simple model based on associative structures, and to adopt a dynamical systems perspective.

A dynamical system evolves in time, going through a sequence of states, or through a pattern of continuous changes. Each state of a dynamical system may be represented as a point in N-dimensional abstract space – state space – the axes of which correspond to variables in the system. The temporal evolution of the system may be portrayed as a trajectory in the state space. [See also Van Gelder: "The Dynamical Hypothesis in Cognitive Science" *BBS* 21(5) 1998.]

The dynamical perspective has proven to be very useful for the analysis of artificial neural networks/connectionist models. Hopfield (1982)-type neural networks, for example, which are based on Hebb's rules of learning are, in fact, programmable dynamical systems. Connectionist systems, although still seriously limited, have some desirable properties with respect to the representation of language (see for example, Elman 1991; 1992; 1995a; Plunkett & Marchman 1993; Pollack 1991; Smolensky 1991; Smolensky et al. 1992; and the other papers in Reilly & Sharkey 1992, Sharkey 1992, and Touretzky 1991).

Most important, Elman (1995a) introduces the notion of trajectories in phase space, not only to linear orders in sentences but to hierarchical structure and recursion; the approach we sketch here is in some respects similar to his. Assume first that there is a space of meanings, in which particular regions correspond to concepts. Call this conceptual space or CSpace. Words and phrases in syntactic space, or SSpace are linked to these concepts. As the linguistic system develops, the configuration of points in SSpace initially reflects the organization of CSpace; the two may and will diverge over time. In a dynamic representation of SSpace, points correspond to the words and phrases of a language and proximities correspond to similarities in the use of words and phrases in sentences. Words may be clustered in the syntactic space, each cluster representing groups of words of similar use; clustering may be based on syntactic, semantic, and/or morphological similarity.

Each phrase and sentence is represented as a trajectory in SSpace, where the order of words in a sentence corresponds to a temporal sequence in which a trajectory crosses these points. Traversing a trajectory in linguistic production or comprehension contributes to a flow in the syntactic space. Each trajectory may be assigned a weight, which corresponds to the ease with which this trajectory is traversed.

Assume that initially, the distribution of the weights over the space is flat and relatively high. Acquisition of syntax is equal to differentiating the weights in such a way that regions corresponding to grammatical sentences in a language acquire relatively low weight and those corresponding to ungrammatical sentences retain relatively high weight. The weight of each trajectory drops with the use of the sentence corresponding to this point. The weight also drops with the drop of other trajectories in the neighborhood, by a process similar to a diffusion. SSpace may thus be described as a landscape, with hills corresponding to ungrammatical sentences and valleys corresponding to grammatical sentences.

Originally, the position of words in the syntactic space corresponds to their position in the semantic space, that is, it is dictated by the meaning of the concepts they denote. There is, however, a process of self-organization in the syntactic space. Words that are parts of similar trajectories move closer together. Trajectories connecting those regions acquire even smaller weight. Hence, syntactic generalizations can form in terms of categories.

In the Pulvermüller model, the state of the brain corresponds to a specific pattern of activation of neural assemblies. Neural assemblies are also dynamical systems. We do not know exactly how to use this fact, but we are exploring an approach within which this view of neural assemblies could be used to produce dynamics that in principle could handle syntax. The dynamical perspective sketched here is of course not a syntactic theory, but it may provide a perspective on how neural assemblies can deal with temporal sequences to represent syntactic knowledge.

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Experimental and theoretical evidence for a similar localization of words encoded through different modalities

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Abstract: In his target article, Pulvermüller addresses the issue of word localization in the brain. It is not clear, however, how cell assemblies are localized in the case of sensory deprivation. Pulvermüller's claim is that words learned via other modalities (i.e., sign languages) should be localized differently. It is argued, however, based on experimental and theoretical ground, that they should be found in a similar place.

In his target article, Pulvermüller presents a theory of word localization. He introduces the notion of cortical cell assemblies as functional units that exhibit an activation state with proper sensory activation, which then reverberate in their own circuit. In addition, a Hebbian function is proposed that emphasizes the correlation between cellular events. The author uses these two concepts to make some interesting predictions as to where words should be represented in the cerebral cortex.

The appeal of Pulvermüller's theory is that it integrates neurolinguistic data with current trends in connectionism. However, two points must be considered when evaluating this approach. First, recent data demonstrate that cell assemblies do not differ according to modality as Pulvermüller believes. Second, the nat-

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ural convergence zones of the primary cortices may offer a better explanation of the localization of words. Both these points will be examined in further detail.

First, Pulvermüller states that "if a language is not learned through the vocal and auditory modalities, but through manual and visual modalities (sign languages), cortical localization of cell assemblies representing meaningful elements should be different" (sect. 3.1). It has recently been reported, however, that deaf and hearing subjects show very similar brain activation when perceiving language (Petitto et al. 1997).

In their study, Petitto's group used positron emission tomography (PET) to assess the language pathways of 21 subjects (11 were profoundly deaf and were using sign language to communicate and the remaining were hearing controls). Differences between their groups showed a recruitment of cells reaching the primary visual area in addition to the use of the traditional speech area. Also, when meaningful signs were compared to a baseline fixation point, the deaf subjects exhibited a left temporal-occipital activation in addition to the activation of the visual cortex that was found in both groups. According to the authors, this showed that the hand movements were processed as linguistic elements, hence their processing in the same brain areas. Moreover, when comparing the signed nouns and appropriately generated signed verbs condition with the visual baseline, both groups exhibited left inferior prefrontal cortex activation, believed to be the localization of the semantic memory. Leaving aside the issue of cortical reorganization, these data suggest that the cortical assemblies involved in different language modalities are very similar.

A lesion study by Bellugi et al. (1989) reported similar results. They found a deficit concordance between hearing and deaf brain damaged subjects. This study revealed general similarities between the localization of lesions and linguistic behavior of the subjects, in contrast to Pulvermüller's claim that different modalities should yield different word localizations. One of the strongest results in this study was that even if sign languages are spatial, right hemisphere damage does not affect linguistic abilities (Bellugi et al. 1989). This implies a linguistic rather than a spatial dimension in the use of gestures in sign languages. Therefore, both studies discussed here strongly suggest that different language modalities (signed and spoken languages) use the same cell assemblies for meaningful elements. This is contrary to Pulvermüller's hypothesis.

In addition to these experimental data, one can arrive at the same conclusion theoretically: cell assemblies should be the same even when different modalities are used to encode the information. By definition, association cortices, where higher cognitive functions like language reside, get their inputs from higher-order motor and sensory cortices (Kupfermann 1991b). This definition seems intuitive because primary cortices feed into second-order sensory and motor cortices. They, in turn, perform an integration of the information and later feed into the association cortices. A convergence zone might be defined as the intersection of cortical regions radiating from the primary cortices. These convergence zones map almost perfectly onto the associative cortices of the brain, especially in the parietal-temporal-occipital cortex (Kupfermann 1991b). In accordance with Pulvermüller's discussion of word localization, it is not surprising that words encoded through these modalities will be found in this zone. For example, hearing the word "dog" and seeing one would be likely to activate cell assemblies in a region between the auditory and visual cortices.

But what would happen in the case of sensory deprivation? According to the notion of convergence zones just proposed, the word localization should be the same. In the case of the parietal-temporal-occipital cortex influenced by three primary cortices (the visual, the auditory, and the somatosensory), a deprived auditory cortex, in the case of congenitally deaf individuals, would not shift the position of the convergence zone produced by the somatosensory and the visual cortices alone. It is important to mention, however, that the unused cortex is not believed to be silent. It would perhaps no longer play the role of primary cortex, and consequently not participate in the formation of the convergence zone.

To summarize the hypothesis formulated here: we agree that words are represented in the cerebral cortex near the primary cortex of the modality through which they are encoded. However, because multiple modalities often interact, it is reasonable that most words are located in an area intersecting the span of activity of those modalities. Contrary to Pulvermüller's hypothesis that word encoding through different modalities should locate in different regions of the cortex, deficits in one modality (i.e., sensory deprivation) forcing an encoding through a different modality should not locate words differently. This also agrees with lesion studies and the brain imaging literature. Pulvermüller's theory of word localization should be reconsidered in light of these observations.

Word versus task representation in neural networks

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Abstract: The Hebbian view of word representation is challenged by findings of task (level of processing)-dependent, event-related potential patterns that do not support the notion of a fixed set of neurons representing a given word. With cross-language phonological reliability encoding more asymmetrical left hemisphere activity is evoked than with word comprehension. This suggests a dynamical view of the brain as a self-organizing, connectivity-adjusting system.

Pulvermüller's (Braitenberg & Pulvermüller 1992) theory of language based on the Hebbian principle of associative learning is brilliant. This principle implies the engagement of cell assemblies, which include neurons in cortical areas where correlated neuronal activity occurs during learning. Words would be represented by distributed cell assemblies that form during learning and are comprised of those neurons that then show correlated firing. For example, a word referring to an object that is usually perceived visually would then be represented by a cell assembly with members beyond the perisylvian region, including the occipital lobes and the inferior temporal region. The representation of a verb referring to actions will include neurons in motor and premotor areas related to the execution of the body movements to which the verb refers.

Though satisfying, this theory is so perfect that it can be shaped to explain whatever experimental observations are being made; hence it is difficult to falsify. The following experimental example demonstrates the difficulties one encounters when translating some of Pulvermüller's theoretical considerations into experimental predictions.

We measured event-related potential correlates of phonological encoding as compared to lexical access and semantic categorization in 14 German and 14 Italian subjects (Angrilli et al., submitted). Within a two-stimulus reaction time paradigm, stimulus pairs had to be matched with respect to semantic identity (word-picture) in a word comprehension task or with respect to the phonological (word) representative of the picture of objects in a rhyming task. The slow negative potential prior to the second stimulus was considered an electrocortical correlate of the activation produced by the presentation of the first stimulus. As illustrated in Figure 1, this activation is specific to the language-related task and not specific to the words presented. With cross-language reliability, we found that whereas phonological encoding (rhyming) evoked a more pronounced left- than right-hemispheric negativity, little asymmetry was found in the word comprehension task.

From these and other studies (e.g., Eulitz et al. 1996), we con-

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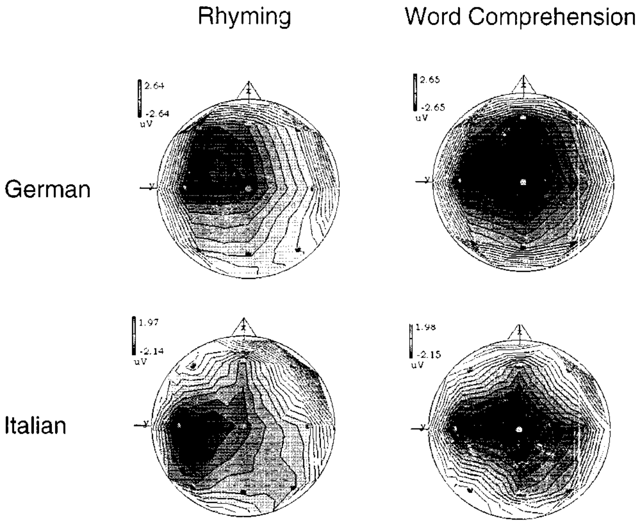

Figure 1 (Elbert et al.). In the phonological encoding task of the German experiment, two pictures of objects were presented with an ISI of 2 sec. The subject's task was to decide by pressing a button whether the words represented by the picture rhymed. For the Italian sample, two words were presented; for the second of these the subject had to decide whether the words were phonologically similar (rhymed). In the word comprehension task a 1-s word presentation was followed after 2 sec by a picture of an object. The subject's task was to decide whether the picture matched the word.

The maps show the change from baseline prior to the presentation of the second word, that is, while the representation of S1 was active. Because the same words were presented in both tasks, unique word representation would predict identical scalp distributions for rhyming and word comprehension. Rhyming produced an asymmetric map, however, irrespective of whether a picture (German study) or a word (Italian study) was presented.

clude that the neural network activated by the presentation of a word does not have a unique representation, but depends on the level of processing invoked by a specific task. One experimental condition may enhance word representations on a semantic level (as in the word comprehension task) and another condition on the word form level (as in the phonological encoding task). Yet another task might activate word representations on their syntactic level (Levelt 1989). [See also Levelt: "A Theory of Lexical Access in Speech Production" *BBS* 22(1) 1999.] Depending on the context, the same word or percept can activate a lateralized cell assembly in the left hemisphere, as in rhyming or a distributed network (e.g., in word comprehension).

This illustrates the limits of approaches based on Hebb's rule: It seems impossible to define which neurons are included in a cell assembly representing a word and which are not. A network may operate in different modes, recruiting one set of neurons in a reverberating circuit for a word representation in one task and another set on another task. Accepting this would render the concept of a fixed set of neurons representing a given word useless.

If the brain is viewed as a dynamic, self-organizing system that permanently adjusts the connectivity among its excitable units and can even alter its numbers, then it is not the representation of words, objects, actions, and so forth that would be localized, but the activity related to a specific task performance. Somatosensory perception would concentrate activity in the postcentral gyrus, in posterior parietal cortex, and SII; rhyming would center activity in the left hemisphere perisylvian region, whereas word comprehension would require widespread, bilateral activity.

This point is further illustrated by research on cortical representational plasticity (Bunomano & Merzenich 1998; Elbert & Flor, in press): modified by task and experience, the cortex can preferentially allocate neural elements to represent and process any relevant input source. The somatosensory cortical representational map is not the body surface, but is similar to the "language" the brain uses to process sensory experience. Like the dynamic adjustments of language, the map may adapt to different sensory experiences and demands. One and the same neural network can store different concepts, operating in different modes; that is, different "languages" may be coded in the synaptic weights of the network. A network in primary representational zones may respond with one spatial pattern of activity in one condition and a different pattern in another (Birbaumer et al. 1997).

Similarly, a word might have one representation in a syntactic task but another during semantic processing. Hence Pulvermüller's view might not be sufficient to describe brain functioning. It may adequately model one given set of data but fail to explain another one. We may ultimately have to adopt a position akin to the one in quantum mechanics where for an electron, the model of a particle can be adequate to explain one set of data and the model of a wave might be needed to explain observations under different experimental conditions. The concept of a word representation may explain data only from certain distinct, very simple paradigms; the concept of task-dependent organization or the interaction between the two views may be needed in experiments that go beyond the framework presented by Pulvermüller.

Other brain effects of words

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Abstract: Pulvermüller's discussion needs more explanation of how the proposed assemblies remain assembled after formation and how they can be accessed later among all the possible assemblies, many of which involve many of the same neurons. Alternative Hebbian strengthening mechanisms may provide additional information, and, developmental studies of the assemblies might provide insights into their evolution.

1. Given that Hebbian neuronal (and glial?) assemblies are created by defined inputs, how do the assemblies know they are assemblies? That is, why do they persist after the input that created them ceases, and how do they persist in the face of later multiple inputs that are likely to encompass many of the same neurons? And how does any later input evoke the ignition of just those same neurons (and glia)?

2. Assembly is virtually guaranteed experimentally by the response to the simplest inputs such as single words: activation of broad patterns in brain scans that light up on the order of a few percent of the cortex. There is no way to accept that the input of a single word would activate such a large fraction of the neurons unless the group activation process is the normal response.

Grouping of responses is also indicated by the folklore that, on the average, each neuron is only five synapses away from every other neuron in the cortex. In this connection, it would be interesting to try to learn about the different groupings that are evoked by related inputs. This could be done by comparing the brain scans when just the first, then the first two (and so on) letters of a word are given to a subject. This looks into the overlap phenomenon discussed by Pulvermüller. What differences would be expected in brain scans resulting from reading and hearing the following input words – school, schism, and schedule – where the latter word could have different pronunciations in England and the USA?

On the other hand, the fact that seeing only the first few letters of a word can create a whole word in our minds also shows that a group can be normally activated by those first inputs. The group must have been strengthened by repetitions and reverberations

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because otherwise, the signal given by the first inputs would have no special ending in our minds.

Moreover, such experiments should be done developmentally, meaning they should be carried out on children starting from, perhaps, age 1 through to brain maturity around age 18, with measurements being made at least every year. Such measurements could perhaps get at the role of the inferior parietal lobule discussed by Geschwind (1965); its being called "the association area of association areas" clearly predicts that most inputs will activate significant areas of the perisylvian region. Its developmental status has not been adequately probed. According to a remark I have heard attributed to Yakovlev, this is the most recently evolved part of the posterior brain, as evidenced by the pushing down of the end of the Sylvian fissure going from monkeys to humans, so it is very likely to be involved in one of the fundamental differences between the species: language.

3. There could be alternative Hebbian mechanisms. The model being developed in the target article depends strongly on using a Hebbian picture of synaptic events. The use of the Hebbian strengthening of synapses might be amplified by considering that the strengthening could be biochemical, biophysical, or anatomical. Such different mechanisms might lead to appreciably different pictures of assemblies and their permanence. Current considerations of Hebbian mechanisms stress biochemical aspects relating to the substances being created and transported in either the forward or reverse direction. There is an enormous literature that does not need surveying here.

A biophysical alternative is that the export of so much excitatory material would increase substantially the demand for excitation-linked substances. That could result in their being synthesized in such amounts that the concentration along the strengthened path would reach a value so great that novel extensions would be created, paralleling the first one. That means that the strengthening would be by an increased *number* of synapsing branchings between the connected neurons as an alternative to increasing the *strength* of the synapse between them.

An anatomical alternative could stem from recent reports (e.g., Gould et al. 1998) that there is replication of neurons in adult primates. This raises the possibility that there can be a strengthening of communication along a particular pathway resulting from an increasing number of both excitatory and receptor neurons. That would multiply the connectivity along the given pathway, thereby strengthening the kind of connection whose functioning is being enhanced.

4. Other input contributors could be words that have an experiential or emotional context that could alter the assembly as, for example, when the word "injury" calls up the fact that the individual has a broken leg. That would mean that a brain scan would show activation of, say, motor or sensory areas. So, the condition of the body can also figure in the extent of the connections made to create the assemblies.

5. The role of available energy in Hebbian strengthening is not usually sufficiently considered. Many studies have emphasized the probable role of reverberation in solidifying responsive networks (e.g., King & Kutas 1998). In that case, reverberative strengthening of an activated path could lead to even less energy being available for other paths. Reverberations would thereby increase the differential response of synapses. Indeed, reverberations could be responsible for a major portion of the energy demand of the brain whose 10-fold greater demand (than an equivalent weight of body) otherwise still lacks explanation. Perhaps this is one version of what Crick and Mitchison (1983) could have had in mind in their explanation and analysis of the restoration processes that happen during sleep.

Hebb's other postulate at work on words

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Abstract: The correlative coactivation of sensory inputs, Hebb's "second rule," probably plays a critical role in the formation of word representations in the neocortex. It is essential to the acquisition of word meaning. The acquisition of semantic memory is inseparable from that of individual memory, and therefore the two probably share the same neural connective substrate. Thus, "content" words are represented mainly in postrolandic cortex, where individual perceptual memories are also represented, whereas "action" words are represented in frontal cortex, with executive memories. The activation of a memory network may not necessarily entail the high-frequency oscillatory firing of its cells, though reverberation remains a plausible mechanism of short-term memory.

Hebb's famous postulate ("When an axon of cell A is near enough to excite a cell B and repeatedly . . .") has generated hundreds of experiments and torrents of ink. Despite its appealing logic it has yet to receive conclusive empirical proof. On page 70 of his book, Hebb (1949) postulates another "rule" that, in addition to the previous one, is supposed to be critical for the making of cell assemblies and for perceptual integration. He rightly attributes this second postulate to prior theorists, and formulates it as follows:

> Any two cells or systems of cells that are repeatedly active at the same time will tend to become "associated," so that activity in one facilitates activity in the other . . . what I am proposing is a possible basis of association of two afferent fibers of the same order – in principle, a sensori-sensory association. (Hebb 1949, p. 70)

This second rule does have considerable experimental support, and I have argued elsewhere (Fuster 1995) that it constitutes a fundamental principle of the formation of memory in the neocortex. It is the main principle that Pulvermüller seems to adopt to support his neurolinguistic reasoning, with the extra proviso that correlation is used as a criterion of coactivation. In his conceptual framework, "synchronous convergence" – as I call the principle – is implicitly or explicitly at the root of the associative networks or assemblies of cells that presumably represent words.

To anyone who recognizes the basic neurobiological dichotomy between cortex dedicated to perception (postrolandic) and cortex dedicated to action (prerolandic), the evidence of "content" and "action" words in posterior and frontal cortex, respectively, is not surprising. Even less surprising is the relative confinement of "function" words to the left perisylvian cortices and, I should add, the massive fiber tracts that undercross the rolandic fissure; for these structures, like those words, probably play a crucial role in syntax. The experimental evidence Pulvermüller summarizes is remarkable nonetheless, in part because it is technically quite difficult to obtain.

The meaning of real words, action words, and content words is inextricably related to individual memory, a point that Pulvermüller touches on lightly. This is a point that can hardly be ignored in the interpretation of the data he reviews and it should probably bear heavily on his anatomical inferences. Words are semantic memories that have accrued from individual experience in the learning of language. Thus, after language learning, there presumably remain in the cerebral cortex underlying associations between word meaning and individual memory. This would imply that the cortical distribution of a word is tied to the idiosyncratic distribution of associated memories, and thus to the diversity of cortical memory networks in different individuals. Consequently, the distributions of words of any given category in different individuals may be grossly similar but are unlikely to be identical. The representations of words are likely to be as diverse as the life experiences that provided them with meaning. Could that be the reason the distribution of real words is apparently more widespread and more variable than that of pseudowords or phonemes?

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Moreover, could the relative constancy of function-word distribution be an expression of the relative constancy, perhaps innateness, of a universal grammar?

That the ignition of a memory network leads to the reverberation of activity between the associated components of the network is a plausible notion (Fuster 1997b). This is clearly a putative mechanism of active or "working" short-term memory, though it has not yet been conclusively demonstrated. Of course, oscillatory activity might be an electrical manifestation of the reverberatory "binding" of assemblies in active memory. But then one could argue the other way, theoretically and even empirically. Because of differences in the length of re-entrant circuits in a network, multiple reverberation frequencies are likely to supervene over a resting oscillatory frequency when the network is activated; a given cell or cell group may thus become solicited by several simultaneous re-entrant inputs from different parts of the network ("frequency attractors"). The result may then be desynchronization, a "washout" of the prevailing oscillation at rest. We have indications that this is indeed the case, at least in certain neuronal populations of somatosensory cortex during active memorization of tactile stimuli in a haptic memory task. During active memory, some cells that oscillate at rest show an increase in transitions of firing frequency – without an overall average increase – and a reduction in the amount of time they stay in an oscillatory state (Zhou et al. 1997).

Also plausible is the notion that cells in certain regions of the cortex (especially the prefrontal cortex), which play a key role in the temporal organization of behavior (Fuster 1997a), undergo phasic and sequential firing changes in correlation with the implementation of successive component acts. It is no less plausible to extend this principle to the syntax of language and to postulate the successive recruitment of certain neuronal populations at the service of the temporal structure of language. Furthermore, several groups of cells may serve as a short-term neuronal pushdown store to convert temporal order into meaningful subordinate order in language expression, thus accounting for the subordinate role of embedded sentences. Neurons such as the one in Pulvermüller's Figure 10 could be part of such a pushdown store in the behavior of the monkey. To substantiate the operation of such stores, however, correlated groups of cells would have to be shown to exhibit exponential decay of firing after each perceptual item in a sequence leading to consequent action. The neuron of the figure would do for one item at one time, as it apparently did in our monkey. But many correlated neurons like that one are needed, at different times, and with decaying firing frequency, to substantiate the speculative pushdown store of Pulvermüller. Thus far our methodology has simply not been geared to discover them, although they may indeed be there.

Words do not stand alone: Do not ignore a word's role when examining patterns of activation

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Abstract: Pulvermüller traces the differences in brain activity associated with function and content words. The model considers words displayed primarily in isolation. Research on letter detection suggests that what distinguishes function from content words are their roles in text. Hence a model that fails to consider context effects on the processing of words provides an insufficient accounting of word representation in the brain.

Pulvermüller postulates that the degree of laterality of brain responses to words depends on their semantic properties. Concrete content words, often associated with easily imaged concepts, should yield only weakly lateralized cell assembly activity, whereas more abstract function words, which fail to reference particular images, should evoke highly lateralized activity. The physiological work cited by Pulvermüller provides reasonable support that brain activity in response to these two classes of words differs as suggested. However, in discussing these patterns of activation, the author acknowledges that attributing the diverging patterns of cortical activity simply to the semantic properties may be problematic because words falling into these two classes tend to differ on a variety of dimensions (word frequency, word length, abstractness, etc.).

In particular, this position largely ignores the potential effect of differences in the structural (syntactic) roles associated with the function and content words. To study structural roles, though, it is necessary to examine both behavioral and biological response patterns to target function and content words in text, rather than in isolation. Although features such as frequency, imagery, and even meanings often operate independently of context, structural role is achieved in the context of a sentence. Pulvermüller notes that target words observed in context may be affected by semantic and syntactic relationships that could corrupt physiological patterns, either by artificially defining class differences or by masking real processing differences. Indeed, most of the neurological work on response patterns to function and content words has studied words presented in isolation, that is, not in actual text. (A few exceptions are discussed by Pulvermüller [e.g., Neville et al. 1992; Pulvermüller 1995a], but often the "context" studies failed to control important confounding factors.) It is our position that this interest in "purity" of presentation may obscure one of the most relevant factors distinguishing these word classes.

In light of this shortcoming, we draw Pulvermüller's attention to a program of behavioral research that (in addition to supporting the suggested division between function and content words) points out the salience of a sentential role for the understanding of response patterns to these two classes of words: The structural role of a word in a sentence is of primary importance and response patterns to words are likely to be affected substantially by the embedding context. Koriat and Greenberg (1994) propose that during the act of reading, readers process text for both structure and meaning. Although meaning extraction is paramount, clarifying sentence structure is a necessary component for obtaining and organizing meaning. According to this account, the processing of structure leads the way to the processing of meaning, so that the interpretation of individual units is constantly subordinated to the encompassing phrase structure (see also Bock 1990). Function words or morphemes are assumed to be markers of important structural units.

The phenomenon that informs this position is the missing-letter effect. Readers are less likely to detect a target letter, for example, *t,* in a function word such as *the* than in a content word such as *tie.* In general, letter detection in prepositions, conjunctions, and articles (function words) is more difficult than in nouns, verbs, and modifiers (content words). For example, Healy (1976) and Drewnowski and Healy (1977) found that readers consistently missed more *t*s in *the* (about 62% of all errors) than in content words containing *t,* whereas Greenberg and Koriat (1991) found more misses of *f* in *for* (27%) than in short content words also beginning with *f,* such as *fun* (5%).

Initially, the missing-letter effect was thought to reflect the familiarity of a word rather than its function in a sentence (Healy 1976). The recent work of Koriat and Greenberg (1991; 1994; 1996), however, points to the role of the word in a sentence as the primary factor in letter detection performance. Evidence favoring this conclusion is plentiful. Briefly, Greenberg and Koriat (1991) observed that detecting an *n* in *on* depended on whether *on* appeared in a structural role as in "on his way" (42% errors) or as a modifier, as in "on switch" (17% errors). Moravcsik and Healy (1995) found that *t* in *the* was more difficult to detect when used normally as an article (37% errors) than as a noun (2%; e.g., "the definite article the"). Similarly, Saint-Aubin and Poirier (1997) replicated the effect in French: The word *or* produced more omission errors when it was used as a conjunction (meaning "however") than when it was used as a noun (meaning "gold"). Moreover, even

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more subtle changes in the relative contribution of a function word to structure resulted in differences in letter detection, for example, in a critical structural role *for* produced 27% errors, whereas in a noncritical structural role it showed only 3% errors (Greenberg & Koriat 1991). Muesseler et al. (submitted) recently found that although various forms of the German definite article all produced more errors (about 13%) than matched content words (about 2%), the effect was more pronounced when the article introduced a subject noun phrase than when it introduced an object noun phrase. A nominative subject phrase is more significant than the object phrase to the organization of a sentence (e.g., see Van Dijk & Kintsch 1983).

Given these results it might be wise to examine the activation of cell assemblies for various orthographic patterns as the sentential role of those patterns is shifted. Certainly, before committing ourselves to a model of how function and content words are represented by brain activity, the effect of a word's structure and meaning role in text must be systematically examined.

Pulvermüller suggests that categorizing words may be less useful than seeing words on a continuum, but he does not specify how the context affects the activity of a particular word as its function changes. A variety of questions arise. Specifically, how would the cell assemblies respond to words that carry both function and content morphemes? How would they handle cases when the orthography alone does not give away the status of each component? Also, in many languages suffixes carry syntactical information. How are these suffixes distinguished from other similar letter endings that are part of the stem of a content word? Finally, and most important, how would Pulvermüller's proposed system accommodate different responses to the same real words when the roles of words, even function words, change with context?

As Pulvermüller suggests, it may be difficult to make a binary distinction between vocabulary classes based on semantic criteria. Our results in fact favor a position in which words are placed along a *continuum* between those that carry mostly semantic information and those that carry mostly structural information. The placement of a word on this continuum will of course vary depending on its contextual environment. This "continuum" view is also consistent with grammaticalization theory in linguistics, which asserts that grammatical words or morphemes have their origin in content words (e.g., nouns and verbs) that have acquired syntactic characteristics.

It is possible that one must distinguish between the representations of structural and semantic properties of a single word depending on its embedding sentential context. Indeed, there is evidence that the position of a content or function word in a sentence influences the electrocortical activity associated with it (Van Petten & Kutas 1991; see also Roesler et al. 1998).

Pulvermüller acknowledges this point, but he views context as obscuring the "real" distinctive patterns of brain activity for function and content words. Indeed, context probably does alter patterns, but given the letter detection results reported, it would appear to be a shortcoming if a model of brain activity were satisfied with clear and distinguishable patterns, while ignoring context.

Which phonology? Evidence for a dissociation between articulatory and auditory phonology from word-form deafness

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Abstract: Pulvermüller's Hebbian model implies that an impairment in the word form system will affect phonological articulation *and* phonological comprehension, because there is only a single representation. Clinical evidence from patients with word-form deafness demonstrates a dissociation between input and output phonologies. These data suggest that auditory comprehension and articulatory production depend on discrete phonological representations localized in different cortical networks.

Pulvermüller argues that "most word representations consist of two parts: a perisylvian part related to word form and a part located outside the perisylvian areas representing semantic word properties" (sect. 7). The word form is the sound structure of words consisting of phonemic articulation for speech production and acoustic analysis for speech comprehension. In Pulvermüller's view, these two phonological codes are neither distinct nor represented in different anatomical areas. Nor is the word form a supplementary abstract phonological representation (Blumstein 1995). It is instead a single distributed system that represents both motor and acoustic codes: "The Hebbian view implies that the motor and acoustic representation of a word form are not separate, but that they are strongly connected so that they form a distributed functional unit. For this unit to function properly, both motor and acoustic parts need to be intact" (sect. 3.1). According to this view, a lesion within perisylvian areas should impair both speech production and auditory comprehension, because there is only a single representation. This model challenges the classical dichotomy of function between the anterior (articulatory) and posterior (auditory) phonological areas (e.g., Geschwind 1970).

It is true that lesions to anterior or posterior perisylvian areas do not clearly predict articulatory or auditory deficits, respectively. Lesions to either area can be accompanied by either deficit, and often both deficits occur regardless of the site of the lesion (Blumstein 1995). Nevertheless, the clinical evidence still suggests that auditory and articulatory phonology are relatively independent representations and therefore localized separately in the brain.

The distributed word-form circuitry proposed by Pulvermüller does not predict the dissociations commonly founded in clinical data, for example, word-form deafness. These patients have difficulty in recognizing spoken words and repeating heard words in spite of an intact ability to detect and discriminate heard phonemes (Franklin et al. 1996) and normal performance on audiometric tests (Ellis & Young 1988). They fail at the auditory lexical decision task (Howard & Franklin 1988) and confound words with similar pronunciations (e.g., "garden" and "pardon"). Word-form deafness has thus been considered a "prelexical" problem (Kohn & Friedman 1986).

Though speech comprehension is drastically impaired, speech production, reading, and writing are intact; if they are impaired, it is not as severe as the deficit seen in speech comprehension (Buchman et al. 1986, patients 2 and 3; Howard & Franklin 1988). This dissociation means that articulatory phonology can be accessed and retrieved in spite of an impairment at the auditory phonological lexicon, a dissociation that is not predicted by Pulvermüller's word-form model.

Word-form deafness has been considered a distinct deficit from both pure word deafness and transcortical sensory aphasia. Patients with pure word deafness are unimpaired in the auditory lexical decision task, and can repeat spoken words without being able to define them. Following Kohn and Friedman's (1986) terminology, pure word deafness is considered a "postlexical" deficit, as the impairment has been localized between the phonological lexicon and the semantic system, both of which are intact. Transcortical sensory aphasia, on the other hand, is characterized by impaired language comprehension affecting both spoken and written language, anomia, and other more generalized semantic deficits (Berndt et al. 1987). Word-form deafness has been associated with dysfunction in the processing of rapidly presented phonological information (Miller 1987). In support of this hypothesis, some patients show an improvement in speech comprehension if the experimenters talk slowly (Albert & Bear 1974). We can therefore classify word-form deafness as a unique and selective deficit that impairs speech comprehension in the auditory modality, but leaves intact speech production as well as reading and writing.

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The dissociation between input and output phonology is present in other syndromes as well. Anarthric and dysarthric patients have problems articulating words, but nevertheless show normal performance in tests assessing phonological skills, speech comprehension, and reading (Baddeley & Wilson 1985). Finally, Pulvermüller's single phonological representation does not address other dissociations, such as those seen in dyslexia. Patients with phonological dyslexia are unable to read nonwords, but show few problems when articulating or comprehending speech (for a review, see Galaburda 1993).

The cognitive processes and neural architecture of phonology are still under investigation. However, neuropsychological evidence to date suggests that articulatory phonology and auditory phonology constitute two relatively independent representations. These systems are localized in separate cortical networks and can be selectively impaired, as word-form deafness shows.

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What else should a neurobiological theory of language account for?

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Abstract: We critique five points that impede the target article's far-reaching efforts toward formulating a neurobiological theory of language. Neurolinguistics amounts to no more than neurology in linguistics in this account, because it assumes "perceptual representational isomorphism," processing autonomy and "meaning," thereby aiming primarily at justifying modular concepts in terms of associative principles.

1. Neurolinguistics should amount to more than neurology in linguistics. Neurolinguistic investigations of linguistic processes use mainly linguistic categories. They do not attempt to justify the plausibility of linguistic hypotheses, not to mention the neurological reality of linguistic theories. But neuronal data should provide an empirical ground on which linguistics can base its speculations. This has already been the case in word recognition (e.g., Balota 1990) and sentence parsing (Altmann 1989; Hawkins 1994), where processing constraints lead to stronger hypotheses. Thus, a language model should be built on a neurological basis *despite* (actual) linguistic speculation.

The target article takes many controversial issues for granted. Center embeddings, for example, are said to be a "linguistic universal." On the contrary, "there is a correlation between the perceptual difficulty of center embeddings and their frequent ungrammaticality in English and many other languages" (Hawkins 1994, p. 5). Center-embedded sentences may be tolerated in German, but not in English or Portuguese. As Hawkins states, the same holds true for subject-object-verb (SOV) languages, with Japanese accepting and Persian rejecting center embeddings.

2. The "perceptual-representational isomorphism" assumption. The target article is based on an almost direct connection between "words" and "meaning" – although it is not indicated what a word or a meaning should be. As stated elsewhere (Pulvermüller et al. 1995a, p. 367), "in brain terms, lexical access most likely corresponds to the ignition of a cell assembly representing a word." Thus, the author's arguments seem to be based on what Seidenberg (1990, p. 34) called "perceptual-representational isomorphism": For each representational unit in the mind there is a corresponding basic perceptual unit in speech and reading. However, that approach has been systematically challenged (for reviews, see Balota et al. 1990). A serious problem faced here concerns the relationships between words and their constituents (morphemes). That there is generally as simple a processing for "morphologically complex" words as for noncomplex words (Schreuder et al. 1990) seems to show that "word representation" is not yet (or no longer) a solid ground.

3. The autonomy assumption. The target article also lacks a critical note on the assumption that information about a word should be accessed *after* that word has been recognized, context playing almost no role in that process (the autonomy assumption). It seems instead that we should believe things happen this way, because all methodological concerns are about *isolated* words. Nevertheless, there is evidence that context (parafoveal information) is intrinsic to word recognition and comprehension (Balota 1994; Schustack et al. 1987). On the other hand, the difference between open-class and closed-class words, as indicated by Garrett (1988), may be an indirect rather than an essential one. As Bock and Levelt state:

> open class words by and large occur less frequently than closed class words, they are learned later in language acquisition, they are longer, and they are more likely to bear stress. Such factors, alone or together, could create a predisposition to error that has nothing to do with word class per se. (Bock & Levelt 1993, p. 26)

It accordingly seems more productive to examine how and how often words combine, rather than comparing data on isolated words (e.g., Kutas & Hillyard 1980a).

4. The "meaning" assumption. The notion that words *have* a meaning – what Lakoff and Johnson (1980) call the "container metaphor" – is now hard to maintain. It seems that "meaning" consists of the process of meaning (Clark 1992). Words should be seen as information tokens that, among others, to some extent guide the meaning process. Function words have an extremely important role to play as information about how to process a text/discourse more efficiently (Halliday & Hasan 1976). Considering this, Dillinger (1997) suggests that it is better not to differentiate the tokens, but the processes in "text-based processing" and "knowledge-based processing." This is far more interesting for accounting for sentences like Pulvermüller's: "It will provide preliminary answers to the 'where' question" (sect. 1, para. 4), without a complex representational hypothesis about "where" as a function word inserted in a name slot. Here, "where" simply recalls the localization of neuronal correlates of psychological processes of word comprehension in the brain, which is the point Pulvermüller is trying to make.

5. Justifying modular concepts in terms of associative principles. We believe that the target article attempted in part to justify symbolic and modular theoretical notions, such as lexical access, in terms of associative principles (Hebb's assemblies). This attempt is doomed to fail, partly because network modeling has already advanced the hypothesis of explaining language without the notion of lexical access (e.g., Seidenberg & McClelland 1989).

We believe that the fundamental problem of neurolinguistics is still to explain serial order in behavior. This is not yet possible in terms of purely associative devices. Sequencing of neuronal discharges cannot be explained exclusively in terms of feedback connections (Abeles et al. 1993; 1994). Serial order requires a mixed architecture, composed of both feedback and feedforward connections. Feedback connections generate oscillatory and synchronic activity. But to originate sequencing patterns, feedforward connections are required. In other words, the system must be hierarchically structured. There is evidence that feedforward connections in cerebral cortex are predominantly prewired genetically, whereas feedback connections are subject to activity dependent on plastic modifications (e.g., Singer 1995). This is of interest because most connectionist approaches that have succeeded in modeling serial order have somehow incorporated the architectural principle of the cerebral cortex (Elman 1990; 1995b) or made use of synchronizing oscillators (Shastri & Ajjanagadde 1993).

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In addition, to be defined, a sequence needs boundary markers. Pöppel (1970; 1978; 1985) has suggested that this may be achieved by means of a hierarchically organized system of oscillators with two frequencies. Higher frequencies may be used to define events, which are then automatically ordered and integrated up to a temporal boundary given by the period of the lower frequency oscillation. There is both theoretical (Theunissen & Miller 1995) and empirical (McLeod & Laurent 1996) evidence that oscillatory and synchronizing components may be informationally dissociable. Synchronizing mechanisms may serve informational goals of categorization and abstraction, whereas oscillatory mechanisms may work as timing devices or "Zeitgebern," which are used to define behavioral sequences.

It seems that the enormous authority acquired over the course of centuries by a way of thinking of language in symbolic terms inhibits Pulvermüller's efforts. To get any further we should probably first try to shake off arbitrary (mis)conceptions in linguistic theory, some of which are based on common sense rather than on scientific knowledge.

Cell assemblies as building blocks of larger cognitive structures

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Abstract: Pulvermüller's work in extending Hebb's theory into the realm of language is exciting. However, we feel that what he characterizes as a single cell assembly is actually a set of cooperating cell assemblies that form parts of larger cognitive structures. These larger structures account more easily for a variety of phenomena, including the psycholinguistic.

Pulvermüller is to be congratulated for his accomplishment in extending Hebb's cell assembly theory into the realm of language and for showing that meaningful and supportable predictions can be made about measurable neural activity. Without undermining his accomplishments, however, we do feel that adjustments in both the terminology and the conceptualization of his work reveal a more powerful and flexible cognitive system.

In 1949, Hebb, in his landmark book *The organization of behavior,* developed the concept of the *cell assembly.* In his original conception, a cell assembly consisted of a number of neurons that responded to a set of similar stimuli and could sustain activity for about 500 milliseconds (Hebb 1949). Cell assemblies, though powerful themselves, are also ideal building blocks for larger cognitive structures (Holland 1998; Kaplan et al. 1990). The recombination of subsets of building blocks into larger structures yields a vast number of potential combinations. Just as a modified Hebbian synaptic learning rule can be used to form cell assemblies, the same learning rule can be used to create an associative link between two assemblies through a set of mediating connections. Thus, when one assembly becomes active, another is likely to become active because of this link.

When a number of cell assemblies become linked in this way, longer sequences are encoded. When many distinct sequences pass through a given set of assemblies in such a way that each assembly can be reused in multiple sequences, a more complex structure evolves. This structure is similar to the *cognitive map* that Tolman proposed (Tolman 1948). This cell assembly interpretation of Tolman's cognitive map concept has been proposed as a general purpose knowledge structure, useful not only for storing information used in navigating an environment (Chown et al. 1995; Kaplan & Kaplan 1982; Levenick 1991), but also for encoding algorithmic and story structures of many kinds. It appears to be equally suitable for the generation and parsing of language.

Hebb focused on cognitive structures with direct sensory and motor content. Because a neuron is more likely to be connected to those nearby, a notion of neural distance exists. Some neurons are close to the sensory and motor apparatuses, whereas others are farther away. Neurons that are close to the sensory interface are well placed to become members of cell assemblies with concrete, sensory content. These assemblies then become the inputs for neurons farther away from the sensory interface, where assemblies with diminished sensory content will form.

From the simple notion of distance emerges both the concept of depth and a hierarchical structure. In such a hierarchy, depth equates with abstractness, moving from basic-level categories (e.g., *tree,* Rosch et al. 1976) to those so abstract they have little or no sensory content (e.g., *justice*). Both the cognitive map and the hierarchy are directly applicable to Pulvermüller's work in language. The pattern of neural activity generated by a noun, a verb, or a grammatical function word that Pulvermüller uses in his argument is not a result of what we view as a single cell assembly. Rather, we would characterize the pattern as the result of the activation of a set of strongly associated assemblies.

The phonemic representation of a word in perisylvian cortex probably involves a sequence of cell assemblies where each represents a phoneme. The same phonemes in a different order would, after all, generate a different word (e.g., "cat" and "tack"). As the sequence of phonemes is recognized, activity may then collect in another assembly sitting at the next level of a hierarchy and representing the whole word. Note that this hierarchical relationship is based on the grouping of a sequence. A categorical hierarchy is also available so that "cat" may be an animate noun, or more traditionally, an animal.

The phoneme-based word assembly has strong associations with potentially many semantic correlates. By keeping the phonemic and semantic assemblies separate, yet highly associated, the system can readily deal with homonyms by using contextual cues to resolve the competing interpretations. A set of separate cell assemblies can account for a number of other phenomena as well. Many concepts simply do not have simple verbal correlates. People can learn and represent nonsense words. Because one can have a word without a concept, or a concept without a word, the assemblies are separate.

If we might be a bit more speculative, we conceptualize a set of *word maps* composed of cell assemblies rich in semantic content, and a set of word maps composed of phoneme-based cell assemblies. These two maps are highly associated and traversal between them is often easy and consciously seamless.

By keeping the maps separate, the system has a more powerful and flexible structure. There are links within each map as well as links between the maps. Among other things, the word maps encode the likelihood of connections between phonemes. If two phonemes never connect in the language, a word in which they do connect will seem unnatural (which may explain the "phonological rules of the language" that Pulvermüller [sect. 4.2, para. 7] mentions). In word maps, words can be combined to form multiword units whose semantic content is unrelated to the base words, as in "The Big Apple," "kick the bucket," and other idiomatic expressions. It is difficult to explain how this could be the case if the maps were not separate.

Finally, hierarchical and map structures go a long way toward explaining how a system as complex as language can be learned in the first place. Preverbal children obviously have sophisticated representations of the world around them, and children undergo an explosive growth in vocabulary. A high school graduate knows 60,000 words (Pinker 1994) and probably knows most of them by age 5. It is difficult to account for this unless children are, at least in part, building larger structures from already learned building blocks, both semantic and phonemic.

Pulvermüller's findings are indeed encouraging. We believe it

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would be worthwhile to explore the application of his methods toward these more complex cognitive structures, opening up fascinating possibilities for the explanation of many complex psychological and psycholinguistic phenomena.

Homogeneous neural networks cannot provide complex cognitive functions

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Abstract: Within the Hebbian paradigm the mechanism for integrating cell assemblies oscillating with different frequencies remains unclear. We hypothesize that such an integration may occur in cortical "interaction foci" that unite synchronously oscillated assemblies through hard-wired connections, synthesizing the information from various functional systems of the brain.

According to Hebbian concepts, if synaptic strengthening occurs between neurons, they will form a cell assembly that exhibits synchronous ("well-timed") activity (target article, sect. 2, para. 14), that is, it will acquire a common oscillation frequency. This corresponds with one of the basic ideas of the Russian neurophysiological school. In the first third of our century Vvedensky (1906) and Ukhtomsky (1935) proposed that connections between nervous structures are promoted through the correspondence in their frequency characteristics, that is, in equalizing their excitation cycle rate (the "functional lability" parameter). Recent studies of synchronized spatiotemporal patterns during perception and learning (Gray & Singer 1989; Viana Di Prisco & Freeman 1985) have demonstrated a role of synchronous oscillations in the neural coding of specific information. But complex behavior requires integration of different sensory modalities or motor commands. According to Hebb's principle, this integration can be explained by the overlapping of neuronal populations (target article sect. 2, para. 19). It seems unlikely that in this process of integration these populations will form a homogeneous network oscillating at the same frequency because they provide completely different types of information from relatively independent brain functional systems. So the problem of associating cell assemblies oscillating with different frequencies arises. A possible mechanism for this integration has been proposed in our studies (Ivanitsky 1993).

The integration may occur in certain cortical centers – "interaction foci" – where connections from various brain regions converge. This is based on our EEG studies of brain connectivity during cognitive operations using a method elaborated in our laboratory. The method develops the idea that synchrony of brain potentials revealed in the exact coincidence of EEG spectral components in different cortical areas promotes brain connections. The areas having a maximal number of such components are considered interaction foci. The topography of the interaction foci is specific to particular cognitive operations. For example, the focus was most prominent in the right parietal and temporal regions in the performance of spatial tasks and in the left central area with verbal tasks (Nikolaev et al. 1996).

From the physiological point of view, the focus may perform functions analogous to those of a command neuron in lower animals (Kupferman & Weis 1978; Sokolov 1979). The focus is hypothesized to consist of groups of neurons with different frequency characteristics, each of them tuned to peripheral groups of neurons of identical frequency (see Fig. 1). Within the focus, the groups of neurons must be joined by connections formed in a different manner: Because they work at different frequencies, the synchronization principle, that is, the equal excitation cycle, cannot be applied here. These connections should be fixed (hard-wired); that is, they are determined by structural changes in synapses, which are effective at any phase in the neuron excitation cycle, except at the absolute refractory phase. The concept of hard-wired and labile connections in mental functioning was first proposed by Bechtereva (1980).

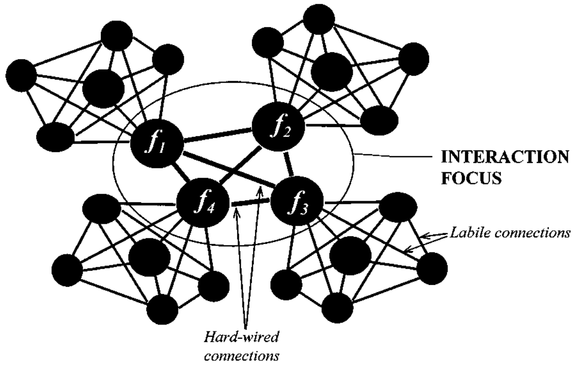

Figure 1 (Ivanitsky & Nikolaev). A hypothetical scheme for an interaction focus. The focus consists of groups of neurons distinguished by their different intrinsic frequency parameters (f_1, f_2, f_3, f_4). The groups are connected with peripheral neuronal groups via labile connections based on their identical frequency characteristics, (the "synchronization principle"). Within the focus, the groups are linked by hard-wired connections based on structural changes in synapses. This structure provides the main function of the focus: the synthesis of information circulating in different neural networks.

The main advantages of the interaction focus is its high information capacity, which overcomes one of the major difficulties of the suggestion that cognitive functions are provided by homogeneous neural networks. The concept of the interaction focus is in strong agreement with the findings of Damasio (1994), who concluded that the active brain areas revealed by fMRI in psychological testing were merely regions to which different types of information converged. The term "focus" has been used in a similar sense by Gevins et al. (1994).

Another interesting point of the target article is Pulvermüller's hypothesis about the representation of words with particular meanings in corresponding sensory and motor cortical areas. This may be so if a word has a very concrete, unambiguous sense or occurs within a certain context. However, if a word is abstract or has many meanings, then its representation cannot be restricted to any particular area and will instead be represented in whole cortex, which serves as an "associative memory" (sect. 2, para. 3).

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Dondersian dreams in brain-mappers' minds, or, still no cross-fertilization between mind mappers and cognitive modelers?

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Abstract: Pulvermüller identifies two major flaws of the subtraction method of neuroimaging studies and proposes remedies. We argue that these remedies are themselves flawed and that the cognitive science community badly needs to take initial steps toward a cross-fertilization

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between mind mappers and cognitive modelers. Such steps could include the development of computational task models that transparently and falsifiably link the input (stimuli) and output (changes in blood flow or brain waves) of neuroimaging studies to changes in information processing activity that is the stuff of cognitive models.

> We may be able one day to use brain waves as indicators of the beginning and end of a mental process; but in general it has seemed necessary to let the timed process start with a sensory stimulus and terminate in a muscular response.
>
> Robert S. Woodworth (1938)

Pulvermüller's identification, in sections 4.1 and 4.2, of two major flaws of the subtraction "logic" underlying neuroimaging studies is laudable. We are sceptical, however, as to whether the two remedies he proposes can solve these problems. Any trained cognitive psychologist knows what Sternberg proposed to solve Donders's subtraction method problem of mental chronometry: the dream of simple mental arithmetic, where one can arbitrarily insert and delete processes into tasks as if the mind were a "Legoland." Some also know what McClelland (1979) proposed to solve problems of Sternberg's additive factors logic. Does Pulvermüller ignore all this, or does he think his two remedies would solve the fundamental flaws of neuroimaging subtraction logic studies, the results of which serve as positive evidence for his Hebbian model – despite these flaws?

To avoid "Problem I" of neuroimaging subtraction logic – that a difference in more than one psychological process may be attributed to each pair of conditions, making it difficult to attribute a physiological contrast to one of them – he sees *only one remedy:* choosing maximally similar experimental conditions while keeping the task constant. However, the history of subtraction and additive factors logic in mental chronometry teaches one that such a proposal is pointless without task or process models that transparently and falsifiably link the "similarity of experimental conditions" to (1) the cognitive (or neurobiological) processes underlying performance in the task at hand and (2) the dependent variables provided by brain imaging techniques. Pulvermüller's Hebbian cell assembly model is anything but such a task model. It neither tells one how "similar" two conditions are nor which psychological processes underlie similarity between conditions, stimuli, or tasks; that is, why two conditions or tasks are psychologically (or neurobiologically) more similar than two others. Computational process models and the approach of "functional overlap modeling" (Jacobs & Grainger 1994) could answer these questions, but only if one major problem is solved: determining how exactly changes in blood flow or electrical activity map onto changes in the information processing activity that is the stuff of computational/cognitive modeling (Jacobs & Carr 1995). This central challenge is not answered by Pulvermüller's model and one may therefore ask what function his model should serve in the process of cross-fertilization between mind mappers (whose methods are flawed as noted by Pulvermüller) and cognitive modelers (whose models do not [yet?] speak to the data collected by neuroimaging studies).

Pulvermüller's proposal to avoid "Problem II" of the subtraction "logic" could be an even bigger "Dondersian dreaming pill" for brain mappers than his remedy we discussed above. The physiological double dissociation method he proposes to test more risky predictions to avoid Problem II could be even more flawed than its neuropsychological analogy. Our little "Gedankenexperiment," summarized in Table 1, will make this clear. It is a triviality not yet considered by many PET researchers, that one and the same difference vector can result from completely different sets of two raw-score vectors. With two tasks – A and B – and a resulting difference vector as shown in Table 1, it is often implied that task A activates location L1 and task B activates location L3 (for example, naming animals vs. naming tools). However, this conclusion is justified only if the difference vector results from the raw score vectors presented as possibility I in Table 1. Two of the many other possibilities are shown in sections II and III of Table 1. Only possibility I would support the notion that the two tasks produce a kind of double dissociation, task A activating location L1 and task B activating location L3 (see note 1). In II and III, however, the conclusions would have to be rather different: In II and III only one of the two tasks produces a topographically specific activation pattern, whereas the other activates all brain areas with equal strength. Unfortunately, the currently available blood flow measurement techniques that exploit task differences provide nothing more than the difference vector. No doubt, such a difference vector can provide useful information about the relative activation levels of two tasks, but – and this should be kept in mind – the difference vector does not support any conclusion that goes beyond this. For a neuropsychological model that tries to pinpoint cell assemblies as storehouses for particular types of information or as processors for particular steps of cognition, such a statement about relative activation levels is of limited use.

For completeness, it has to be added that other brain activation measures, such as event-related potentials derived from the magneto- or electroencephalogram (MEG or EEG), do not necessarily suffer from these restrictions. With these methods, a baseline level of activity can be measured before each trial and it can be "seen" – by comparing pre- and poststimulus patterns – if a task activates relative to this baseline one particular cortex area only or the whole cortex with equal strength (see, e.g., Heil et al. 1997). Moreover, the polarity of slow event-related brain potentials provides clues about the cause of an activity change – whether the cell assembly is in a state of relative activation (negative polarity) or in a state of relative deactivation (positive polarity) (see, e.g., Bauer et al. 1998).

In conclusion, Pulvermüller's challenging target article suffers from a lack of information concerning the lessons to be learned from 130 years of history of subtraction and additive factors logic in mental chronometry. Pulvermüller should therefore ponder the

Table 1 (Jacobs & Rösler). *Hypothetical patterns of brain activation that could be triggered by two different tasks and would result in the same difference pattern*

	I			II			III		
	Brain Location			Brain Location			Brain Location		
	L1	L2	L3	L1	L2	L3	L1	L2	L3
Task A	10	5	5	10	5	0	10	10	10
Task B	5	5	10	5	5	5	5	10	15
Diff (A − B)	5	0	−5	5	0	−5	5	0	−5
Diff (B − A)	−5	0	5	−5	0	5	−5	0	5

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fact that it took 100 years for Sternberg to wake up mental chronometrists from their Dondersian dreams (with a viable methodology and model). We look forward to seeing the first signs of a cross-fertilization between mind mappers and cognitive modelers in the author's reply to our commentary.

NOTE

1. A physiological double dissociation conforming to a crossover interaction could fail to exclude all possible single-locus models for the same reasons as a neuropsychological double dissociation fails to exclude all possible single-process models: It is not difficult to imagine a situation in which two tasks depend on the same process but are negatively correlated, for example, when tasks depend on information sources that are necessarily inversely related (Dunn & Kirsner 1988). Whether the reversed association method, proposed by Dunn and Kirsner as a better alternative to the flawed double dissociation method in mental chronometry, can also be applied to brain imaging studies is an interesting but open question.

Thought as word dynamics

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Abstract: A Hebbian model for speech generation opens a number of paths. A cross-linguistic scheme of functional relationships (inspired by Aristotle) dispenses with distraction by the "parts of speech" distinctions, while bridging the gap between "content" and "structure" words. A gradient model identifies emotional and rational dynamics and shows speech generation as a process where a speaker's dissatisfaction gets minimized.

Pulvermüller's target article communicates the power of a Hebbian approach to word dynamics. First, it accounts in an associationist way for clause generation, where a speaking subject's prior history provides the template for later connections between concepts. Second, through the mechanism of weighted activation, light is shed on meaning. Indeed, in contrast to the classical view, where the overall meaning of a clause results from serial processing of the words composing it, in the Hebbian framework the meaning of a sentence is a global three-dimensional packet of intermixing atomic meanings as provided by words (the concept is reminiscent of the scholastic notion of the *complex significabilis* where words combined evoke a "state of affairs" – see Jorion 1997b). Such an approach is close to what the semantics of languages such as Chinese force on the linguist and underlines how often our current reflections derive from familiarity with a single Indo-European language.

Pulvermüller revives Aristotle's "subsumptive" (see Hogan 1998) approach to language. With the Greek philosopher, in steps of increased semantic significance, concepts are first associated in pairs (to constitute atomic, then molecular propositions); they are then composed into reasoning (of a syllogistic nature), and finally concatenated into full-blown discourse (see Jorion 1996). In Aristotle's approach, our modern distinctions among "parts of speech" are cosmetic and of no functional consequence.

Pulvermüller's elementary dichotomy between "concrete" and "abstract" can be usefully bridged by distinguishing a set of functional relationships with cross-linguistic validity. These cover relations (1) between words and the empirical world, (2) between the words themselves, and (3) between the universe of words and the person of the speaking subject. Here is a brief exposition of such Aristotelian functions:

1. the demonstrative such as in "this," "I" (Jakobson's shifters), establishing a direct relationship between words and things of the empirical world;
2. the anaphoric, relating one or more words to one or several others, previously uttered: "which," "as mentioned before," "whatchamacallit," and so forth;
3. the categorematic, that is, the universal collectives, "mammals," "people of a friendly disposition," which abstract collections of the empirical world into concepts;
4. the determinants (our adjectives, verbs, adverbs) – encompassing the Chinese "modifiers" ("white," "in Santa Monica") and markers of belonging ("the boat's," "her"), restricting universals to one or more specific instances;
5. the syncategorematic: the copula, the associative connectors, and quantifiers of the logician's atomic proposition ("are," "some") or compatibility modulators ("despite," "meanwhile, back in the forest");
6. the continuity markers ("some time before," "then"), a separate function attempting to grasp our awkward intuition of time;
7. the highlighters, used for stressing parts of our speech ("clearly," "See what I mean?" "jolly," "bloody");
8. the adhesion markers, ("I am certain that," "I can't visualize that"), allowing speakers to specify a degree of personal commitment to their own utterances (ranging from the noncommittal quotation, "Someone told me about Jesus," to the assertion of identification, "I believe in Jesus") (see Jorion 1990, Ch. 21; 1996).

In addition to the Hebbian "correlational" logic ruling the connections between content words, Pulvermüller suggests that there is a second neural mechanism (sect. 3.3.1), delinking these time structure words from the might of repeated co-occurrence. Together, these two constitute the requisite infrastructure for the functional approach delineated above. It is interesting that the Hebbian perspective achieves a synthesis between rational and emotional dynamics habitually seen as divergent principles of discourse generation. I have shown (Jorion 1994) that a subject, its history stored as memory, and an environment, together constitute a single possibility space where behavior constantly aims at minimizing a dissatisfaction level. A framework for behavior is thus provided, replacing final causes (targets) by efficient causes in a gradient model where intentions (and worries) constitute potential wells. The gradient model applies to speech just as it does to any type of behavior. Indeed, a word is a memory trace like that potentially generated by every percept; it is associated – in each of its possible uses – with an affect value. The emotional dynamic of speech production follows a gradient leading to the satisfaction of the speaker. External circumstances (such as the words of an interlocutor in a dialogue situation where several dynamics interact) or inner circumstances (such as one's own moods and feelings) fuel such a continuing process that only death can interrupt (Jorion 1997a).

Thus is vindicated an approach first sketched by both the German positivists and the American pragmatists: rationality developed for the species as an adaptive way to safeguard itself, and the individual exercise of rationality contribute to relieving emotional stress. With ANELLA (Associative Network with Emergent Logical and Learning Abilities), I have attempted to show how the utterance of sentences generates, out of necessity, a coarsely syllogistic mode of reasoning, while at the same time bringing peace to the speaker (Jorion 1989).

What, where, and how "big" is a word?

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Abstract: Hebb's theory of cell assemblies is a precursor of the neural network approach used as an implicit hypothesis by most contemporary neuroscientists. Applying this model to language representation leads to demanding predictions about the organization of semantic categories. Other implications of a Hebbian approach to language representation, however, may prove problematic with respect to both neurolinguistic concepts and the results of neuroimaging studies.

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The basis of Hebb's theory is a functional unit of neurons (the "cell assembly"), which becomes associated by coactivation in time. This association can occur between both adjacent and distant neurons. Excitatory input to one or a few neurons can be sufficient to activate all neurons in the assembly, a process called "ignition." Pulvermüller cites many neurophysiological studies of the visual cortex, showing that Hebbian neural cell assemblies may exist at a neuronal level. Pulvermüller goes on to postulate cell assemblies on the level of "groups of neurons," whose interaction is detectable with surface EEG or MEG techniques at a spatial resolution of several centimeters, but he says nothing about the size of these "groups of neurons" or of a cell assembly (e.g., what is the size of the circles in Fig. 3? Do they represent single neurons or groups of neurons? How many neurons do they consist of?). Assemblies for different stimuli may partially overlap; another dimension in localization uncertainty is thereby added to the concept. That certain stimulation paradigms can elicit high-frequency electrocortical responses in the EEG is not evidence for stimulus-specific cell assemblies because the same change in frequency response could have been evoked by several partially stimulus-specific cell assemblies, making it impossible to infer the number and spatial extent of the assemblies (e.g., Klimesch 1996).

Another problem that surfaces when applying Hebb's theory to language processing is predicting hemispheric representation of content words. One of the best documented results from neuroimaging studies (PET and fMRI) is the strongly lateralized left inferior frontal activation during verb generation tasks (e.g., Herholz et al. 1996; McCarthy et al. 1993; Warburton et al. 1996; and others). This is one of the most consistent and reproducible findings, despite variations in experimental design (most study protocols have used sophisticated hierarchical subtraction paradigms, e.g., Warburton 1996). These results were confirmed by comparing neuroimaging data with results from the Wada Test (Pardo & Fox 1993) and intraoperative mapping (Herholz et al. 1997). The verb generation task is probably the only paradigm that has ever been tested in a multicenter PET study for its reproducibility and sensitivity (Poline et al. 1996). Sensitivity is in general less a question of type-I error correction, as proposed in the target article, than of scanner type and data acquisition technique (see Poline et al. 1996). Moreover, studies using volume of interest approaches (Herholz et al. 1996; Thiel et al. 1998), which are subject to less severe type-I error correction than voxel-based statistics, have not reported right hemisphere involvement beyond superior temporal activations. Although Pulvermüller mentions some evidence for right-hemisphere involvement detected in fMRI studies, he does not cite any references.

Further evidence for the lesser role of the right hemisphere in language function comes from neuroimaging studies in aphasics. Although activation of the right homologue to Broca's area can be observed in aphasics (Ohyama et al. 1996; Weiller et al. 1995), recent follow-up studies (Heiss et al. 1997; Karbe et al. 1998) have demonstrated that the only patients who showed satisfactory recovery from aphasia were those who reactivated their left hemispheric language areas (especially the left superior temporal gyrus), in contrast to patients with persisting right Broca activation, as suggested by many neuropsychological studies (reviews in Cappa & Vallar 1992; Gianotti 1993). Moreover, the double dissociation noted by Pulvermüller between word processing problems in Broca's aphasics' agrammatism (predominantly problems with processing function words) and amnesic aphasics (problems with retrieval of content words) is evidence for different representations or sites of processing within the left hemisphere but not for a left-right axis, because both syndromes occur predominantly after left hemisphere lesions.

Another problem is the lack of theoretical foundation for the concept "word." Pulvermüller distinguishes phonological word form and word meaning (the latter being subdivided into further categories) and, to some degree, word function. From a psycholinguistic viewpoint, word representation and processing are much more complex. For example, according to the logogen model first described by Morton (1980), word form representation varies with whether it is phonologic or graphemic, and whether the process concerns word input or output. There is much evidence (from double dissociations) that these representations are distinct and can be selectively impaired (Marini & Blanken 1996; Patterson & Shewell 1987). Furthermore, each lexicon is supposed to have its own "buffer" for rehearsal processes (e.g., the "phonological loop," processed via Broca's area, according to Vallar et al. 1997).

By integrating these concepts, more distinct predictions about cell assemblies could be developed based on, for example, graphemic word form representation and processing and input versus output processing (as in lexical decision tasks [input] versus verb generation [output] experiments). Connectionist models and semantic networks consisting of semantic features interconnected with different associative strengths and activated by spreading activation mechanisms also have a long tradition in psycholinguistics (Collins & Loftus 1975; Murre & Goebel 1996) and are comparable to Pulvermüller's concept of cell assemblies (the neurons representing single features and the assemblies forming the specific combination of features of a single word). These models are not mentioned at any point.

An unanswered question concerns how different levels of attention can be integrated in the concept of cell assemblies. Pulvermüller's model assumes a sufficient level of attention to the word to be processed, so that the "entire assembly will be active" (sect. 2, para. 8). But, according to Craik and Lockart's (1972) "levels-of-processing" view, semantic information can be processed at different "depths" (the word "lemon" could arouse only the category "fruit," or also its taste, form, etc., or it could be recognized only as a word). Although Pulvermüller mentions that cell assemblies must be structured in a hierarchy of different levels of elaboration, he does not define in a specific case what "the entire cell assembly" represents, and which instance (like some higher attention system) controls the level to be activated.

Semantic typing via neuronal assemblies

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Abstract: One of the main aspects of a neurobiological theory of language is the problem of meaning (or semantic content) in the brain. A full explanation of meaning requires a combined approach to semantic typing and the semantic success of cerebral states or processes. Pulvermüller presents his Hebbian model of language in the brain (HML) as an account of semantic success. If his proposal turns out to be viable, however, it may also promote a theory of semantic typing.

Semantic typing versus semantic success. In his well-designed argument for a Hebbian model of language in the brain (HML), Pulvermüller suggests that word meanings are acquired by associative learning, so that "neurons related to a word form become active together with neurons related to perceptions and actions reflecting aspects of its meaning" (sect. 3.3). I shall argue that if this approach turns out to be theoretically viable, Pulvermüller's argument is too modest. This is because he seems to be content with a hypothesis about semantic success in a Hebbian account, although his theory might help to explain semantic typing, too. Bogdan (1989, p. 697) introduced the distinction between semantic success and semantic typing in his argument against Fodor's psychosemantics: "The analysis of semantic success tells us in what conditions a semantic type . . . applies or tokens successfully; it does not tell us what makes the type in question *semantic.*" To explain semantic typing (or the having of concepts) one would have to specify the internal constraints on the organi-

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zation of information processing that account for semanticity (or aboutness). This is a matter of "intentional design," of how information from the world is organized "in formats which allow the information to be about aspects of the world" (Bogdan 1989, p. 699). To explain mere semantic success (or concept application), it is enough to demonstrate under what conditions a concept tokens successfully. Hence, as an account of semantic typing, the HML would have to answer the question: "In virtue of what can brain states be about anything at all?" As a theory of semantic success, it would also show how (or, at least, *that*) the brain states *succeed* or *manage* to be about this or that. If a neurobiological model of language can only account for semantic success, it must be supplemented by an external explanation of semantic typing.

Although Pulvermüller is not completely explicit on this subject, in his section on word categories he seems to assume "meaning" as a linguistic concept (sect. 3.3) and to confine himself to a description of the "mechanism" (sect. 3.3.3) of its cerebral realization. Meaning (for concrete content word he just discusses reference) is a relation between the word and the token of the world it denotes (sect. 3.3.1), and the story of associative learning just describes how certain cerebral states come to represent both the word (form) and the accessible features of its referent. The question of what *makes* the internal mechanism a concept, that is, a type of state with aboutness, is neglected in favor of a description of the conditions of successful concept tokening. To see if the HML may contribute to a theory of semantic typing beyond this description of mere semantic success, I will take a closer look at Pulvermüller's analysis of concrete content words.

Hebbian semantic typing. Pulvermüller (sect. 3.3) implicitly clings to a causal theory of reference fixing, that is, he thinks the reference (or "meaning") of, for example, the content word "mouse" is learned by the build up of neuronal assemblies resulting from the combined appearances of visual or other sensory perceptions of real mice and the word form "mouse," perhaps in a setting of ostensive definition. Frequent coactivation of word-form assemblies and perception-and-action-related referential assemblies leads to a compound phonological-semantic assembly (the "higher-order assembly," HOA), which can hitherto be "ignited" by exclusive inputs to the phonological or semantic part of the representation. The HOA combines represented features of a word with those of the object it denotes and thus strongly resembles Freud's (1891) pioneering model of the "Wortvorstellung." If the semantic part of the HOA is the semantic information structure of the HML, then the special feature of the HML is that this information structure is systematically correlated not only with types of items in the world, but also with the phonological features of the word that denotes this item type, namely "mouse." This HOA can be understood as the cerebral correlate of the mouse-concept or semantic type (more clearly, one would talk about a "mouse-proto-concept," because the concept of a mouse comprises more than just reference).

Pulvermüller's covariance does not hold between a mouse and a mouse-assembly, but rather between a mouse (or the word form "mouse") and an HOA. This would enable him to work out Hebbian hypotheses on semantic typing in addition to semantic success. For example, what makes the mouse-concept semantic are the internal constraints of associative learning in neuronal assemblies together with the causal history of acquisition of the mouse-HOA that establishes an internal connection between an object-representation and a word-representation. And the same totality of conditions prepares a platform for turning information *from* the world into information *about* the world: Once the HOA is established, mouse-related information from the world will "ignite" it and thus transform the further processing of this information into the cognitive context. What finally makes it information *about* the world is that it is cognitively handled as a concept, that is, the activated HOA has to be integrated into groups of related semantic HOAs as well as HOAs serving other than semantic cognitive functions. The architecture and interactions of these patterns of HOAs would have to be spelled out in a Hebbian fashion.

As indicated above, questions of general theoretical consistency have been left open here. For example, a purely causal account of meaning may be insufficient for the explanation of how cognitive systems come to acquire meaning in the first place; this may call for a consideration of motivational or even teleological features at the roots of intentionality. But Pulvermüller's theory of the HML may well be compatible with a philosophical approach to the conditions of meaning acquisition that differs from the purely causal one.

Unifying cell assembly theory with observations of brain dynamics

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Abstract: Empirical evidence suggests that high frequency electrographic activity is involved in active representation of meaningful entities in the cortex. Theoretical work suggests that distributed cell assemblies also represent meaningful entities. However, we are still some way from understanding how these two are related. This commentary also makes suggestions for further investigation of the neural basis of language at the level of both words and sentence planning.

This target article is a major contribution to neurolinguistics. Pulvermüller's arguments span many levels, from fundamental aspects of cell assembly theory, via neuro- and psycholinguistics, to the very complex aspects of experimental design (to say nothing of the actual psychophysiological techniques he uses). At the same time, the author maintains a degree of detachment from the actual results obtained, so that he does not overstate his case. It is clear that the conclusions reached require more and better controlled experiments before they are firmly established. Nevertheless, a strong case is mounted that the theory of cell assemblies (and others of Hebb's ideas) provide an important way of understanding word processing by the brain.

There is one area where Pulvermüller's arguments do not seem completely convincing, although this does not undermine the overall argument in a fundamental way. This is the "how" question: I accept the *empirical* evidence that coherent, mainly high frequency EEG activity can indicate activation in the brain of the representations of meaningful entities. At the *theoretical* level I also regard the cell assembly concept as our best model for the representation of those meaningful entities. However, I think we are some way from a fully rigorous view of the relation between the theoretical and the empirical accounts of the representation of meaning in brain dynamics. I am not convinced by the argument that high frequency EEG activity is the *necessary* consequence of maintained activity in cell assemblies. My doubts arise from both factual and theoretical considerations. In terms of fact, as Pulvermüller admits, we simply do not know the repertoire of conduction delays in axons connecting cortical loci a few centimetres apart. In the work of mine cited (Miller 1996), much longer conduction times were assumed to be common than are assumed in the target article. This issue is likely to have an important influence on the frequency range of activity generated by active cell assemblies.

This brings me to the theoretical uncertainty. The formalization of cell assembly theory is, to the best of my knowledge, not sufficiently developed to determine what exactly this influence would be. For example, one may ask: What is the quantitative relation between the patterns of neuronal activity in neurones, the repertoire of conduction delays between neurones, and the frequency and relative timing of activity in the different neurones in an active cell assembly? What is the number of neurones present in a cell assembly and the degree of their synchrony when the assem-

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bly is active? I suspect that these large questions have not yet been adequately addressed, or if so, the work is not widely known. Until agreement has been reached on these matters, we cannot predict the EEG signs to be expected of activity in cell assemblies.

Apart from this, I would like to make two suggestions for expansion of the cell assembly approach to neurolinguistics developed by the author.

(1) As pointed out by Pulvermüller, experimental analysis of the brain's representation of word types can be taken much further than described here. One such subdivision comes to mind, which might generate feasible experiments. Most "concrete" words refer to visual objects, and from basic neurobiological principles, would have a representation in the right as well as the left hemisphere. However, a few concrete words refer to *sounds,* whose temporal characteristics are not unlike those of speech. These are words such as "babble," "whistle," "clatter," and so on. The names of many common birds may also have associations that are primarily of this auditory type (because we hear, but rarely see them). Such concrete words should have a representation confined much more to the left hemisphere than do concrete words referring to visual objects. Whether this idea could be defined with sufficient specificity to allow a well-controlled experiment to be carried out would be better judged by the author than by me.

(2) The last section, on syntax and grammar, was an interesting venture into new territory. I would like to suggest a way of approaching the neural aspects of such high level linguistic features in terms of cerebral laterality. There is a variety of evidence that the "meaning of a sentence" is represented in the right hemisphere. This comes from the effect of unilateral brain damage on a subject's appreciation of things like metaphor, humour, or indirect inferences in sentences (see Miller 1996, pp. 199–200). Such meaning, accumulated over the span of a sentence, appears to be a form of Gestalt, which, like visuospatial Gestalts, has a predominant right hemisphere representation. Such Gestalts have complex "simultaneous" structure, but no temporal structure. Syntax and grammar, on the other hand, involve the finer temporal structuring of linguistic elements (including word endings, function words, word order, etc.) and this is probably a left hemisphere function. Fluent speech is presumably achieved by a synergy of these two aspects of sentence planning, the right hemisphere providing the semantic framework for the sentence (a slow succession of Gestalt-like ideas), while the left hemisphere coordinates the finer structure of the actual words in the sentence. If so, one would expect interhemispheric communication via the callosum to be required for coordinating the two aspects of sentence planning. Although this is a preliminary hypothesis at present, it may be capable of generating incisive experiments on the neural basis of higher-level discourse planning.

Words – sentences = ?

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Abstract: Pulvermüller advocates an experimental design in which well-matched tokens from various word categories are presented in list form to subjects making rapid lexical decisions about these stimuli. Implicit in this paradigm are several problematic assumptions. We conclude that such experiments are not likely to tell us much about the biological bases of human language.

Pulvermüller seems to believe that our chances of understanding the biological bases of human language will improve dramatically if we remove the contaminating effects of sentences and carefully measure the biological response to isolated words. In Pulvermüller's words:

> If words are presented in sentences or in sentence-like word strings, it may well be that not only the effect of a stimulus word is seen in the neurophysiological response, but a complex blend of the effects of the critical word, its preceding words, and their semantic and syntactic relations. The various context effects may therefore either artificially produce word class-difference, or they may mask real processing differences between word classes (sect. 4.3).

Pulvermüller cites Pulvermüller et al. (1995a) as an example of the type of experimental design he is advocating. In this study, words from the function and content categories were carefully matched (in frequency, length, etc.) and presented in lists. Subjects made rapid lexical decisions to these stimuli.

Implicit in this paradigm are several problematic assumptions. The first is the assumption that the absence of a sentence context does away with context altogether, thereby eliminating a primary source of "contamination" in learning about the biological response to words themselves. But linguistic context is not the only potentially contaminating type of context: Words (or any other stimulus) are *always* presented in some sort of context – linguistic, task, stimulus, social, environmental, and so forth. For example, by having subjects make lexical decisions, Pulvermüller et al. introduced a context that might have profoundly altered the response to these words.

A second questionable assumption is that by presenting words in isolation, one has also isolated the properties of "wordness" that one wants to study. Distinctions between content and function words and among the grammatical categories noun, verb, article, and so on, are primarily defined with respect to the different *functions* that words play *when in sentences.* The epistemological basis for expecting these different functional roles to manifest themselves when words are presented outside this functional context (i.e., in word lists) is not clear to us.

Third is the assumption that by matching words along potentially confounding dimensions, one has succeeded in isolating the difference of interest. It is, alas, *futile* to try to match word categories on all relevant dimensions (in part because it is impossible to identify all the relevant dimensions). The implication is that there will always be other variables in addition to word class that are correlated with this factor and perhaps causally related to any observed differences between conditions. But the problem is even more severe than that. Even if one were to do so successfully, matching stimuli in this manner would not produce the experimental paradigm that allows inferences about differences between word classes. Why not? Because the very nature of stimulus selection has severely limited the scope of the allowable inference. The logic of statistical inference tells us that randomly sampling larger and larger numbers of words from the two categories should produce progressively more reliable differences, if such differences exist in the sampled populations. However, what Pulvermüller is in effect advocating is a *nonrandom sampling of fewer and fewer items from these categories.* The end result is two lists that are not representative of the categories of interest.

Given these considerations, is it surprising that a survey of the word-class literature reveals a remarkable pattern of inconsistency? Restricting ourselves to a few representative event-related potential (ERP) studies in which word lists were presented, we find that Garnsey (1985) found no differences in the ERPs to content and function words, and Pulvermüller et al. (1995a) found that the two word classes both elicited negativities with peaks around 160 and 200 msec, respectively, but that these peaks were left-lateralized for function words only. Osterhout et al. (1997) found that function words elicited a left-lateralized negative peak at 350 msec and content words elicited a right-lateralized negativity peaking at 400 msec.

Pulvermüller suggests that these disparate results are caused by inadequate controls in most studies. We offer an alternative interpretation: Having removed words from the only context in which the word-class distinctions have relevance, the varying results reflect little more than the specific stimuli presented and the

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influence of the various task contexts on these stimuli. Our contention is that when sentences are subtracted from words, the nature of the residual is not clear. Observed differences might have more to do with associative memory than with language (e.g., some words have associations to visual experiences whereas others are associated with motoric experiences).

The approach called for by Pulvermüller can be contrasted with that taken by Osterhout et al. (1997). We contrasted ERPs to words when they appeared in normal text and in a randomized version of this text. Rather than attempting to control word frequency and length, we allowed these factors to vary naturally. This design allowed us to determine whether word-class differences were consistent or inconsistent across text conditions. Furthermore, by correlating length and frequency with any observed ERP differences across word class, we could determine the strength of the relationship between these factors. We found that the most salient difference between word classes (the latency of a negative-going component that peaked between 280 and 400 msec) was highly correlated with word length and frequency; these factors accounted for more than 90% of the latency variance in many subjects. This result was obtained regardless of text condition. But suppose we had found striking differences as a function of text condition. Should we then accept the word list results as more representative of the "true" differences between word classes? We think not, for the reasons noted above.

Most of the interesting properties of human language (including the word-class distinctions) apply to words in sentences and larger discourses. A neurobiological model of isolated words and their associations is not a neurobiological model of language. Pulvermüller might respond by claiming that we have taken his quotation out of context, thereby obscuring its meaning and purpose. He would be right. Which is, of course, our point exactly.

Flexible neural circuitry in word processing

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Abstract: ERP studies have shown modulation of activation in left frontal and posterior cortical language areas, as well as recruitment of right hemisphere homologues, based on task demands. Furthermore, blood-flow studies have demonstrated changes in the neural circuitry of word processing based on experience. The neural areas and time course of language processing are plastic depending on task demands and experience.

Pulvermüller's target article makes several very valuable points. First, it indicates the centrality of the learning process, and the multiplicity of cortical areas involved in the analysis of words. Second, it suggests that brain-based word categories may be different from a priori definitions based on grammatical distinctions. Third, it takes seriously data that provide both accurate localization (from blood flow and metabolism) and time course information (from electrical and magnetic activity) in the analysis of the neural circuitry of word processing.

We will concentrate our comments on processes involved in word generation and we hope to clarify some of the issues raised in the target article. In the spirit of this Hebbian account, the networks involved in word processing ought to have quite separate input areas for processing different modalities, but similar neural areas for semantics and phonology. Although there is some dispute about the exact areas involved, it seems clear overall that similar neural areas process semantics and output regardless of the input modality. Moreover, the circuitry involved is flexible, and depends on task demands and experience.

Consider the left inferior frontal area. It appears to be active not only during the generation of uses, but in monitoring semantic categories (Posner et al. 1988), in classifications such as animate/inanimate (Demb et al. 1995), and manufactured versus natural (Abdullaev & Posner 1998). There is evidence from cellular data (Abdullaev & Bechtereva 1993) and from scalp electrical recording that the activity in this area begins 200 msec after the input of a visual word. The more posterior activity also found in semantic tasks tends to appear much later (Posner & Pavese 1998). The time course information can be important in attempting to go from activation to function. Skilled readers fixate a word for only 250–300 msec. Abstraction of the word meaning occurs during this brief time (Sereno et al. 1998) as the distance of the next saccade depends on the meaning of the currently fixated word. This suggests that the frontal activity may convey information on lexical meaning to the eye movement system.

Pulvermüller argues that a double dissociation would be better than subtraction in indicating how a brain area might be related to function. In our studies we have expanded the subtractive ideas, in the direction suggested by Pulvermüller, by using identical lexical items to study different neural loci dependent on task demand. We examined dissociations by asking subjects to press a key if a word was manufactured and fit into a sentence frame (Posner & Pavese 1998). Whereas lexical tasks activated frontal areas, sentential tasks activated posterior areas as suggested by the time course data. Moreover, the ordering of the two tasks modulated the frontal and posterior activations. Besides this temporal modulation, the left frontal activity seems to be dependent upon both task demands and stimulus presentation (Price et al. 1994). We suggest that, depending on the task and processing, selective and flexible activation of cortical areas associated with word processing can occur.

The lexical access system proposed by Pulvermüller, which necessitates simultaneous access of the phonological and semantic code, is too rigid. For example, in passive viewing of a word compared to fixation (Petersen et al. 1988), no activity was found in the left frontal or posterior sylvian areas that Pulvermüller argues automatically decode the phonology of a visually presented word. Furthermore, neurological deficits have demonstrated that phonological impairments can occur in the absence of reading (e.g., Coltheart & Coltheart 1997) or writing deficits (Shelton & Weinrich 1997). Access to semantic meaning also occurs in the absence of normal phonological processing (see Coltheart 1996). For example, a patient may read the word "*yacht*" as "*ship*" (Shallice 1988) demonstrating phonological deficits with intact semantic meaning. Behavioral data has also suggested that phonological information demonstrates little to no priming in the processing of either picture or word meaning under both short and long stimulus onset asynchronies (Damian & Martin 1998). Recent evidence suggests that phonological access occurs not automatically, but rather when the parameters of the experiment encourage the use of phonological information (Verstaen et al. 1995).

Pulvermüller very accurately suggests that event-related potential (ERP) studies have often provided evidence of right hemisphere activity. Although blood flow studies have not shown entirely left hemisphere activity (e.g., Price et al. 1994), they are more lateralized than the ERP data. In our studies (Abdullaev & Posner 1997), we have shown two conditions where right hemisphere activity becomes prominent. Subjects practiced a list of 100 items and were asked to give the same response to an item. After the first time through the list, we found right frontal activity that we attributed to retrieval of the previous episode (see Tulving et al. 1994). We then asked subjects to give novel responses to the same list. The left posterior activity was still present, but a right homologue was added for generating the novel response. These results suggest that right hemisphere activity can be recruited to aid word processing. This result is reminiscent of behavioral studies demonstrating a role for the right hemisphere in distant associations (Chiarello 1998). The neural circuitry and cognitive processes involved in word processing are more flexible than a single, rigid Hebbian representation for each word. For example, blood flow studies of this same task have suggested that the neural circuits that take over for a well-practiced list differ from those for a novel list (Raichle et al. 1994).

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The combined data from the above studies suggest that the areas involved in processing words can change based on experience, task demands, or strategy. We find the idea of activation of multiple cortical areas as a Hebbian representation important, but we wish to stress that both the areas and time course of these activations are somewhat plastic, depending on task demands and experience.

Only time can tell – words in context

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Abstract: We raise the possibility that the roles words typically play in sentence context, rather than their motor or visual associations, determine the organization of language in the brain. We also discuss time-sensitive functional imaging approaches that allow experimentation both on isolated words and connected language.

Language learning begins as a receptive process of connected speech flow, with no set rules or principles about how to analyze it, or any knowledge of the relevant categorizations. Learning language as a system of connected structures rather than as lists of words may have important consequences for the functional organization of the brain: the separation of words into categories like living versus nonliving objects and nouns versus verbs, as cited in the literature on aphasia, could emerge from the distinct roles these word types typically have in a sentence context, rather than from their motor or visual associations, as suggested by Pulvermüller. The importance of context is supported by simulations where simple three-word sentences (Ritter & Kohonen 1989) and complete Grimm's Fairy Tales (Honkela et al. 1995) were used as input to an artificial neural network, providing with each word only the word immediately preceding and immediately following it. The result was a self-organized map with distinct clusters of nodes representing animate objects, inanimate objects, verbs, function words, and so forth.

The target article emphasizes motor and visual associations of isolated words in studies of language organization in the brain. However, isolated words are both rather unnatural and somewhat ambiguous as stimuli. If there is no predetermined context, the human mind readily creates one. For example, the word "mouse," presented in isolation in PET, fMRI, EEG, or MEG experiments, can evoke quite arbitrary associations (and corresponding brain activations), such as a mouse seen in a picture, sensation of stroking a pet mouse, the sound of a mouse running on the floor, and so on, which may certainly all be considered semantic, but only in a fairly broad sense.

Time-sensitive imaging techniques like EEG and MEG allow focusing on brain processes associated with an analysis of words both in isolation and in context. Following the presentation of isolated words, the left superior temporal cortex is active 200–600 msec after word onset (Salmelin et al. 1996), which could reflect phonological processing, in agreement with Pulvermüller's view (sect. 3.3, para. 1). However, when one performs the classical N400 paradigm, where the semantic appropriateness of the final word of the sentence is varied (Kutas & Hillyard 1980b), using MEG, the same left superior temporal region shows systematic dependence on the semantic congruity of the sentences (Helenius et al. 1998). The left perisylvian activation accordingly, cannot be interpreted as solely phonological because it obviously has a strong semantic component.

Furthermore, EEG and MEG make it possible to mark different types of words within connected text or speech and to average brain responses to the selected categories. One can thus separate classes according to their motor or visual associations, whether they are living or nonliving, according to their role in the sentence (subject-verb-object), or according to any other criterion, and let the brain show whether it is particularly sensitive to one or the other division. Differences in processing could express themselves in location, timing, or activation strength. Obviously, these results can be compared with brain activations evoked by the same words presented in isolation. The spatial and temporal resolution of stimulus-locked MEG responses should also allow Pulvermüller to verify or dismiss his theory of language learning: Word processing in deaf (no auditor input) and blind (no visual input) subjects appears critical in this context (sect. 3.1, para. 2).

Pulvermüller emphasizes the role of EEG and MEG essentially in the analysis of gamma band rhythmic activity (sect. 6). Although cortical rhythms are certainly a very interesting and potentially important part of brain function, caution may still be warranted in interpreting them. For example, the higher gamma band activity seen in the left temporal cortex in response to real words (in contrast to pseudowords; Fig. 8) was interpreted as a reflection of "additional high-frequency neuronal processes not involved after pseudoword presentation" (sect. 6); however, this difference arose from a suppression following pseudowords and the essentially stable activity level for real words, which makes the interpretation somewhat ambiguous. Also, single-cell and even multi-unit recordings are conceptually almost as far from the macroscopic EEG and MEG measures as interactions of a few particles are from temperature or pressure. Reverberation of activity between neuronal populations within a cortical region of a few square centimeters could well result in a cancellation of the macroscopic signal or a summation of the signals to show an overall higher level of activity, with no obvious oscillatory content.

In conclusion, presenting isolated words as visual or auditory stimuli, or producing them, are useful tools for studying cognitive processes. However, this may not be the way language is organized in the brain: Some linguistic distinctions or classifications we make may be totally irrelevant for the brain, or their apparent existence may be only an emergent property of the underlying network (as the Grimm's tales example shows). Making use of the many imaging techniques currently available and, with an open mind, allowing the individual brains to inform us about their function, it seems possible to find solid answers to how the brain perceives and produces language. Time will tell.

Bihemispheric representation, foveal splitting, and visual word recognition

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Abstract: Pulvermüller's account of lexical representation has implications for visual word recognition, given the claim we make that a foveally presented word is precisely split and contralaterally projected to the two hemispheres, and that this splitting conditions the whole process of visual word recognition. This elaboration of Pulvermüller's account raises issues of hemispheric differences and collaboration.

In this commentary we examine implications for visual word recognition. Although stored lexical representations may be rather more labile than Pulvermüller suggests, given the plasticity of even somatosensory coding (cf. Elbert et al. 1995), the claim remains that content words are represented bihemispherically as an orchestration of activity in functionally different parts of the brain that are relevant to the individual word. This account raises two related issues: How is the (visual) stimulus itself to be incorporated into this account, and what is the division of labour between the two hemispheres?

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Normally, for a range of activities, the two hemispheres cooperate in processing. There are differing hemispheric propensities, and even examples of apparent exclusivity of processing (expressive phonology is relevant to current concerns); the general case, however, is that each hemisphere is capable of conducting a particular processing task in some fashion, but that cooperation produces a superadditive effect.

When a word is read, it is typically fixated somewhere within its length. It is now clear that a word falling across the fovea is initially split precisely about the vertical midline and the two parts are then contralaterally projected to the respective hemispheres, rather than being directly projected bilaterally; bilateral projection of the fovea occurs in many animals, but not in humans (see Brysbaert 1994; Shillcock & Monaghan 1998a, for review and discussion). It is also clear that processing directly relevant to word recognition begins prior to any potential complete sharing or copying of information between the two hemispheres. We argue that this initial splitting of a word conditions the processing of written words and demonstrate that it provides a coherent account of data concerning the privileged processing of the outside letters of words, the optimal fixation point, and the principal subtypes of dyslexia (Shillcock & Monaghan 1998a; 1998b). Coordinating the two parts of a word requires callosal transmission. Theorising about such transmission requires an appreciation of the computational task of identifying one word out of 50,000+ words in the lexicon. We show that a word split at or near its optimal fixation point is divided into two independently maximally informative parts, and that such a splitting of a word is in fact an informationally attractive starting point for word recognition. Within this account, the initial splitting is taken to persist, such that the ipsilaterally presented part of the word is represented in each hemisphere with less speed, accuracy, or authenticity and that the two hemispheres cooperate, each concentrating at least initially on the relevant, contralaterally presented part of the word. In the normal case, callosal transfer then involves orthographic/graphemic and semantic information; in the impaired case, interhemispheric coordination is desynchronised and transfer may rely more on semantic information.

Pulvermüller's account of lexical representation may be extended to accommodate the fact that different parts of a word are projected to different hemispheres: the *pl* and *an* of *plan* are projected to the right and left hemispheres respectively, given a typical central fixation. (We ignore here the need to accommodate the presentation of a word in a single hemifield.) This distribution of visual information will interact with the existing hemispheric differences discussed by Pulvermüller. As one example of the implications of this analysis, consider the case of deep dyslexia, in which an abstract word may typically be misreported as a more concrete word. If dyslexia involves desynchronisation of the two hemispheres (see, e.g., Davidson & Saron 1992), then the RH (right hemisphere) functions more independently than in the normal case, partially activating its own semantic hypothesis on the basis of the part of the word viewed. The relative specialisation of the RH for concrete words biases the representations it creates toward that type of word and means that an incorrect identification, arising from the two hemispheres comparing their partially activated semantic representations, is moved in the direction of being a more concrete word. Thus, *plan* may be misreported as *flan* (involving an orthographic error, too). This account echoes Coltheart's (1980) right hemisphere hypothesis concerning deep dyslexia.

In conclusion, the reasoning behind Pulvermüller's account of lexical representation may be usefully grounded in the anatomical details of visual processing in the case of visual word recognition.

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Early effects of semantic meaning on electrical brain activity

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Abstract: When words are read, the visual cortex is activated, independent of whether visual or motor associations are elicited. This word-evoked brain activity is significantly influenced by semantic meaning. Such effects occur very early after stimulus presentation (at latencies between 80 and 130 msec), indicating that semantic meaning activates different neuronal assemblies in the human visual cortex when words are processed.

Pulvermüller reviews results on how electrical brain activity and metabolic measures reflect the processing of words in the human brain. The content and meaning of semantic input, it is claimed, determines which cortical areas are activated: Whereas words referring to motor action yield activation that includes neurons in the motor cortices, words representing visual stimuli activate neurons in visual areas. Thus, differences in activated brain regions and processing should depend on whether stimulus material elicits visual or motor associations.

I wish to draw attention to the fact that, in addition to the effect of the content of a given word, the presentation mode of semantic stimuli is crucial. As expected, reading words will activate the visual cortex. Such word-evoked brain activity is significantly different from that evoked by meaningless stimuli, however (Skrandies 1998). Components reflecting processing in primary visual areas demonstrate the activation of different neural assemblies by meaningful material. Most important, neuronal activation during reading is very specific, as different semantic meaning yields different electrical brain fields. The connotative meaning of words can be quantified by the semantic differential (Osgood et al. (1957; 1975), and Skrandies (1998) showed how words belonging to Osgood's classes of "evaluation," "potency," and "activity" activate different neuronal populations in the visual cortex. In this study, 22 healthy adults were examined using word stimuli that had been matched for length and frequency of occurrence, and only connotative meaning was varied systematically. The results indicate that semantic meaning affects the pattern of activation within the human visual cortex when stimuli are read by the subjects, and this specific activation is not restricted to words that elicit visual associations.

It is important to note that most effects of semantic meaning and the activation of different neuronal assemblies occur quite early after stimulus presentation, between 80 and 130 msec (Skrandies 1998). This is in contrast to numerous studies that are also mentioned in the target article. As described in Pulvermüller, section 7 in lexical decision tasks, differences in evoked activity between words and pseudowords are not seen before 200 msec after stimulus onset (Pulvermüller et al. 1995a), and most word class-differences occur around 200 msec post stimulus onset. In a similar line, effects of content and function words were reported with components at 280 and 350 msec latency (reviewed in sect. 5.1).

At first sight, very early semantic effects may come as a surprise because most electrophysiological experiments using linguistic material have reported much larger latencies (e.g., Kutas & Hillyard 1980b; Pulvermüller, target article). Experiments on reading, however, illustrate that language processing is a rapid process because subjects are able to read and comprehend more than 1,000 words per minute. During normal reading, most of the time is needed for programming and the execution of saccades (Epelboim et al. 1994). When rapid serial visual presentation is employed (Potter et al. 1980), processing time drops to 51.3 msec per word for aloud oral reading, and it decreases to 36.3 msec per word with silent reading (Rubin & Turano 1992). This indicates that human subjects are able to comprehend words very rapidly. Although reading times cannot be equated with latencies of elec-

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trophysiological components, this rapid processing agrees with the finding of early semantic effects in brain mapping experiments (Skrandies 1998). Components of brain activity evoked by visual input with latencies on the order of 100 msec certainly reflect cortical activation, as has been demonstrated by studies using dynamic random dot stereograms that are processed only after binocular fusion in the human visual cortex (Skrandies 1991; 1997). With human intracranial recordings one finds that the earliest signals from the retina can reach the striate cortex with latencies smaller than 50 msec (Ducati et al. 1988), a finding that is in line with intracranial source location data (Pascual-Marqui et al. 1997). In addition, studies on discrimination of meaningful material have shown that components with latencies of about 100 msec are sensitive to task relevance and stimulus type (Skrandies 1983; Skrandies et al. 1984).

In summary, there is ample evidence that words are processed in visual cortical areas of the human brain very shortly after stimulus presentation, independent of possible visual associations elicited by semantic meaning.

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On computational and behavioral evidence regarding Hebbian transcortical cell assemblies

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Abstract: Pulvermüller restricts himself to an unnecessarily narrow range of evidence to support his claims. Evidence from neural modeling and behavioral experiments provides further support for an account of words encoded as transcortical cell assemblies. A cognitive neuroscience of language must include a range of methodologies (e.g., neural, computational, and behavioral) and will need to focus on the on-line processes of real-time language processing in more natural contexts.

Understanding the interaction between the perceptual modalities and the cortices that subserve them is a goal that has too long played second fiddle to the more popular goal of "finding the boxes in the head." Although many perceptual/cognitive functions exhibit some degree of cortical localization, the continuous communication between these "modules" is at least as important as their anatomical separation. Indeed, if Pulvermüller is right about the Hebbian transcortical cell assembly being the brain's primary "unit of representation," then a solitary punctate region of cortex whose averaged activity correlates with a broadly defined class of perceptual/cognitive tasks may *not* be especially relevant for understanding perception and cognition. Instead, what we should study are more specific environmental instances (ecologically valid combinations of stimuli) and sequences thereof, and *the multiple cortical regions that participate* in representing those environmental instances.

Pulvermüller's shortcoming is that he unnecessarily limits his evidence predominantly to one methodology (neuroimaging), when a wide range of methodologies provide insight into "words in the brain's language." This commentary points to the relevance of two areas of cognitive neuroscience that Pulvermüller barely mentions: neural modeling and behavioral experiments. By also looking at computational and behavioral results, one can see a more complete picture of how a proposal like Pulvermüller's may be manifested at multiple levels of description: from the individual synaptic weights that *produce* the cell assemblies to the motor output that *is produced by* the cell assemblies.

Neural networks. If Pulvermüller's proposal is correct, it indicates that one's representation of a word includes multi-modal information not traditionally considered linguistic (e.g., perceptual features, motor routines). He suggests that our mental representation of a word might best be described as a pattern of activation widely distributed across a disparate set of information processing units. In the field of neural networks, this notion of a "distributed representation" has made significant advances since Hebb's original thesis (far more than is implied by Pulvermüller's brief nod to the neural network literature; Gutfreund & Toulouse 1994).

As far as they go, the neuroimaging results are substantial. However, the descriptions of the physiology of these cell assemblies, the spread of neural activation throughout them, and their temporal dynamics, are left somewhat vague and impressionistic. This is, of course, less a criticism of Pulvermüller's review than a reflection on the lack of precision of current neuroimaging techniques. These limitations will undoubtedly be somewhat remedied with improved technology. For now, though, further insight into these more specific issues can come from the study of biologically plausible artificial neural networks. Far more in-depth analysis and experimentation can be performed on artificial neural networks than will ever be possible with real brains.

Of particular interest are attractor networks, which represent words as distributed representations and have some temporal dynamics leading to the full ignition of a cell assembly (McRae et al. 1997). Moreover, models that can integrate sensory information from separate modalities during learning (de Sa & Ballard 1997) can provide examples of possible developmental trajectories for Hebb-inspired accounts of lexical acquisition.

Behavioral experiments. As important as it is to "zoom in" on the subcomponents of the cell assembly, we also need to see the "wide angle" view that includes what neural representations are good for: behavior. Of course, some behaviors are better than others at elucidating the temporal dynamics of a cell assembly attempting full ignition. For example, Munakata et al. (1997) use a developing distributed representation to explain how some infants who are still making the classic A-not-B error in their *reaching* behavior actually show signs of being aware of the correct solution in their *eye movement* behavior. Behaviors, such as eye movements, that are sensitive to probabilistic information can provide converging evidence on the partially activated representations (cell assemblies) that are computed in real time while the brain gravitates toward a stable state to encode an environmental instance.

As another example, when adult participants are instructed to "pick up the candy," they never *reach* for incorrect objects, but they often *look* at incorrect objects whose names have similar phonology such as a candle (Tanenhaus & Spivey-Knowlton 1996). Additionally, as Hebb himself predicted, oculomotor representations are activated when participants are imagining an event or remembering an object. While listening to a story about a train going past, participants made predominantly horizontal eye movements; and when asked to recall a missing object on a grid, there were eye movements toward the vacated square (Spivey & Geng 1998).

Summary. To study anything in "the brain's language," we must be as opportunistic with *our* information sources as the brain is with *its*. We need convergence of methodologies. We need to map out in detail the cycle from perception to action. In contrast to neuroimaging, neural modeling simultaneously allows the spatial and temporal resolution necessary to explore how a particular cell assembly might approach its stable state over dozens of timesteps (Tabor et al. 1997). Moreover, behavioral experiments allow us to observe the pragmatic consequences of these cell assemblies, realized as motor output grounded in the same environment as the original perceptual input, thus completing the cycle.

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The neurobiology of knowledge retrieval

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Abstract: Recent investigations have explored how large-scale systems in the brain operate in the processes of retrieving knowledge for words and concepts. Much of the crucial evidence derives from lesion studies, because word retrieval and concept retrieval can be clearly dissociated in brain-damaged individuals. We discuss these findings from the perspective of our neurobiological framework, which is cited in Pulvermüller's target article.

The issue of how large-scale systems in the brain operate in the process of retrieving knowledge for word forms and for the concepts those word forms designate has been vigorously investigated in recent years. It has been spurred by intriguing and sometimes counterintuitive findings indicating, for example, that distinct neural systems may be relatively specialized for the retrieval of knowledge relating to different grammatical classes (e.g., words for concrete entities versus words for actions), levels of specificity (e.g., words for unique entities versus words for nonunique entities), and conceptual categories (e.g., words for animals versus words for tools); that within a particular domain of knowledge (e.g., unique entities such as persons and places), the neural systems that operate word form retrieval may be distinct from those that operate retrieval of concepts; and that the relative segregation of such neural systems varies considerably from one knowledge domain to another (e.g., the segregation appears to be minimal for actions and tools, and maximal for unique entities). These findings have prompted new theoretical accounts anchored to neural, linguistic, and psychological constraints.

Pulvermüller has chosen to base his discussion on evidence from functional imaging (PET, fMRI), ERP, and EEG/MEG studies, as these approaches have yielded valuable clues about knowledge retrieval. The lion's share of the evidence, however, still derives from lesion studies, and it is important that such evidence not be given short shrift. In regard to some of the most challenging questions, the lesion approach actually offers unique possibilities. For example, consider the distinction between retrieval of concepts versus retrieval of words. Simply put, there is a difference between knowing and retrieving the meaning of a concept (its functions, features, characteristics, relationships to other concepts), and knowing and retrieving the name of that concept (the specific word form). We have emphasized this distinction (Damasio 1989c; 1990; Damasio & Damasio 1992; 1993; 1994; Damasio et al. 1990; 1996; Tranel et al. 1997a; 1997b; 1998), as it has crucial implications for the neurobiology of knowledge retrieval; it can be difficult to interpret the results of studies in which "naming" and "recognition" are not clearly separated.

The evidence to support this distinction, which is by now quite powerful, derives almost exclusively from studies of brain-damaged subjects, and there is a straightforward reason why this happens to be the case. Normal subjects, when exposed supraliminally to a particular stimulus – say, for example, a picture of Bill Clinton, or a line drawing of a pitchfork – engage processes aimed at retrieval of both concepts *and* words. In fact, one cannot willfully stop one's brain from attempting to retrieve the word form along with the meaning. In brain-damaged individuals, however, the two processes can be clearly dissociated: subjects may have a profound inability to retrieve word forms and yet retrieve meanings normally. Traditionally, this has been characterized as a dissociation between naming and recognition (Damasio 1990; Damasio et al. 1990; Goodglass et al. 1997; Hart & Gordon 1992; Hillis & Caramazza 1991; Humphreys et al. 1997; Warrington & McCarthy 1994; Warrington & Shallice 1984). Our point is that lesion studies permit the unequivocal teasing apart of brain-behavior relationships that cannot be dissociated easily in normal subjects.

Pulvermüller correctly points out that the Hebbian concept of cell assemblies constituting functional units, and neural networks subserving associative memory, has influenced modern large-scale neuronal theories of language and other cognitive functions. However, with regard to our current framework emphasizing the key role of "third-party" (what we term *intermediary* or *mediational*) neural units for knowledge retrieval (see Damasio & Damasio 1994; Damasio et al. 1996; Tranel et al. 1997a; 1997b), Pulvermüller is unsure how such a system could be explained by associative learning or other biological principles. We would like to clarify the issue.

The intermediary neural sites operate as implicit catalysts for the explicit retrieval of varied aspects of knowledge that are necessary and sufficient to constitute a mental representation of the concept or word form. The retrieval of explicit aspects of knowledge occurs in temporally correlated fashion, but in separate early sensory cortices. We do not believe that the explicit mental representation of concepts or word forms occurs at the intermediary sites, or that the sites constitute "centers." Rather, each site is seen as part of a multicomponent system, each part containing neurons and circuitry necessary for the optimal retrieval of concepts and word forms.

The process would work as follows. When a stimulus depicting a given entity (say, a hammer) is shown to a subject, an intermediary region becomes active and promotes the explicit sensorimotor representation of knowledge pertaining to the hammer, which occurs in certain early sensory cortices and motor structures. This constitutes the conceptual evocation for the given tool. This in turn activates a different intermediary region, which promotes (in the appropriate sensorimotor structures) the explicit representation of phonemic knowledge pertaining to the word form that denotes the given tool. The process can operate in reverse to link word form information to conceptual knowledge. In short, the intermediary regions for lexical retrieval hold knowledge about how to reconstruct a certain pattern (e.g., the phonemic structure of a given word) in explicit form, within appropriate sensorimotor structures. When concepts from differing categories are evoked, say, those of persons or those of animals, intermediary regions that are different from those related to word form retrieval for the "tools" category are engaged. In our view, this provides a parsimonious and testable explanation for category-related dissociations of knowledge retrieval, in neurobiological terms not available in some of the models adduced by Pulvermüller.

We believe the structure and operation of the intermediary regions are flexible and modifiable by learning, and that their anatomical placement is such that it permits the most effective interaction between the regions of cerebral cortex that subtend perception, and those required to represent explicitly the images that define the pertinent conceptual and word form knowledge. We believe there are two overriding reasons why retrieval of knowledge for different kinds of entities would be correlated with different neural sites. One pertains to the overall physical characteristics of the entity, which determine the sort of sensorimotor mapping generated during interactions between an organism and the entity as it was learned. The other pertains to the fine physical characteristics and contextual linkages of an entity, which permit the mapping of an entity at an appropriate level of specificity (e.g., at a subordinate level for unique items such as familiar persons; at a basic object level for nonunique items such as animals). The intermediary systems process preferentially certain physical characteristics and contexts of entities, and because entities within a given conceptual category tend to share more of those characteristics than entities outside of it (see Humphreys et al. 1997; Kurbat et al. 1994; Medin et al. 1987; Small et al. 1995; Tranel et al. 1997c), lesions at a particular site are more likely to impair the recognition (or naming) of stimuli from that category, rather than another. This account also explains why in functional imaging studies, certain neural regions are preferentially and prepotently activated by stimuli from certain conceptual categories.

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Structure and dynamics of language representation

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Abstract: The important Hebbian architecture for language may not be the phonological networks of perisylvian cortex, but rather the semantic networks of limbic cortex. Although the high-frequency EEG findings are intriguing, the results may not yet warrant a confident theory of neural assemblies. Nonetheless, Pulvermüller succeeds in framing a comprehensive theory of language function in the literal terms of neuroanatomy and neurophysiology.

Pulvermüller has articulated his theory of language representation within the modern connectionist terms of neuroanatomical structure, and he presents evidence for functional connectivity in the concrete terms of neurophysiological dynamics.

More could be said about structure. For example, the differentiation of sensory and motor neocortices from paralimbic cortices in mammalian evolution has resulted in the greatest intermodal connectivity being retained in paralimbic regions (Pandya et al. 1988). It is certainly good Hebbian reasoning to recognize that words for vision or action are likely to engage representations distributed across the appropriate sensory or motor neocortex. But the interesting theoretical question for cortical representation is not concrete, stimulus- or action-bound representations, but abstract ones. From a straightforward connectionist analysis, supramodal integration must be required for words to achieve abstraction. The connectional anatomy of the human cortex shows that this integration is most likely to be found at the paralimbic core. Consistent with this reasoning, observations with aphasia have shown that whereas deficits of language articulation or perception occur with lesions of anterior or posterior neocortex, deficits of language semantics invariably involve damage to limbic networks (Brown 1988).

Thus, by focusing on "perisylvian" cortex, Pulvermüller seems to overlook the primary architecture for Hebbian self-organization in language development, an architecture that is dependent on corticolimbic reverberation to consolidate memory. The early maturation of speech perceptual and articulatory networks is certainly relevant to left hemisphere competence in the syntactic structure of the native tongue. But language, above all, requires memory. Words emerge as cognitive elements from the temporal-limbic traffic that integrates the grammatical capacities of neocortical networks with the general semantic capacities of paralimbic networks. Whereas motor and sensory neocortical networks are relatively isolated within each hemisphere, the dense connectivity of paralimbic networks includes extensive transcallosal connectivity as well. A greater right hemisphere contribution to semantics than to grammar would be expected on the basis of this pattern of connectivity alone.

However, the right hemisphere's contribution to semantics can also be approached with a more specific anatomical analysis. Studies of semantic priming using visual field presentation in normals have suggested that a word presented to the right hemisphere primes a broader set of semantic domains than one presented to the left (Beeman et al. 1994). It was observed many years ago that focal lesions of the left hemisphere produce focal sensorimotor and cognitive deficits, whereas equally focal lesions of the right hemisphere produce more diffuse deficits (Semmes 1968). The logical implication is that functional networks are more distributed on the right than the left, and this more holistic structural organization may be integral to the right hemisphere's holistic attentional skills (Tucker & Williamson 1984). EEG coherence studies have provided converging evidence, suggesting that there is greater similarity in EEG frequency modulation across right than left hemisphere regions (Tucker et al. 1986).

Thus, the extension of semantic representation beyond the left hemisphere may be more fundamental than Pulvermüller's account of bilateral representation of visual and action associations. In cortical network topography, the medium may be the message. A direct isomorphism may exist between the structure of hemispheric cortical networks and the structure of hemispheric semantic networks.

More needs to be said about dynamics. If it were true that we could analyze the dynamic functional assemblies of cortical networks through measuring high-frequency EEGs, we should see a revolution in cognitive neuroscience. Maybe we will. But there is a long history of searching for gamma band activity in the human EEG, and the few positive findings (Sheer 1989) have proven difficult to replicate. It may be significant that the new findings reported by Lutzenberger and Pulvermüller analyzed current density data, which may increase the sensitivity to focal electrical fields (Lutzenberger et al. 1997; Pulvermüller et al. 1997). Yet the current density measure has been found to be highly unstable with the sparse electrode arrays used in the Lutzenberger and Pulvermüller studies (Srinivasan 1996).

Although I am critical on several points, I like the way Pulvermüller talks. Whether it is a cloak or a mold, a scientist's language is revealing. For example, in the words of some ERP (event-related potential) researchers, a brain wave difference is described as showing that two cognitive conditions are "associated with nonidentical brain states." Seeing this tortured, timid language, we can know that these ERPers will not venture far into the terra incognitio of the wet stuff. Similarly, in today's rush to wedge each cognitive paradigm into the fMRI scanner, we often find familiar parts of the old box-and-arrow maps of mental activity grafted onto brain parts. Yet the words with the pictures just don't sound like brain. The excitement with the new images seems to cause the investigators to lose hold of the cognitive framework with which they trained, and to slip all too quickly down the slope of vapid modularity.

Pulvermüller, on the other hand, casts his psychological theory, and his experiments, in the literal terms of anatomical connections and neurophysiological activity. This is beyond metaphor and artifice and into the neural description of mind. Although the story may not be straight yet, Pulvermüller casts it squarely in the brain's language.

Locating meaning in interaction, not in the brain

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Abstract: Pulvermüller's attempt to link language with brain activity appears to depend on the assumption that words have context-independent meanings. An examination of everyday talk contradicts this assumption. The meaning that speakers convey depends not only on word content, but also, and importantly, on the location of a "word" in an ongoing sequence of turns in talk.

Linking language to neurological activity is an ambitious project, and its success depends on an adequate conception of language. Although not completely explicated, it appears that Pulvermüller's approach depends on a view of language in which words have particular, context-independent meanings. We offer a cautionary note concerning serious problems with this view of language.

Pulvermüller's assumptions about language ignore Wittgenstein's (1958) investigations of language and Putnam's argument against the tendency to think that "*what goes on inside our heads* must determine what we mean" (Putnam 1981, p. 22, emphasis in original). Putnam (1988) has argued that "*reference is a social phenomenon*" (p. 22) and "language is a form of cooperative activity,

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not an essentially individualistic activity" (p. 25). But rather than rehearse philosophical arguments, we use the bulk of our commentary to analyze examples of spontaneous talk.

We take it that Pulvermüller's goal is to explain how people understand talk. He proposes that word meaning is related to the activation of cell assemblies associated with a phonological word form. Of course, Pulvermüller recognizes that some words have more than one meaning, but his solution to this problem, that some word forms are associated with different semantic cell assemblies, is inadequate. First, there is the nontrivial problem of what causes one semantic cell assembly to be activated while another is inhibited. This is not a minor problem; perusal of any dictionary shows that most words have many meanings. But there is a more fundamental problem. The set of dictionary definitions does not exhaust the meanings that a speaker can convey by using a word in a specific turn at talk. Examples of spontaneous talk clearly illustrate this.

When people talk to one another, they use sounds that correspond to the linguistic notion of "words" along with other vocal (nonwords) and visual behaviors to produce and recognize meaning. The meaning a speaker conveys by uttering a particular sound-word depends not only on the word used but also on the location of the word in a sentence of utterances. Consider two examples of transcripts of tape-recorded spontaneous talk that illustrate this point with respect to the word "what":

1 G: and there's like this one spot I felt total I was the total threesome
2 but (pause) I didn't care
3 (2 second pause)
4 R: WHAT?
5 G: nobody else was even there (pause) it was me that guy and
[Nicole]

6 R: [I see]

Based on research on the analysis of spontaneous speech, the two second pause (line 3) between speaker G's turn and R's response probably conveys that R is having some difficulty with G's turn. When R finally does speak, she says "WHAT?" with a questioning intonation and in a louder voice than the surrounding talk (indicated by upper case). R's "WHAT?" conveys that she does not understand something about G's previous turn and that R wants G to clarify her previous turn. G proceeds to do so. R in line 6 overlaps the end of G's turn (shown by [ ]) with "I see," indicating that she now understands. This response clearly supports our interpretation of "WHAT?" in line 4.

A speaker produces a very different meaning by using "what" in another sequence:

1 C: guess what I'm drinking?
2 D: what?
3 C: iced cappuccino

It may appear that C in line 1 is asking if D can guess what C is drinking. Thus, when D in line 2 utters "what?" one interpretation is that D thereby conveys that he wants C to identify the thing that C is drinking. However, if C really were asking whether D could guess, then D should have responded affirmatively or negatively, and "what?" does not seem to do so. A different and preferred interpretation is that in her first turn C is checking whether D wants to be informed of something, and D's "what?" in line 2 gives C the go-ahead.

Speakers R and D both uttered the word "what," yet each conveyed a different meaning by doing so. We are not claiming that "what" is polysemous and that, somehow, one of its meanings is decoded on specific occasions of use. Rather, we suggest that speakers can use *any* word to produce an extremely wide and potentially unlimited range of meanings, and that an important resource for so doing is the placement/location of a word in a particular sequence of turns at talk.

A critic might argue that the word "what" in the two examples really does have the same meaning but the utterances differ because meaning is determined by the sentence context. According to this criticism, our two examples of "what" are actually two different truncated sentences, which convey different meanings. But how do we know that? Even if truncated sentences were involved, there is nothing about the word that indicates the meaning of that sentence. Moreover, it is not evident how a listener could determine *on the basis of the word alone* whether it was part of an utterance or a full utterance. Note, in this regard, that in our second example the "what" in the first line is part of an utterance, whereas in the second line the "what" is a full utterance. It is the location of a "word" in a particular sequence of turns at talk, rather than some internal characteristic of a lexical item, that determines its status as a word or utterance.

In sum, the meaning a speaker conveys by uttering a word and the status of a "word" as a word or utterance are in part dependent on the specific sequences of turns in speaking, in which the "word" is embedded. The essentially context-dependent and interactional nature of talk poses problems for the view that words have context-independent meanings located in brains. If the meaning of words depends on their location in an ongoing sequence of turns in talk, then the social nature of language must be central in any model of language.

Gamma band suppression by pseudowords: Evidence for lexical cell assemblies?

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Abstract: The EEG and MEG studies cited in the target article found reduced gamma band power following pseudowords in comparison with words. Pulvermüller interprets this power difference in terms of reverberating lexical cell assemblies. An alternative interpretation in terms of latency jitter in the gamma band following pseudowords is proposed that does not appeal to lexical cell assemblies.

Pulvermüller's lexical cell assembly model is an ambitious effort to integrate neurophysiological and psychological hypotheses about how the brain represents lexical information. The core hypothesis is that words are cortically represented as Hebbian cell assemblies. We wish to examine the empirical evidence for this hypothesis and focus on a central issue regarding the interpretation of the EEG and MEG experiments cited in the target article: gamma band suppression by pseudowords. We are not the first to draw attention to this issue (cf., Klimesch 1994) and it is explicitly addressed in Pulvermüller et al. (1996a), Pulvermüller (1996), and Lutzenberger et al. (1994). We believe this issue deserves sustained consideration.

A prediction of the lexical cell assembly model is that there should be increased gamma power following the onset of lexical stimuli relative to suitable nonlexical controls. When formulated in this fashion, that is, as a relative difference in gamma power, rather than an actual increase over prestimulus baseline gamma power, the EEG and MEG data appear to be consistent with the prediction. Inspection of the MEG data illustrated in target article Figure 8, shows a reduction in 30 Hz gamma power for pseudoword controls relative to baseline. Similar results were obtained in the EEG experiment first reported in Lutzenberger et al. 1994.

Two types of explanation have been proposed. Lutzenberger et al. (1994) suggested that gamma suppression following the pseudoword, "could be explained if cell assembly ignition is assumed to last for several seconds, so that it can bridge the interstimulus

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interval . . . Word-induced 30-Hz activity would then also 'contaminate' the baseline" (p. 118). Gamma suppression by pseudowords is also discussed in Pulvermüller et al. (1995) and Pulvermüller (1996). If we have understood correctly, the explanation is that gamma power for both words and pseudowords is suppressed relative to the prestimulus baseline by the presentation of the stimulus, and that the relative lack of suppression for lexical stimuli is caused by subsequent reverberation of the cell assembly following ignition. Both explanations appear to assume that there is a difference in gamma power between the two conditions, and this assumption may not be warranted.

In what follows, we suggest a possible explanation in which the apparent pseudoword gamma suppression results from relatively greater latency jitter in the time course of the gamma activity following the presentation pseudowords. Pulvermüller's procedure for quantifying gamma power uses averaging in the time domain, specifically, computation of average RMS gamma band power for a specific poststimulus interval within each experimental condition. This average is then normalized, that is, expressed as a proportion of baseline power, and log transformed. Interpreting these averages as reflecting an actual difference in RMS gamma power presupposes that the time course of the gamma power changes in each experimental condition is fairly consistent from trial to trial. Figure 1 illustrates schematically how latency jitter in individual "trials" can affect an average waveform. Figure 1, Panel (a) shows three schematic "trials" consisting of a nominal waveform with a peak amplitude at 400 msec poststimulus and two variations, one in which the peak occurs 100 msec earlier and one in which it occurs 100 msec later. Figure 1, Panel (b) compares the average of these three jittered "trials" with the nominal waveform and shows that the jitter results in the average peak having lower amplitude than the nominal trial. If the nominal waveform were observed in three trials in one experimental condition, for example, Word, and the jittered waveforms were observed in three trials in a second experimental condition, for example, Pseudoword, then the log normalized gamma power in the Word condition would be relatively higher than in the Pseudoword condition between 300 and 500 msec poststimulus as in Figure 1, Panel (c). It would, however, be a mistake to conclude on this basis alone that the peak gamma amplitude in each trial was different. The peak gamma power in each trial is the same, it just occurs at different times.

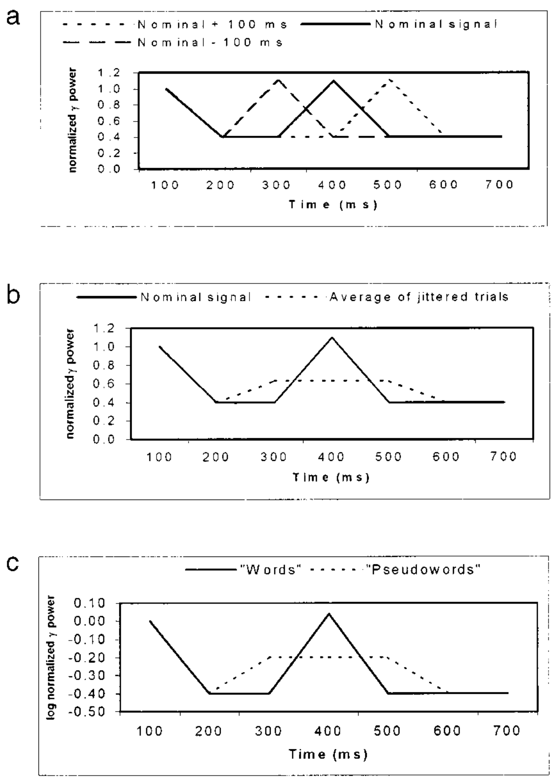

Figure 1 (Urbach et al.). Effects of latency jitter on time domain averages.

The effect of latency jitter is a general issue in the interpretation of amplitude differences in waveform averages. It is of particular concern for Pulvermüller because the amplitude difference is interpreted as reflecting a difference in relative gamma power. This power difference is interpreted in terms of reverberating lexical cell assemblies. If there is no difference in the magnitude of the gamma power, but the same peak power occurs at different latencies, then it is not necessary to postulate a physiologically distinct mechanism such as lexical cell assemblies to account for the observed difference in the average power.

Latency jitter seems to be an explanation in principle, and given the design of the experiments, it is not implausible to think that the time course of lexical decision is more variable for the pseudowords than for the words. The words are controlled on several dimensions, all of which will tend to reduce variability between individual words. The pseudoword controls, however may be more or less similar to real words either orthographically or phonologically. Pseudowords that share a high number of features with real words would tend to be more difficult to reject than pseudowords that do not. It might be possible to get some evidence for or against this suggestion by comparing the variability in the reaction times for pseudowords with the variability in the reaction times for the words in the lexical decision task for the EEG study. Although the points above have been made in the context of interpreting gamma power differences between words and pseudowords, they also apply to amplitude effects in the scalp topography for different classes of words.

It should be noted that if the gamma power difference between pseudowords and words is a function of latency jitter, then this means that the time course of gamma power changes is sensitive to a cognitive manipulation. Our view is that event-related changes in frequency band power hold a good deal of promise as a measure in experimental cognitive psychology. However, it appears that further research is required before the EEG and MEG experiments discussed in the target article can be interpreted as strong empirical evidence for the lexical cell assembly hypothesis.

A spy to spy on a spy: From type to token representation with cell assemblies

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Abstract: The idea of representing words with cell assemblies is very appealing. However, syntactic sequences need to be represented as well. This cannot be done by using the activity levels of assemblies. Instead, structural relations and operations between assemblies are needed to achieve serial order in syntactic word strings.

Pulvermüller makes a strong case for the idea that words are represented in the brain by cell assemblies, distributed over different sections of the cortex. However, as the author correctly notes in the final section of the target article, a complete theory of "language in the brain" cannot do without syntax, that is, the ability to represent syntactic (word) strings.

In the final section, the author proposes that such sequences can be stored by means of the decaying activation of the cell assemblies involved. Thus, if the string A-B-C is stored in that order, the activity level of the assembly C will be the highest, followed by that of B and A (see Fig. 10). Using this difference, the string could then be retrieved in the order C-B-A, which would create a pushdown store.

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However, the idea of storing sequences of cell assemblies in terms of their activity levels has fundamental flaws, in particular, because sequences with repetitions cannot be stored in this way. Thus, in the sequence A-B-C-A, the assembly A has both the highest and the lowest activity level, which is obviously impossible. Hence, the sequence will be stored as B-C-A, because the highest (last) activation of the assembly A overrides the lowest (first) activation of A. The difficulty results from the fact that representation in terms of cell assemblies is a form of "type representation," and to store a sequence such as A-B-C-A one needs a form of "token representation."

To illustrate this fundamental issue, consider the sentence "A spy to spy on our spy who searches for their spy."[1] Here, one word (of the type "spy") occurs as four different tokens. If we concentrate on one grammatical category, there are three occurrences of the noun "spy" in this sentence. The first occurrence (token) of the noun "spy" is right at the beginning of the sentence, so in Pulvermüller's model the cell assembly for the noun "spy" should have the lowest activity level of all the assemblies representing this sentence. But the noun "spy" is also the last word in the sentence, so the cell assembly for "spy" should have the highest activity level, as well. And for the second occurrence of the noun "spy," the cell assembly for "spy" should have an activity level that is between the lowest and the highest for the cell assemblies representing the sentence. It is obvious that the three different activity levels required here for the assembly "spy" (lowest, highest, and in between) cannot be found at the same time in one assembly. In fact, because the last activation of an assembly will override the previous ones, the assembly for "spy" will have the highest activity level of all the assemblies representing the sentence. Because the three occurrences of the noun "spy" cannot be distinguished in the model proposed by the author, the meaning of the sentence will be lost entirely.

To ensure representation of syntax with cell assemblies, a fundamentally different approach is needed. This can be illustrated with a model of the production of a context-free language, implemented with attractor neural networks (Van der Velde 1995). Attractor neural networks (ANNs) are good models of cortical cell assemblies (e.g., see Amit 1989; 1995).

The pushdown stack in this model is an ANN consisting of three parts. In the central part the symbols (words) of the language are stored. The left and right parts are of equal but variable size. A stack memory with an ANN is different from a standard computer stack. In the latter case each symbol is represented individually. Thus, for example, *AABB* is represented by *A - A - B - B*, repetitions included. This is a form of token representation. In contrast, in an ANN each pattern can be stored only once. That is, storing patterns in ANNs are forms of type representation. Therefore, a symbol is stored in an ANN as a token by embedding it in other patterns.

For example, the string *AABB* is stored in the following manner. First, the pattern r_0Ar_1 is stored in the ANN, with r_0 in the left part, A in the central part, and r_1 in the right part. The patterns r_0 and r_1 are random patterns, generated by the network itself or by an external source. To store a new symbol, in this case the second A, another random pattern r_2 is generated. Then, the pattern r_1Ar_2 is stored in the network, with r_1 in the left part, A in the central part, and r_2 in the right part. This process is repeated for every new symbol stored on the stack. Thus, *AABB* is stored as $r_0Ar_1, r_1Ar_2, r_2Br_3, r_3Br_4$. The last B is the top of the stack. This symbol is retrieved by presenting r_4 to the right side of the ANN. As a result, the ANN will settle in the attractor state representing r_3Br_4. The pattern r_3 can now be used to retrieve the next symbol from the stack by presenting it to the right side of the ANN.

One can also "remove" the top symbol B from the stack and store a new symbol, say A, in its place. To do so, a new random pattern r_5 is generated and the pattern r_3Ar_5 is stored in the ANN. Yet, r_3Br_4 is not actually removed; it is still a pattern stored in the ANN. Thus, the ANN now contains $r_0Ar_1, r_1Ar_2, r_2Br_3, r_3Br_4, r_3Ar_5$. However, using the procedure outlined above, a retrieval of all the symbols from the stack will now give *A - B - A - A* (in that order). The first B is by-passed, because after activation of r_3Ar_5, r_3 is presented to the right part of the ANN, which activates r_2Br_3 and not r_3Br_4.

This example illustrates how (syntactic) sequences of cell assemblies can be represented. Because a cell assembly represents a word as a type, a new set of assemblies is needed. These assemblies are used to represent the order in a sequence. A sequence of words can be represented by forming the appropriate (temporary) associations between the order assemblies and the word assemblies (using, for example, a form of fast Hebbian learning). To this end, structural operations between and within the cell assemblies are needed, so that the sequence of words is stored and retrieved in the correct order. It is important to note that operations of this kind can be found in the visual cortex (Van der Velde 1997). In the visual cortex, these operations ensure that representations of shape, color, and position are related to the same object. In my view, the operations needed to store and retrieve linguistic sequences will turn out to be of a similar kind.

NOTE

1. From the BBC television series "Blackadder Goes Forth" ("General Hospital").

Author's Response

Toward a cognitive neuroscience of language

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Abstract: In this response to multidisciplinary commentaries on the target article, "Words in the brain's language," additional features of the cell-assembly model are reviewed, as demanded by some of the commentators. Subsequently, methodological considerations on how to perform additional tests of neurobiological language models as well as a discussion of recent data from neuroimaging, neuropsychological, and other behavioral studies in speakers of spoken and sign languages follow. Special emphasis is put on the explanatory power of the cell-assembly model regarding neuropsychological double dissociations. Future perspectives on neural network simulations, neuronal mechanisms of syntax and semantics, and the interaction of attention mechanisms and cell assemblies are pointed out in the final paragraphs.

Let me first thank the colleagues who commented on the target article. These contributions from linguists, psychologists, biologists, and neurologists, as well as from philosophers, computational scientists, and anatomists were extremely helpful. Discussions of this kind are important for the developing field one might want to call the "cognitive neuroscience of language."

The only fundamental objection to the research strategy proposed in the target article is raised by **Bierwisch.** He discusses the claim that language mechanisms can be explained exclusively by associative learning plus neuroanatomical and neurophysiological facts and finds it premature. Human knowledge and behavior, however, are undeniably determined by experience resulting in learning, and by the structure and function of the nervous system, which is itself determined by the genetic endowment.[1] In some forms of learning, genetic and environmental factors

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do interact according to a more or less fixed time table. Imprinting, for example, can be defined as associative learning in a critical period, that is, when certain neuroanatomical and neurophysiological preconditions are met. Such "mixed forms" are included under associative learning and neuroanatomical/physiological factors. One might argue that there are forms of learning that psychology text books would classify as nonassociative. These include elementary perceptual learning such as habituation and sensitization (which are probably of minor importance for language), but also imitative learning, which may play an important role in language acquisition (Kupfermann 1991a). The latter form of learning, however, is based on a co-occurrence of sensory stimuli and would thus be considered a form of coincidence or correlation learning covered by Hebbian associative mechanisms. In summary, associative learning (including coincidence and correlation learning) plus anatomical and physiological prerequisites specified by genetic information appear to be the only determinants of language mechanisms. It is difficult to see what third factor Bierwisch might have had in mind.

The determinant **Bierwisch** probably considers most relevant is the knowledge specified by Universal Grammar (UG), which, according to many linguists, is necessary for language learning (or, as proposed by Chomsky 1980 [see also Chomsky: "Rules and Representations" *BBS* 1(3) 1980], for the growth of language in our brains). This information must nevertheless be materialized in some way in the brain; it may take the shape of a pattern of neuroanatomical connections between Broca's and Wernicke's areas (Deacon 1992a;b), the length of branches of dendrites therein (Scheibel et al. 1985; Jacobs et al. 1993), a myelination and plasticity schedule for these and other areas (Pulvermüller & Schumann 1994), specific neuronal dynamics (Pulvermüller 1993), or still unknown anatomical or physiological properties. As proposed in the target article, it is important to determine where, why, and how universal linguistic knowledge is organized in the brain and how the inborn neuronal structures and processes interact with activity patterns caused by the environment. The postulates in the target article are no doubt incomplete, and some may turn out to be wrong. However, there is no alternative to the proposed research strategy of spelling out linguistic structures and processes in the language of neuroanatomy and neurophysiology, at least if the general goals of explaining language and understanding the brain are accepted.

This Response is structured in the following way: I will first discuss the cell-assembly concept and possible alternatives in light of questions raised (sect. R1). Special attention will be paid to basic properties of cell assemblies, assemblies representing homophones and synonyms, feedback regulation of cortical activity, representation of semantic word classes, plasticity, high-frequency brain activity, and brain structures involved in word processing. Alternative and complementary models will also be discussed in this section. In section R2, methodological issues regarding physiological double dissociations, processing of single words, and possible artifacts will be addressed. The physiology of word processing will be dealt with in some detail in section R3, because several colleagues reported relevant results that have been treated too superficially in the target article. The next section (R4) will address the relevance of cell-assembly explanations of neuropsychological syndromes. Although this was not the topic of the target article, the excursus is necessary, because commentators have suggested that the cell-assembly model of language may be incompatible with neuropsychological data. The opposite may well be true: The cell-assembly model seems indispensable for explaining neuropsychological syndromes. In section R5, behavioral data relevant to the proposed model will be featured briefly. Section R6 will address sign language, and the last section (R7) will discuss extensions of the present proposal concerning semantic and syntactic mechanisms and the neurobiology of attention. Table R1 presents the structure of this Response together with information about which commentaries are addressed in the individual sections.

R1. Cell assemblies: Details, additional mechanisms, and alternatives

R1.1. Organization of cell assemblies. Questions about cell-assembly organization and development are raised by **Epstein, Ivancich et al.,** and **Kalbe & Thiel.** One concerns how many neurons one cell assembly includes. This is relevant, because it should be possible to detect assemblies by large-scale neuroimaging. However, instead of speculating about the size, one may want to look at empirical results and consider that rather surprising brain responses could be predicted and can now be explained by the cell-assembly model. This encourages the view that cell-assembly activation can lead to detectable brain responses picked up by EEG, MEG, PET, and fMRI. Thus, one can propose an optimistic strategy for future experiments, namely, to seek enhanced activity (relative to an adequate control condition) where the model predicts it. This would then provide additional support for the model, regardless of the exact size of the neuron sets.

Another possibility is to make calculations and estimates of assembly size, their activation dynamics, and the way these translate into brain waves and metabolic changes. All these estimates are problematic, but here is one of them[2]: Cell-assembly size is currently estimated to lie between several hundred and about a million neurons (Palm 1982; 1993). Notice that a considerable range is necessary, in part because the relation of inclusion may hold between assemblies. The assembly representing a word should include representations of the sounds that are part of the word. The latter subassemblies would thus be much smaller than the former. However, let us take 10^6 neurons as a typical size of assemblies. The cortex includes more than 10^{10} neurons. If a significant proportion of these become active – as, for example, during an epileptic seizure – voltage changes of some 100–500 μV can be recorded at the surface of the head (Rockstroh et al. 1989). Let us therefore assume that synchronous activity of all cortical neurons will yield an EEG voltage change on the order of 1 mV. If this is correct, then simultaneous activity of 10^6 neurons (that is, about 1/10,000 of the cortical population) should lead to an EEG voltage change of some 0.1 μV. This calculation is admittedly based on rough estimates. The real values may differ from 0.1 μV by a factor of 10 or more. However, this estimate clearly shows that the activation of a cell assembly will not lead to very pronounced voltage changes in the EEG. On the contrary, these changes are likely to be so small that they can just be detected by noninvasive measures of electrocortical activity; the same may hold for metabolic imag-

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Table R1. Structure of this Response and overview of where comments are addressed. The left column lists section and sub-section headings (some of which have been abbreviated). At the top, the commentators' names are listed in alphabetical order. The "x"s indicate in which paragraphs the comments are being addressed

	Bierwisch	**Chapman**	**Code**	**Cullicover & Novak**	**Dubé & Cohen**	**Elbert et al.**	**Epstein**	**Fuster**	**Greenberg & Nisslein**	**Grossi**	**Haase & Rothe-Neves**	**Ivancich et al.**	**Ivanitzky & Nikolaev**	**Jacobs & Rösler**	**Jorion**	**Kalbe & Thiel**	**Kurthen**	**Miller**	**Osterhout & Bersick**	**Posner & DiGirolamo**	**Salmelin et al.**	**Shillcock & Monaghan**	**Skrandies**	**Spivey et al.**	**Tranel & Damasio**	**Tucker**	**Turnbull & Carpendale**	**Urbach et al.**	**Van der Velde**
R1. Cell assemblies																													
R1.1. Organization			x				x					x		x		x													
R1.2. Regulation							x					x				x											x		x
R1.3. Word types	x	x		x				x			x				x			x		x	x		x				x		
R1.4. Cort, distribution				x				x													x				x				
R1.5. Plasticity						x	x													x		x							
R1.6. High frequency								x			x		x			x		x			x								
R1.7. Meaning cortex					x		x						x			x		x		x	x		x		x	x			
R1.8. Hemispheres																						x							
R1.9. Subcortex															x										x	x			
R1.10. Local CAs													x							x					x				
R2. On method																													
R2.1. Double diss.														x															
R2.2. Single words						x			x		x								x	x	x		x				x		
R2.3. Artifacts																										x		x	
R3. Word physiology																													
R3.1. Content/function		x																	x										
R3.2. Nouns/verbs																													
R3.3. Affect meaning		x																					x						
R4. Neuropsychology																													
R4.1. Relevance										x	x					x									x				
R4.2. Double diss.										x										x		x			x				
R4.3. Re-assemblies			x																										
R5. Behav. experiments																													
																								x					
R6. Sign language																													
					x																								
R7. Future perspectives																													
R7.1. Neural networks				x							x				x									x					x
R7.2. Syntax	x			x					x		x	x							x								x		x
R7.3. Meaning	x			x		x		x										x		x			x		x		x		
R7.4. Attention						x														x									
R7.5. Final statement																	x												

ing as well. Consistent with this, the word-class differences we found in studies using event-related potentials were in the range of 0.5 to a few microvolts. Although it is not presently possible to fulfill **Jacobs & Rösler**'s wish to determine "how exactly changes in blood flow or electrical activity map onto changes in . . . information processing activity," this and similar estimates may inspire neuronal modelling of cognitive processes.

Cell assemblies are envisaged to consist of local clusters of neurons. This is related to a proposal by Ojemann, who found that electrical stimulation at particular cortical sites may disturb processing of a word, but stimulation a few millimeters apart from these critical sites does not (Ojemann 1983; 1991). The local neuronal clusters may be analogous to what Hubel (1995) calls ocular dominance and orientation columns. A circle in Figure 4 of the target article would accordingly denote a relevant fraction of the neurons included in such a column.

Epstein asks an additional question about cell-assembly organization: How can a cell assembly persist in the absence of input? If the synaptic changes induced by Hebbian learning are long-lasting, their weight changes will persist. In addition, stimulation of an assembly by external input (from outside the brain) is only one possibility to get it active. The other option is to activate it via cortico-cortical connections. Cell assemblies may activate each other so that a sequence of ignitions results. If later input activates only a small number of assembly neurons plus additional neurons outside

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the assembly, it will still ignite because of the strong assembly-internal connections. This mechanism was used by Hebb to explain gestalt completion (the fact that a cat partly occluded by a tree is nevertheless perceived as a cat). The neurons outside the assembly will probably soon become silent again, because they lack fellow neurons that help them stay active. In contrast, the assembly will remain active because it allows activity to reverberate. However, if the assemblies and particular external neurons are frequently active together, their activity becomes better correlated and the latter may gradually be included in the assembly.

It is relevant to point out here that the proposed concept of cell assemblies is necessarily fuzzy, that is, any exact boundary of an assembly can only be chosen arbitrarily (see **Elbert et al.**). In simulations using artificial associative memories (Palm & Sommer 1995), one immediately runs into the problem of determining which neurons belong to the assembly and which do not. What one finds are neurons that are connected to many of their fellows by maximal synaptic strength (it is indisputable that these are assembly members) and others whose connections to the rest of the assembly are slightly weaker, and whose inclusion in the assembly is therefore uncertain. Correspondingly, some neurons will always become active together when a certain input pattern is provided; others may only be recruited in 80 or 90% of the cases, depending, for example, on the neuronal sets activated in the past (Milner 1957). In other words, there will be some neurons with high correlations and others whose correlation with these "core neurons" are smaller. To decide whether or not a neuron belongs to the assembly, one must set up critical values for synaptic connectedness or correlation coefficients. For some purposes, it helps to distinguish the kernel of an assembly from its halo (Braitenberg 1978b), but in network simulations arbitrary boundaries need to be introduced for defining these assembly parts as well. And this is not a problem. It is essential to see that fuzziness is intrinsic to the assembly concept and that this is only problematic in the way it is a problem to determine the boundaries of the sun or the Milky Way. The fuzziness of the boundaries of the respective concepts should not obscure the fact that there are stars, galaxies, and perhaps cell assemblies representing these concepts and words.

An important property of cell assemblies is their functional discreteness: An input either will or will not ignite it. If only some of the 100,000 or 1 million assembly neurons are not activated – for example, because they are refractory – the cell assembly can still be considered to ignite. However, if only 10% or 50% become active, one would not call it a "full" activation. The point is that activation of some 50% would rarely occur, because there is a "point of no return": If a critical number of excited neurons is reached (most of) the rest will be recruited because of the strong assembly-internal connections. Functional discreteness is important for modeling language (Braitenberg 1980; Braitenberg & Pulvermüller 1992). [See also Braitenberg et al.: "The Detection and Generation of Sequences as a Key to Cerebellar Function" *BBS* 20(2) 1997.] A word is either produced/accessed as "hat" or "had;" it is either noun or verb; it can be in either the dative or the accusative case. For organizing this, all-or-nothing decisions are necessary. These decisions may correspond to the ignition of one cell assembly (while competing networks are hindered from igniting).

Epstein is right that Hebbian synaptic modification is related to biochemical and neuroanatomical changes. For example, the number of synaptic vesicles or subsynaptic receptors may change, as may the shape of the spine on which the synapse is located (see for example, Braitenberg & Schüz 1998). Dendritic sprouting and the formation of new synapses and subsequent pruning of synapses during critical periods is relevant for Hebbian learning if the synapses with low correlation of pre- and post-synaptic activity are being pruned. [See also Ebbesson: "Evolution and Ontogeny of Neural Circuits" *BBS* 7(3) 1984.] A similar point can be made for recovery from brain lesions, as **Code** suggests. Replication of neurons may also become relevant for learning, as proposed by **Epstein.** However, the implications of this for the present model would have to be explored. I had difficulty understanding **Epstein**'s energy metaphor. He uses it to suggest that strengthening one connection (or path) may lead to weakening another. However, no energy metaphor is necessary here. Any correlation rule implies it (see Tsumoto 1992 for discussion of evidence).

R1.2. Representation of related words and the need for regulation (inhibition). How would assemblies representing related words be organized? **Epstein** and **Ivancich et al.** ask for a more detailed answer to this question. In the case of words sharing their initial consonant, overlap by neuronal populations in the perisylvian part of the assemblies would be assumed. More specificity is possible after saying a word about the hypothesized phonological machinery (Braitenberg & Pulvermüller 1992; Pulvermüller 1992; 1996b): Representations of language sounds are part of assemblies organizing words, and the sound sequence constituting the words needs to be realized as connections between these phonological representations. However, specified in this way, a problem mentioned by Lashley (1951) would occur: The few phonemes (about 50) that are part of a language would be linked by various connections so that the words "tab" and "bat" would include the same subunits, and neuronal connections could not specify in which direction the neuronal phoneme string must be read. This problem can be overcome if context-sensitive sound units rather than phonemes, are assumed to be cortically represented by functional subunits. So whereas one neuron population may represent a word-initial /t/ followed by an /æ/, another may be the counterpart of a word-initial /t/ followed by /i/, and still another may organize a /t/ at the end of a word following an /æ/. Context-sensitive coding of phonemes has been proposed by Wickelgren (1969). It is clear, however, that not all phoneme or letter sequences in words can be coded by replacing letters with context-sensitive triplets including only the left and right neighbors, as suggested by Wickelgren. "Mororoa," for example, would yield the triplets #Mo, mRo, rOr, oRo, rOa, and oA#, which also could produce "Moroa." (This problem arises for only a few English words [e.g., "lullaby"] but it is common in languages spoken on islands in the South Pacific.)

To solve this problem, information about phonemes farther away from the critical one could be included in its context-sensitive representation. Because the different /r/s or /t/s have many of their phonetic features in common, their neuronal counterparts would be assumed to share neurons. Strong activation of one context-sensitive variant must therefore exclude activation of its sisters. Here, an inhibitory mechanism (which could be realized by local cor-

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tical inhibitory connections) must be postulated. According to the motor theory of speech perception and related empirical work (Liberman et al. 1967; Liberman & Mattingly 1985), the sound characteristics of a phoneme vary strongly as a function of its context, while the articulatory movements of context-sensitive variants of phonemes appear less variable. This suggests that whereas the overlap between context-sensitive phoneme representations is located primarily in the anterior perisylvian areas, many of the neurons actually distinguishing the /t/s in "ta" and "ti" are located in the posterior perisylvian region (Pulvermüller 1992). In summary, two words sharing their initial phoneme would have cell assemblies overlapping by part of their initial context-sensitive phoneme representations, and this overlap would be localized mainly in the anterior perisylvian region.

The representation of homophonous words (e.g., "spy"), and the question of how different readings of the same word can be modelled has been addressed by **Ivancich et al., Turnbull & Carpendale,** and **van der Velde.** Instead of responding directly, I will quote from an earlier publication (Pulvermüller 1992), where some hints have been given and even the examples happen to correspond to those in the commentaries:

> Syllables like "spy" have obviously at least two possible meanings with only minor if any relation to each other. How would such homophonous words be organized in a cell assembly model? The syllable may frequently occur together with spiders and spions [*sic*] and the syllable assembly could, therefore, develop connections to the neuronal counterparts of both word meanings (which are located outside the perisylvian cortex). So two assemblies develop that overlap and share the syllable assembly. (p. 184)

There is a problem, however, as correctly pointed out by **Ivancich et al.:** Now perception of "spy" will lead to the ignition of both assemblies. This problem can only be solved if a regulatory or inhibitory mechanism is assumed that allows only one of the overlapping assemblies (probably the one best primed by context) to ignite. For widely distributed assemblies, it is unlikely that cortical neurons provide between-assembly inhibition, because cortical inhibitory cells are small (Braitenberg & Schüz 1998); hence it would be difficult to explain inhibition between neuron populations located far apart.

It was accordingly proposed – following the Theory of Cortico-Striatal Interplay by Miller and Wickens (Miller & Wickens 1991; Wickens 1990; 1993; Wickens & Arbuthnott 1993) – that cell assemblies include neurons in the striatum. The striatum can function as a regulatory device producing a complex pattern of inhibition around activated cells. If all cortical assemblies include striatal neurons, between-assembly inhibition could be wired through the striatum. Now,

> if we assume that the overlapping assemblies include different neurons in the striatum . . . , the strong striatal lateral inhibition could guarantee that only one assembly can ignite at a particular time. However, the ignition of one of the overlapping assemblies would necessarily stimulate the other one to some degree. This predicts that the presentation of a homophonous word form ignites only one assembly and partly activates the other. Assemblies that overlap with regard to their cortical neurons but include distinct striatal cells could also be the basis of different "submeanings" of a particular word. "School," for example, can either refer to a place ("the school in Brentwood"), an event in such a place ("school begins at nine") or a body of persons (the school of generative linguistics) or animals ("school of fish"). These readings are related but nevertheless exclude each other in a particular context. Their possible neuronal counterparts are overlapping cell assemblies that share some of their cortical neurons but inhibit each other via their striatal connections. (Pulvermüller 1992, p 184)

More generally, inhibition between intersecting assemblies may explain a universal feature of language occurring at various levels: The mutual exclusion of two word forms with the same meaning, of two pronunciations of the same word, of two meanings of homophonous words, of two readings of the same word, and even of two interpretations of the same sentence (word string) may all be based on this kind of inhibition. The differences between the mechanisms realizing these types of mutual exclusion may lie primarily in the different cortices where the relevant assembly parts are localized.

This may give the reader an idea of how powerful a cell-assembly mechanism can become if additional subcortical brain mechanisms are included in the considerations. It should be pointed out, however, that the target article was not conceived as a demonstration that all linguistic problems can be solved by cell assemblies. Instead, it focused on aspects and predictions of the model that can be tested and have actually been tested in neuroimaging experiments. (This is a point I will have to stress at several places in this reply.)

R1.3. Distinguishing word types. Many commentators see a discrepancy between the word categories proposed in the target article and current linguistic categories. **Posner & DiGirolamo** find the suggestion that brain-based word-type distinctions differ from established grammatically based word categories valuable; **Jorion** rejects linguistic distinctions between parts of speech as "cosmetic" and favors aspects of the proposed framework. In contrast, **Bierwisch** sees "the real problem" in the fact that the proposed categories are "at variance with the nature of lexical categories," as proposed by linguists; and **Haase & Rothe-Neves** accuse me of not "shak[ing] off arbitrary (mis)conceptions in linguistic theory."

There is disagreement here and it is necessary to clarify: *One* of the important distinctions discussed in the target article – that between content and function words – is important in psycholinguistics (Garrett 1975; 1988) and neurology (Pick 1913). I do not share the opinion that this distinction is a misconception, although the two word classes of course consist of smaller categories that differ, and may, for example, be selectively affected by stroke (Menn & Obler 1990). Another distinction – that between words related to motor and sensory modalities – is less common, but it appears unavoidable for any associationist approach to word processing in the brain. Certainly, not all of these distinctions are taught at school or dealt with in linguistics books. There are also important differences from classical categorization schemes such as the one proposed by Aristotle and summarized by **Jorion.** However, this is neither an argument against the present approach nor is it an argument against other categorizations. The target article focuses on word categories for which a neuroscientific approach yields strong predictions that can be tested experientially by neuroimaging research. Localizational postulates (addressing the where-question) and functional predictions (addressing the how-question) are discussed in

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detail. The data providing evidence in favor of these predictions hence support the proposed brain-based categories; they do not show that other categories are irrelevant.

It is very likely that additional distinctions are also important; it would be very useful, for example, to consider how Rosch's basic categories and prototypes (**Bierwisch**), various syntactic categories (**Culicover & Nowak; Salmelin et al.**), content words with different meanings (**Bierwisch**), or function words with different uses (**Turnbull & Carpendale**) are realized. These questions are raised and preliminary answers are given at several places in this Response: some have been addressed in earlier publications.

A main proposal is that an aspect of lexical semantics (reference) is related to cortical distributions of cell assemblies realizing words. This rests on the assumption that words have meaning. Now, **Turnbull & Carpendale** propose that there is no context-independent meaning of words, and **Haase & Rothe-Neves** even find it hard to maintain that words have a meaning at all; they advocate speaking only about the "process of meaning." I cannot agree with these statements. Without assuming that words have meaning, how could one explain that inserting one single word into a sentence spoken in a particular context can dramatically change the sentence's meaning? It is necessary to make the important *distinction* between *langue* (language) and *parole* (language use) (de Saussure 1916) here (or the related distinction between competence and performance). A word has a meaning in the particular scenario in which it is used; one aspect of this *meaning*$_{-1}$ may be that the word refers to a crocodile in a particular context. The meaning of a word is its use in the language (Wittgenstein 1969, para. 43), that is, the range of its possible uses, and this *meaning*$_{-2}$ includes the property that it can be used to refer to crocodiles (perhaps in any context). Meaning$_{-1}$ and meaning$_{-2}$ are systematically related to each other (Alston 1969; Fritz & Gloning 1992). Without having a meaning$_{-2}$, a word could never be understood in a new context. Arguably, meaning$_{-2}$ is realized as a certain wiring in the cortex, and meaning$_{-1}$ as an activity pattern therein (Pulvermüller 1992).

Classification of words according to their meaning makes it necessary to assume that the classes hold for various individuals speaking the same language. However, **Salmelin et al.** state that words can evoke quite arbitrary associations. It is certainly true that one can hear the word "mouse" and think of an elephant. However, this is probably not the rule. Normally, one is reminded of something mouse-like, and this involves the visual and – depending on one's experience – somatosensory and motor modalities. Some variability over individuals is possible, but there is no arbitrariness. Atypical experiences of an individual can also influence the structure of an assembly realizing a word. **Fuster** correctly points out that the memory networks tied to word forms also store idiosyncratic experiences. However, all people speaking a language share important aspects of their language use (Wittgenstein 1967) and hence many of their word associations. Instead of merely postulating this, it is better to do additional psychological tests. For word associations this has been done in some of our experiments using questionnaires.

Fuster's insight has important implications for future research: If two populations usually use concrete words for different things and therefore have different word associations, their brain correlates for these words may differ. For example, professional soccer and handball players may think of actions performed by the foot or hand when confronted with the words "goal" or "ball." Correspondingly, these populations may exhibit different brain responses (with stronger activation of the motor and premotor areas relevant to hand/foot movements, respectively) when confronted with these words in isolation [see also Jeannerod: "The Representing Brain" BBS 17(2) 1994.] Furthermore, clinical populations such as patients with anxiety or posttraumatic stress disorder may well exhibit very specific brain responses when confronted with words related to their disorders.

Bierwisch calls the distinction between content and function words "vague." This is because only typical examples of the two categories (nouns, adjectives, and verbs vs. articles, pronouns, and auxiliary verbs) were introduced in the target article, but the categories were not defined with regard to all word groups. Bierwisch mentions prepositions as a critical example for which a classification as either content or function words would be problematic. This criticism is not appropriate in the present context, however, for the following reasons: First, to demonstrate brain-differences between two categories, typical examples need to be compared. It is not necessary to treat cases where categorization is questionable. Second, prepositions were excluded from all of our own studies on content/function word differences, for theoretical and empirical reasons (see, for example, Friederici 1982; 1985). Third, the problems and advantages of the function/content word differentiation have been discussed in many recent publications (e.g., Pulvermüller 1995a).

Ivanitsky & Nikolaev ask how abstract (content) words would be represented; this was addressed in section 3.3.2 of the target article. On the abstractness scale, some abstract content words lie half-way between the concrete content words and the highly abstract function words. Such items close to the category boundary are therefore of interest for research on which properties of content and function words are relevant for eliciting different brain responses. In their critique of research on single word-processing, **Haase & Rothe-Neves** seem to overlook that the relevant factors distinguishing word categories can be teased apart in well-controlled neuroimaging experiments (see target article, sect. 5). Ivanitsky & Nikolaev's suggestion (which is related to Damasio's 1989b proposal) that neurons relevant for storing abstract information of objects are located farther from sensory cortices than those related to concrete information sounds plausible. The idea is complementary to the differential laterality hypothesis put forward in the target article.

Any category has typical members (prototypes), members that are less typical, and others that are "on the periphery," and whose inclusion can therefore be questioned. This applies also to the words related to action and vision. A distinction without a sharp boundary does not produce a "trivial 'anything goes' type of theory," as **Bierwisch** believes (Wittgenstein 1967).

R1.4. Cortical distribution of functional units. The narrow localization of function words in perisylvian areas may be determined by Universal Grammar, **Fuster** suggests. I fully agree. Language-relevant genetic information determines that cortical neurons sending their efferent fibers to the ar-

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ticulators are primarily housed anteriorly to the foot of the central sulcus, and signals from the ears are sent to cortical neurons in the superior temporal gyrus. Further genetic information specifies that these areas are connected indirectly via closely adjacent areas (Broca's and Wernicke's). Hence, neuronal coactivation in these primary cortices causes activity patterns in the perisylvian region; word form representations develop therein. Because most function words do not correlate highly with nonlinguistic stimuli or actions, their assemblies do not change their cortical distribution. It has already been pointed out in the target article that genetic information may be necessary to determine laterality. In addition, anatomical characteristics of the language areas (Hayes & Lewis 1993; Jacobs & Scheibel 1993; Scheibel et al. 1985), which may suit these areas better for representing language (Greenfield 1991) may also be genetically preprogrammed. Last, there must be a genetic determinant of babbling (Locke 1989; 1991; 1993). Thus, language-relevant genetic information (Universal Grammar), plays an important role in placing function words in perisylvian space. The broad distribution of electrocortical responses to content words probably reflects the semantic variability of words rather than differences between individuals, because equally specific topographical responses have been found for different subcategories of content words.

Fuster emphasizes that Hebb's second learning rule is most relevant for explaining memory and language mechanisms in the human brain. According to this rule, frequent coactivation of two cells or systems leads to association and subsequent mutual facilitation of neurons, a prerequisite for considering them a functional unit. As far as memory is concerned, Fuster has provided compelling evidence that this second Hebbian principle is correct (Fuster 1995). Those who believe that higher cortical functions can be explained at the level of molecules, membranes or single-cell dynamics without considering information processing in large networks will eventually be convinced by his findings that (1) tonically active neurons can store specific memory contents (Fuster & Jervey 1981), (2) such neurons can be found in distant sensory/posterior and motor/frontal areas (Fuster 1997b), and (3) functional disturbance (transient cooling) of neurons in either the sensory or motor areas leads to a reduction of stimulus-specificity of the neurons in the respective other areas (Fuster et al. 1985). I can only hope that equally strong evidence will some day be available regarding language mechanisms. However, the data obtained by Fuster and his conclusions regarding memory are clearly relevant for any neurocognitive model. For sensory-sensory, sensory-motor, and motor-motor associations established during word learning, specific synaptic strengthening in various parts of the perception-action cycle are necessary.

Why there must be distributed neuron populations in the cortex that are relevant for cognitive processing and how these populations may be organized has hardly been spelled out more clearly than in the work of Damasio and his collaborators, for example, Damasio (1989b) and several more recent publications, among them the commentary by **Tranel & Damasio.** Sensory-sensory associations between neurons in primary somatosensory, auditory, and visual cortices, and sensory-motor associations between cells in primary motor and auditory cortices cannot be direct, because the necessary powerful, direct cortico-cortical pathways are not present, as can be inferred from studies in the monkey (Deacon 1992a; Pandya & Yeterian 1985; Young et al. 1995). Hence association between modalities involves neurons in further areas that Damasio calls "convergence zones" or "intermediary regions." It is by these "third party" neurons that the knowledge about an entity is held together. Most important, Tranel & Damasio consider the union of all these neuronal populations (sensory and intermediary) to be a multi-component network, each part of which is "necessary for the optimal retrieval" of the entities stored. The assumption that activating each part of the distributed system is *a necessary condition* for the respective cognitive operation comes very close to the concept of distributed cell assemblies reaching into sensory and motor cortices and involving many neurons in association cortices. Thus, the notions of cell assemblies and convergence zones appear compatible, if not identical.

There is also agreement about the factors determining where the relevant association cortices should be localized. The modalities through which information is transmitted (e.g., visual or motor), overall and finer-grained characteristics of an object (e.g., whether it is colored and usually moves), and the context in which it frequently occurs (e.g., whether it is grasped by the hand) will certainly be important, as will the placement and specialization of the cortico-cortical information pathways involved. This has been pointed out in earlier associationist work (McCarthy & Warrington 1985; Warrington & McCarthy 1983; 1987; Warrington & Shallice 1984). However, these statements leave many questions unanswered, thus, there is room for diverging empirical predictions.

Predictions of the cell-assembly (CA) and convergence-zone (CZ) frameworks about the involvement of temporal structures in the retrieval and processing of word-related meanings do not differ as far as the temporal lobe in the left hemisphere is concerned (although the reasons for postulating different localizations may differ, see target article, sect. 5.2). There is a discrepancy about the representation of words referring to actions: Damasio postulated that the inferior frontal lobe, roughly Broca's area, houses the convergence zone for verbs (Damasio & Damasio 1992). In contrast, according to CA theory, motor, premotor, and additional prefrontal areas in which meaning-relevant information is processed become relevant. For "to write" and most other action words, this would be the areas dorsal to Broca's area and the motor cortices controlling the articulators. Regarding action verbs, one may argue that the lesion evidence supports the CZ view (Daniele et al. 1994). However, closer examination of single cases (for example, Damasio & Tranel's 1993) shows that areas dorsal to Broca's region are also frequently damaged (because they are supplied by the same blood vessels). Thus, at present the lesion evidence appears to lead to a draw in this case.

Different predictions of the CA and CZ frameworks are also obvious for laterality. The laterality indicator differences for content and function words (see target article, sect. 5.1) are consistent with the CA predictions, but not with the CZ approach according to which left-hemispheric areas should house third-party regions for most words. There is also the following more general difference: Damasio has usually specified one particular area as the convergence zone of a category (e.g., in people – anterior temporal, in animals – middle inferior temporal, tools – posterior temporal); the Hebbian approach would suggest multiple

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convergence zones or association areas for any cell assembly involved in cognitive processing. For example, the relevant binding sites for function words (and all word forms) would be both the anterior and posterior perisylvian cortices. For content words and their associated meanings, the binding sites would include these areas and additional association cortices strongly connected to both perisylvian sites and meaning-relevant primary cortices, in both hemispheres. Clearly, in addition to neuroimaging data, further evidence is needed to decide whether the latter strong predictions are correct (see sect. R4 below). It should be clear, however, that CA and CZ approaches do not differ in the specificity of their predictions or their potential explanatory power, but in that they make different predictions about word processing in the brain.

Salmelin et al. call attention to the fact that neural networks presented with word strings (and nothing else) can learn to categorize these into lexical categories, such as noun and verb (see Elman 1990 and the papers cited by Salmelin et al.). That is, the activity patterns caused by these words, for example, in a hidden layer, will become similar for items from the same lexical category. This occurs because the network stores which other elements frequently co-occur with a particular word. Because words from the same lexical category frequently have the same neighbors in the string (e.g., a noun frequently has the articles "a" and "the" to its left and a verb or a full stop to its right) their representations become similar. These simulations show that there is reason to postulate that syntactic categories develop in the brain during language acquisition. They were not discussed in the target article because they do not lead to topographical predictions. These simulations show that neuronal populations differentiating between lexical categories should eventually develop. They do not allow for predictions about where these differentiating neurons are located.

Most likely, the scenario outlined by **Culicover & Nowak** is more realistic than the Chinese room learning situation addressed by **Salmelin et al.:** The brain acquires semantic representations of (content) words, probably based on correlations between words and nonlinguistic stimuli and therefore involving different cortical areas. In addition, the network is confronted with grammatical word strings so that lexical categories differentiate, probably caused by learning co-occurrences between words. The latter type of associative learning should lead to an inclusion of additional neurons into the assembly – as was pointed out early by Milner (1957) – and, of course, to a strengthening of connections between word representations. The perisylvian cortex (but not the meaning-related neuron populations outside) are arguably the locus of these syntactic wirings. Table R2 presents our predictions as to where in the cortex different kinds of linguistic information are stored (Pulvermüller & Schumann 1994).

R1.5. Plasticity. It is stressed by **Elbert et al.** and **Posner & DiGirolamo** that there should be plasticity of word representations in the cortical network. The Hebbian framework is far from denying plasticity. Plasticity is a necessity in any associationist model and the Hebbian mechanism provides an explanation of it. Word repetition effects and, most important, the word frequency effect in cortical responses (see target article, sect. 4.3) can be explained using the assumption that the more frequently a cell assembly becomes active, the stronger its internal connections become. Posner & DiGirolamo mention recent PET studies in which a verb generation task with the same stimulus words was repeated over and over and a reduction of perisylvian activity was found (Raichle et al. 1994). I am not sure whether this difference needs to be attributed to word repetition and plasticity of linguistic networks. It could just as easily be that a search process for a word matching the task requirements is invoked only after initial presentation. When the stimulus words are repeated, the already primed assemblies can ignite – without further search in the network. Earlier psychophysiological work has shown that word search leads to strong perisylvian activation in the left hemisphere (Rösler et al. 1993). Thus, the PET results mentioned do not allow for strong conclusions on plastic changes of the distribution of cortical networks related to word processing.

Table R2. *Connections and cortical areas most relevant for the storage of different types of linguistic knowledge, as proposed by Pulvermüller and Schumann (1994)*

	Perisylvian areas		Other cortices
	Primary/secondary cortices	Broca & Wernicke	
Long distance connections (A-system)	Word forms	Semantics	
Local connections (B-system)	Phonology	Syntax	

The relevant cortical areas include perisylvian sites, that is, primary areas (1–4 and 41, see Fig. 2, target article), the additional higher-order perisylvian sites (e.g., 22, 31, 40, 44, 45), and extra-perisylvian regions (e.g., association cortices). Long-distance connections linking different perisylvian sites are most relevant for knowledge about word forms, and long-range connections from perisylvian space to other areas are crucial for semantic knowledge, as detailed in the target article. Local connections in the perisylvian areas are important for storing phonological information and syntactic knowledge. It is important to mention that long-range ("A-system") and local ("B-system") synaptic links are mainly localized in upper versus lower cortical layers, respectively (Braitenberg & Schüz 1998). Adapted from Pulvermüller and Schumann (1994).

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R1.6. High-frequency brain response. It is correctly pointed out by **Kalbe & Thiel** that dynamics in the high-frequency (HF) EEG and MEG > 20 Hz do not prove the existence of cell assemblies. The target article states that dynamics in HF responses following linguistic stimuli were predicted based on CA theory. The finding that HF responses differentiate, for example, between words and pseudowords can now be explained in this framework. For one of the results (different cortical topographies of HF responses to words with visual and action associations) it is difficult to see how competing theories (e.g., that global subcortical "clock pulses" determine cortical HF activity) could provide an explanation. The results on HF responses to language stimuli support the cell-assembly framework, but do not prove my view correct, that is, they do not exclude better future explanations.

Why should cell assemblies produce HF activity? **Miller** writes that neurophysiological data (summarized in Miller 1996) indicate slow axonal conduction times. This is correct, but the relevant studies were conducted in small mammals in whom conduction times may well be slower than in humans. In the target article (sect. 2), it was assumed that most cortico-cortical fibers conduct action potentials quite quickly, around 10 m/s: to be on the safe side, let us say 5–10 m/s. This rests on the following evidence: (1) In a neuroanatomical study of axons in the human corpus callosum Aboitz et al. (1992) found that the majority of long-distance cortico-cortical fibers are myelinated and have a diameter of around 1 μm. (2) Estimates of axonal conduction times indicate that 1 μm axons conduct their action potentials at around 5–10 m/s. Of course, these data and estimates can be criticized (see, for example, Miller 1994), but to my knowledge no better data and estimates for humans are available. If a wave of activity reverberates in the short distance- and long distance-loops of the assembly illustrated in Figure 3 of the target article, reverberations between the anterior and posterior language areas (which are some 10 cm apart) will be present after delays of around 20–40 msec (and the local loops may produce even faster reverberations). Thus, if the present concept of a cell assembly producing reverberations is correct, it must generate strong high-frequency responses. It may produce additional low-frequency activity as well, but the relative sparseness of thin myelinated and unmyelinated axons (Aboitz et al. 1992; La Mantia & Rakic 1990) suggests that slow reverberations are less common. This argument is further elaborated and grounded in calculations of round-trip times in various cortico-cortical loops in an article in Miller's forthcoming book on cortical dynamics (Pulvermüller 1999a).

As can be seen when looking at Hebb's simplified illustration of a reverberating cell assembly (Fig. 1, target article), the network will produce multiple reverberatory frequencies when active. The loops formed by neuronal populations 1-2-3, 5-6-7-8, and 9-10-11-12-13-14 lead to gradually longer round-trip times and therefore the frequencies produced by a wave of excitation will affect several frequencies. A single neuron involved in several such loops will probably change between several preferred frequencies. This may be related to **Fuster**'s finding that certain neurons show an increase in firing frequency transitions during active memory epochs. The finding that oscillatory activity decreases when specific cognitive processes are required (Zhou et al. 1997) corresponds to our result from MEG experiments that HF responses sometimes decrease relative to the baseline preceding presentation of the relevant stimuli (see Fig. 8, target article). At rest, there appears to be more activity in a certain HF band, and after a stimulus requiring a specific cognitive operation this activity decreases. A possible explanation is that what is considered a "resting state" is actually used for task preparation, a process necessitating much cortical activity, as demonstrated in many psychophysiological experiments (Rockstroh et al. 1989).

Strong HF activity obtained before stimulus onset may always reflect preparatory processes. However, comparing differences in the responses to similar stimuli (different tactile stimuli, words, and pseudowords) allows much stronger conclusions than just a comparison to the baseline. This fact is ignored by **Salmelin et al.,** who take the decrease of HF activity after pseudowords relative to rest obtained in our first MEG study (Pulvermüller et al. 1996a) as a reason to call the proposed interpretation "somewhat ambiguous." However, no strong conclusions can be drawn from a comparison of a condition in which a well-defined cognitive process occurs, and another condition for which the cognitive processes are entirely unclear and may strongly vary across individuals. Correspondingly, the differences in HF responses between baseline and word/pseudoword processing varied greatly across experiments. Sometimes there was a decrease and sometimes an increase. However, stronger HF activity during word processing relative to pseudoword processing was always obtained. This difference can be interpreted using the assumption that words, but not pseudowords, elicit reverberation in cell assemblies specialized for words.

Ivanitsky & Nikolaev propose an extension in which cell assemblies are envisaged to oscillate synchronously, and cortical "interaction foci" produce synchrony in distant assemblies. Although this idea is interesting, the present proposal assumes that distant cell populations are coordinated by strengthened long-distance cortico-cortical connections through which waves of excitation can travel. **Haase & Rothe-Neves** speculate that whereas neuronal synchronization is related to categorization and abstraction, oscillatory activity is involved in sequencing. The problem with this is not that hypotheses are presented, but that it is unclear which neuronal circuitries Haase & Rothe-Neves have in mind that could produce these cognitive processes and physiological responses. Merely saying that a particular cognitive process is indicated by a physiological response is a good thing, but clarifying the wheres, whys, and hows of the underlying networks is better.

R1.7. Cortices for processing meaning. Which cortical areas engage in the processing of word meaning (or lexical meaning)? Based on PET and EEG data, **Posner & DiGirolamo** favor left inferior frontal areas; **Salmelin et al.** report MEG evidence that the left superior temporal lobe is relevant; in **Tranel & Damasio**'s framework the role of the left inferior temporal lobe should probably be emphasized based on both lesion evidence and PET data; **Skrandies** reports EEG studies suggesting the occipital lobes, and **Epstein** makes reference to the neuropsychological model by Geschwind (1970) and considers the angular gyrus at the boundary of the parietal, temporal, and occipital lobes as important for all word meanings. Figure R1 illustrates how widely the opinions about the loci of word meaning differ. Regarding word semantics, Posner & DiGirolamo's statement that "there is some dispute about

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the exact areas involved" is absolutely correct. And the discussion would have been even more controversial if those who advocate the right hemisphere's role in lexical and semantic processing (Paivio 1986; Zaidel 1985) had participated. In contrast to all of these views, the target article proposes that no single area, gyrus, lobe or hemisphere specializes in semantics; the entire cortex contributes to the processing of word meaning and semantic properties of words determine which areas become relevant. This view follows from Hebbian correlation learning, and is supported by (or, at least, consistent with) the neuroimaging studies summarized in section 5 of the target article. Part of the considerable variance in the studies on word meaning may arise because processing loci change as a function of semantic word type (as detailed in sect. 3 of the target article).

An important issue is raised by **Posner & DiGirolamo:** Different cortical areas may be relevant for processing word meanings and sentence meanings. Posner's recent data strongly support this view (Posner & Pavese 1998). Eventually, we will need a neuroscientific theory explaining why this is so.

A remark is necessary about the distinction between perisylvian and "extra-perisylvian" areas. Above, meaning processes were sometimes attributed to the latter. This is not appropriate. As **Miller** points out, words referring to sounds or sound-producing objects may well have cell assemblies, including neurons related to the cortical processing of these sounds. Thus, the acquisition of their meaning would correspond to the inclusion of additional perisylvian neurons in the already established perisylvian network. In addition, Miller is right that these "sound words," unlike other content words, may be organized as strongly lateralized assemblies.

Word meanings are accessed early. Physiological studies already indicate meaning-related word-class differences around 200 msec following stimulus onset or even earlier (see target article, the early study by Brown & Lehmann, 1979, and the more recent ones by Posner & Pavese 1998 and Skrandies 1998). Early access to lexical meaning has also been stressed by **Posner & DiGirolamo. Skrandies** suggests even earlier access to one type of meaning called *affective meaning* (this will be discussed in sect. R3). The fact that cortical indicators of the processing of meaning are present around the time when word responses diverge from pseudoword responses is consistent with the view that semantic and phonological word features are accessed almost simultaneously. This agrees with the concept of cell-assembly ignition, that is, synchronous or near-synchronous activation of all assembly parts. Axonal conduction times suggest that the relevant delays are on the order of 10–20 msec (see sect. R1.6).

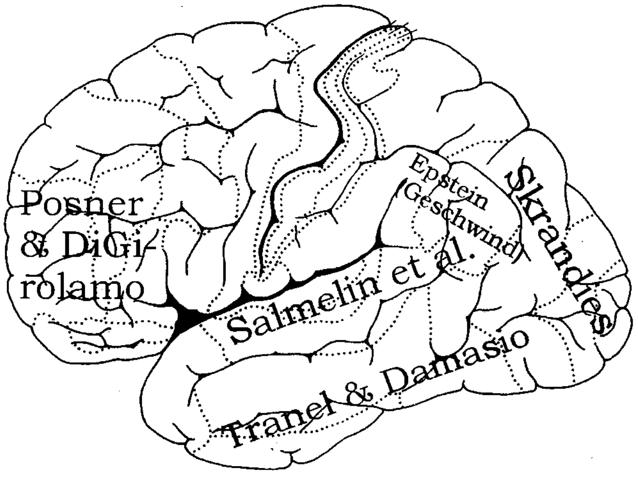

Figure R1. Opinions about the cortical loci relevant for processing word meanings differ widely among researchers. This figure summarizes views put forward in the commentaries. In contrast according to the cell assembly approach, all cortical areas in principle can become relevant, depending on aspects of the meaning of the words (see target article, sect. 3, and Figs. 3–5).

R1.8. Interhemispheric interaction and laterality. Only about half the information about a word presented visually at fixation is transmitted to each hemisphere, **Shillcock & Monaghan** argue. This proposal is grounded in neuroanatomical evidence that there are no bilateral foveal projections in humans (Brysbaert 1994). For identifying the word, interhemispheric interaction would therefore be necessary. I fully agree that these neuroanatomical data support this conclusion. Shillcock & Monaghan further suggest that splitting a word in the middle creates two maximally informative parts and that such splitting actually facilitates word processing. However, one may call for more direct evidence of positive effects of interhemispheric interaction on word processing. Here it is necessary to recall a few studies addressing this issue.

Words were presented in either the left or right visual half-fields. As a third condition, they were presented twice, simultaneously to the left and right of fixation. The surprising result was that bilateral presentation of a word led to faster and more accurate responses in a lexical decision task than unilateral presentation. The responses to bilateral presentation were even superior to the condition in which the language-dominant (left) hemisphere was stimulated directly (right visual field presentation) (Mohr et al. 1994b; 1996; Zaidel & Rayman 1994). In the split-brain patient L. B., bilateral word presentation did not lead to processing improvement (Mohr et al. 1994a), nor was improvement present for pseudowords presented bilaterally in healthy individuals. These results indicate: (1) that information exchange between the hemispheres can improve lexical processing, even relative to processing after presentation to the language-dominant hemisphere alone; (2) that this information exchange depends crucially on the intactness of the callosum; and (3) that it occurs for linguistic stimuli for which a cognitive and neuronal representation can be assumed, but not for uncommon pseudowords of similar perceptual complexity. These data support the postulate that cell assemblies processing words are distributed over both hemispheres (interhemispheric cell assemblies) and that neuronal excitation can summate in these strongly connected neuron populations (Pulvermüller & Mohr 1996).

Miller believes that sentence planning involves both hemispheres. According to his view, sentence meaning is processed in the right hemisphere and syntactic structures are dealt with in the left. Also according to this view, interhemispheric interaction would be necessary for processing sentences. However, although this is certainly possible, one should recall the evidence for bilateral processing already at the level of the processing of single words (sect. 5, target article). Interhemispheric interaction may therefore already occur when words are being processed.

Kalbe & Thiel doubt whether right-hemispheric activity is at all relevant for language. They cite their own study

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of aphasia patients with reactivation of left-hemispheric language areas. It is necessary to stress, however, that there are also patients whose entire perisylvian region in the language-dominant hemisphere has been damaged but who nevertheless reacquire some ability to use words (see, for example, Pulvermüller & Schönle 1993). There is no other possibility here except recruitment of circuitry in the right cortical hemisphere. Even the verb generation task, used frequently because it produces nice left-hemispheric activation foci, sometimes leads to right-hemispheric activation. Kalbe & Thiel assert that this was stated in the target article without citation. However, a MRI study by McCarthy and colleagues (1993) was cited in which left inferior-frontal activation was found during verb generation plus activation of homotopic right-hemispheric areas. Bihemispheric temporal activation related to word frequency was reported by Price et al. (1992). The target article summarizes additional reports on right-hemispheric activation during other word processing tasks (see also the review by Petersen & Fiez 1993). In addition, the physiological studies (EEG and MEG) indicating differential right-hemispheric involvement in the processing of word categories (target article sect. 5.1) cannot be ignored. These data are consistent with bihemispheric but lateralized word processing, as proposed in the target article.

Posner & DiGirolamo suggest that right hemispheric activation is optional and can be recruited for aiding word processing. Optionality of right-hemispheric processes is also indicated by data on neuropsychological patients with lesions in their right nondominant hemisphere who very rarely suffer from overt aphasia. However, it may well be that lesions in the right nondominant hemisphere can lead to fine-grained but specific deficits in word processing that are detectable only in psychological experiments. In this case, the right hemisphere would be optional for passing aphasia tests, but not for achieving good performance in these psychological experiments (Pulvermüller et al. 1998). Future research is needed to clarify the role of the right hemisphere in word processing (see sect. R4).

R1.9. Subcortical circuitry. The possible role of subcortical mechanisms in a network of cortical cell assemblies has been stressed in the discussion of inhibitory processes above. In addition, we (Pulvermüller & Schumann 1994) have suggested that subcortical connections of assemblies through limbic structures such as the amygdala and dopaminergic nuclei in the midbrain are relevant for storing aspects of the affective meaning of words. Although the target article dealt mainly with cortical processes, it is clear that the cortical assemblies may have subcortical tails.

The need to realize affective or emotional aspects of meaning in a brain model of language is also emphasized by **Jorion,** who proposes an interesting functional role: If cell assemblies related to words were associated with the machinery controlling emotions, some words may acquire links to subcortical cell populations producing positive emotions so that they could be used as self-reinforcers during subsequent language use. Schumann (1976; 1978; 1986; 1990; 1997) used a related idea to explain why although some individuals can learn a second language quite easily after puberty, others living in the same environment fail almost completely and remain at a low-level pidgin.

Tucker suggests that different contributions of neocortical areas to language processes may be less relevant than the contributions of limbic and paralimbic structures; paralimbic cortices and nuclei may be relevant for semantics and temporo-limbic structures could relate to syntax. This is certainly a possibility, but it is not yet clear to me how this specialization could be rooted in Hebbian learning or in other biological learning mechanisms.

Memory networks appear necessary for storing both content and function words, and memory processes are important for both semantic and syntactic analysis. Nevertheless, **Tucker's** view is an alternative to the proposal about content/function word representation in the target article.

R1.10. Local cell assemblies. The inner structure of a cell assembly as outlined in the target article would be the following: Local neuron clusters are housed in a small cortical locus represented by circles in Figure 4. These are held together by local cortical connections (probably mediated by local axon collaterals and basal dendrites). Several of these local clusters can be located in one cortical area or in adjacent areas, for example, the anterior perisylvian cortex. Short-distance cortico-cortical axon bundles represented by short lines in Figure 4 are the basis of these semilocal groups. It is important to note that there are long-distance cortico-cortical fibers between these areas allowing for the formation of a distributed functional unit, a (transcortical) cell assembly, as illustrated in Figures 4–6. The neuroanatomical basis of such transcortical assemblies would be axons going through the white matter and reaching apical dendrites of pyramidal cells in distant areas.

It is certainly possible that the local clusters have only weak links and can therefore be regarded as quasi-independent "modules" of cortical processing. In contrast, the present theory postulates that widely distributed functional units are the neuronal counterparts of words. Arguments in favor of this view (and against the localist perspective) include the following: (1) Word presentation induces activity in various cortical areas almost simultaneously. (2) Focal lesions in one of several cortical areas lead to multimodal language disturbances (sect. R4). (3) In terms of the numbers of their synapses, the network of local cortical connections is about as powerful as the system of long-distance links (see Braitenberg & Schüz 1998).

Ivancich et al. propose not to speak about one assembly in which information about word forms and semantics are bound together. They prefer to distinguish two separate cell assemblies linked by mediating connections that make mutual activation of assemblies likely. I am not sure whether this is equivalent to the description in the target article. If so, there is no problem. However, Ivancich et al. may mean that the connections between phonological and semantic maps are somewhat weaker than those linking the aspects of a word form or the features of an object. Access to word forms and word meanings should therefore be dissociable, not only by a cortical lesion – which can, of course, destroy assembly-internal links, thereby separating what is closely tied together in the intact cortex (see sect. R4) – but also in the intact and attentive brain.

In the intact brain, however, it appears that hearing or seeing a word form automatically and immediately leads to its comprehension. As already mentioned, the comprehension process is invoked so fast that physiological signs of the processing of word meanings can be detected some 200 msec after the onset of letter strings or even earlier. In an analogous way, access to word forms may automatically fol-

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low presentation of a picture of an object, as pointed out by **Tranel & Damasio:** "In fact, one cannot willfully stop one's brain from attempting to retrieve the word form along with the meaning." However, **Posner & DiGirolamo** call attention to the evidence that passive viewing of a word did not lead to activation of perisylvian sites provided by one of the classical PET studies on language (Petersen et al. 1988). This suggests that the (perisylvian) phonological machinery does not necessarily ignite together with the representation of the visual word stimulus. Recent PET results, however, indicate otherwise. To quote from a paper by Price et al.:

> This study demonstrates that even when subjects are instructed to perform a nonlinguistic visual feature detection task, the mere presence of words or pseudowords in the visual field activates a widespread neuronal network that is congruent with classical language areas. The implication of this result is that the subjects will process words beyond the functional demands of the task. (Price et al. 1996)

This suggests that passive word viewing lights up cortical sites related to the processing of phonological information.

These data do not refute the concept of an ignition involving assembly parts related to both semantic and phonological knowledge. However, **Ivancich et al.** provide theoretical arguments aimed at such a refutation: "Because one can have a word without a concept or a concept without a word, the assemblies [for phonology and semantics] are separate." This argument is by no means convincing, however. In the case of a word without a concept, that is, a pseudoword such as "sherfel" or "reitoon," there is no correlation between word form and nonlinguistic stimuli, and hence no reason for assuming a higher-order assembly binding phonological and semantic information. The same point can be made for concepts without words. Furthermore, Ivancich et al. suggest that it is easier to deal with homophones and synonyms in a network if phonological and semantic information are only "highly associated" but do not form a higher-order assembly. However, the problems remain the same: the homonyms or synonyms must exclude each other when a homophonous word form is perceived or when an object with two names must be referenced. For such mutual exclusion, inhibitory processes such as the striatal inhibition mechanism described above must be postulated (sect. R1.4).

Also in the convergence zone framework of **Tranel & Damasio,** Hebbian learning mechanisms are one of the driving forces. Because, as these authors correctly point out, words and the concepts they relate to are hardly processed separately, it is imperative to postulate frequent coactivation of their neuronal representations and strong association of neurons in the respective convergence zones. Concept and word representations are accordingly distinct anatomically (perisylvian vs. extra-perisylvian) but form a functional unit.

In conclusion, the concept of transcortical cell assemblies processing word forms and their meanings together in the intact, aroused, and attentive brain appears to be tenable. More arguments in favor of this view will be provided in section R4 below.

R2. On method

R2.1. Task similarity and double dissociations. Two general criticisms by **Jacobs & Rösler** address the methodological remarks in the target article. These authors argue that without a criterion for similarity of experimental tasks derived from a cognitive model, it is impossible to follow my suggestion to choose maximally similar tasks in experiments designed to test word-class differences. This implies that, to realize that verb generation is closer to word reading than to looking at words, it is necessary to have an explicit statement of the subprocesses involved in these tasks. However, the problem addressed by Jacobs & Rösler does not arise in the target article: "Maximally similar" means identical for all practical purposes addressed in this text. If word class differences are searched for, it is best to keep the task – for example, lexical decision or naming – constant rather than comparing generating verbs to reading nouns. For judging task identity, no additional theory is necessary.

The second criticism presented by **Jacobs & Rösler** addresses the concept of a physiological double dissociation. A double dissociation is present if condition 1 produces stronger activity than condition 2 in cortical area A, while in area B condition 2 activates more strongly than condition 1. It was argued in the text that, instead of predicting only an increase or decrease in brain activity or a difference in only one region of interest, the prediction of a double dissociation is stronger. Hence if the corresponding double dissociation manifests itself in a significant crossover interaction of the factors Task × Region of Interest, this allows for stronger conclusions.

Jacobs & Rösler argue that this is only correct if the crossover interaction results from differences in brain activation *across* regions of interest in all conditions. If one of the conditions leads to similar activity values in all regions of interest, they consider the possible conclusions "of limited use" for a neuropsychological or neurobiological model of cognitive function. To illustrate their point, they present three tables in which hypothetical activity levels (or "vectors") are listed. All three tables list physiological double dissociations of "raw score vectors," but the activation values vary across regions of interest only in the first table. According to the other two tables, one of the tasks leads to constant activity across regions of interest. As I understand them, these commentators only consider the physiological double dissociations in the first table meaningful. However, this rests on the assumption that "raw score" values and their variation across areas can be easily interpreted in neuroimaging experiments, but this is incorrect. Different cortical areas have been found to exhibit quite different activity levels after subjects were merely asked to lie down and rest (see, e.g., Martin et al. 1991). For example, in typical resting states spectral power in the alpha-band is usually found to be most pronounced at occipital leads. Hence the finding of strong alpha at location Oz and weak alpha at frontal leads in a particular experimental condition (that is, the pattern to be expected at rest) is not of higher theoretical interest than constant alpha power across these sites. The same argument applies to other physiological measures and imaging techniques. Activation values can only be interpreted relative to an adequate control condition.

Jacobs & Rösler may want to argue that the values they list in their tables are not, as they write, "raw score vectors" but are meant as values relative to a baseline. Let us consider their argument after this reinterpretation: here, the problem is that an adequate baseline is extremely difficult to find. One may argue that a "resting condition" induced by an instruction such as "lie down and think of nothing"

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may be adequate, but it is clear from the history of neuroimaging that this is not correct. PET studies (Metter 1987) have been criticized, because they compared activity during rest between healthy subjects and clinical populations (Bachman & Albert 1991). The mental activity these individuals engage in while "resting" in the scanner are not controlled, and their brain activity patterns are therefore difficult to relate to cognitive processes (or to their absence). This uncertainty, immanent to any "resting" condition, also makes the interpretation of values relative to "rest" difficult. In contrast, interpretating the direct comparison of two well-controlled experimental conditions is straightforward. (See also Posner & Raichle 1995.)

To sustain **Jacobs & Rösler**'s argument, it is necessary to assume that an adequate baseline can be obtained. These authors may argue that this is a problem for PET studies, but no problem in EEG research where the baseline can be obtained immediately before stimulus onset. Yet one can also question whether a pre-stimulus baseline can be considered a "resting" condition. Preparatory processes are known to be linked to electrocortical activity with specific topographies (for example, CNV-like components maximal at frontal leads; see Rockstroh et al., 1989, for review). This is one reason why many investigators of cognitive processes prefer to interpret difference waves elicited by well-controlled conditions (for example, the mismatch negativity; Näätänen 1990; 1995; Näätänen et al. 1978), instead of pre-/post-stimulus differences.[3] This is in line with the proposals in the target article.

Still, **Jacobs & Rösler** may argue that if the baseline before stimulus onset is assumed to reflect "rest," their argument could be sustained. This would be incorrect, too, however, because any stimulus produces not only processes and brain responses specific to task and stimuli, but it necessarily causes brain activity common to the conditions. The polarity and strength of *unspecific activity* – which manifests itself as a pattern of ups and downs (with a specific topography) in the evoked response – is difficult to separate from the specific responses. If a third condition aiming at producing only unspecific activity is compared to the two critical conditions, Jacobs & Rösler's argument could probably be sustained. But as to my understanding this is not what these authors have in mind. Hence, again, in the investigation of higher cognitive functions direct comparison of well-controlled conditions is more conclusive than that of values relative to their pre-stimulus baseline.

R2.2. Presenting single words. Several commentators suggest validating the results with single word presentation using words embedded in sentences (**Greenberg & Nisslein, Haase & Rothe-Neves, Osterhout & Bersick, Salmelin et al.**). I had summarized studies on electrocortical differences between content and function words with both sentences and isolated words (sect. 5.1). In both kinds of study, function words were followed by left-lateralized components which were not present for content words that elicited more symmetrical responses over the hemispheres. This suggests that context does not have an important influence in this case. Also, Osterhout et al. (1997) suggest that random presentation of single words versus in-text presentation of the same stimuli yield a global difference after around 400 msec (content words) and more than half a second after stimulus onset (content and function words). This is consistent with earlier findings (Van Petten & Kutas 1991). Thus, at present there is no indication that the *early* word class-differences in the topography of brain responses (150–300 msec after stimulus onset) found in some of the studies would be affected.

One should nevertheless emphasize that even if in-context presentation were to cancel the differences seen in single word-conditions, this would not falsify the proposed model. Any model of word processing needs to be tested in experiments where single words are processed and confounding factors are as far as possible excluded. It is important to ask how cortical cell assemblies representing words are linked to each other and on what functional principles serial order of words is based. To find out, experiments using coherent word strings are needed. Insofar as the evidence available to date addresses this, it appears that **Greenberg & Nisslein** are right: brain responses to words can indeed change with context (Brown & Lehmann 1979; Rösler et al. 1998), and the processing of sentence meaning is electrocortically distinct from the processing of word semantics (Posner & Pavese 1998). However, it is not generally "more productive to examine the way words combine" (**Haase & Rothe-Neves**). This depends on the purpose of the study. If context effects are sought, in-context presentation is imperative, and if word processing is the target, single words are fine. It is essential in both kinds of experiment to avoid confounds, for example, from the other of the two variables. As a next step, the interaction of context types and word type can be systematically investigated.

Osterhout & Bersick argue against avoiding confounds; they believe "it is impossible to identify all the relevant dimensions." However, it is certainly possible to match stimuli carefully to exclude all *likely* confounds evident from earlier studies (as pointed out in the target article, sect. 4.3). This reflects the standard in experimental psychology. This is more fruitful than not caring about confounds and then trying to get rid of them after the experiment using correlation analyses, as suggested by Osterhout & Bersick. Why not avoid them in the first place? Arguments against their correlation strategy are the following: First, it runs into exactly the same problem of identifying relevant stimulus dimensions. Second, it is not clear whether correlations help when the factors under investigation (such as word frequency and length) are themselves highly correlated. In this case, it is difficult, if not impossible, to separate their influences through correlation (see Osterhout et al.'s 1997 study). Third, correlational analyses are based on special assumptions one may or may not share (such as the linear or exponential increase of one variable with the other). Fourth, if word frequency (or any other variable) varies with the latency of a word-class distinguishing component (as reported by Osterhout et al. 1997), differences in overlap between specific and nonspecific components (e.g., N1, P2) can account for differences in topographies of word-class responses. Thus, as Osterhout et al. (1997) themselves write, any topographic specificity (or non-specificity!) of word-class components observed in such a study "may be wholly or partly due to the effects of component overlap" (p. 165). It follows that the kind of study Osterhout & Bersick suggest is inadequate for investigating topographies of word-class-specific brain responses.

The problems in interpreting the Osterhout et al. (1997) results are even more severe because this study suffers from additional (and unnecessary) confounds, for example, word

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repetition, which strongly influences electrocortical responses (sect. 4.3). Osterhout et al. compared words from different lexical categories, for example, articles, auxiliaries, nouns, and verbs; 100 or more stimuli were taken from each category. There are much fewer than 100 different articles or auxiliaries in English, however, whereas the stories used as stimuli probably included many different nouns and verbs. Apparently, the repetition confound affected word categories differentially. This is another reason why Osterhout et al.'s data cannot provide strong evidence for or against hypotheses about word-class-specific evoked potentials.

What Osterhout et al.'s (1997) study shows is that infrequent and long versus frequent and short words elicit brain responses with different latencies. This is methodologically important because it would follow that averaging of many stimuli varying in frequency (or length) leads to a smearing of specific cortical responses (Pulvermüller et al. 1995a). Thus, it appears imperative not only to match stimuli to these frequencies closely, but to keep the *variance* of these parameters as low as possible. Otherwise, category-specific differences may disappear or appear only at a long latency, when even the longest and least frequent words have elicited their specific components.

Matching stimuli and reducing the variance of stimulus properties implies that the stimulus groups entering the comparisons become smaller. **Osterhout & Bersick**'s concern that these groups may become too small to be representative of the larger category can be met by comparing several pairs of well-matched stimulus sets (or by investigating whether the differences between well-matched items generalize to a less well-matched sample).

Osterhout & Bersick also question the appropriateness of talking about "out-of-context" presentation when stimuli are presented randomly. Clearly, the "context" in an experiment can also influence word responses. But this context is the same for all kinds of stimuli. In coherent text, different word kinds have quite different contexts. This is the reason for speaking about a confound.

Finally, if words have different meanings, one can ask which of them becomes relevant when the words are presented in isolation. This can be clarified by priming studies or simply by asking experimental participants (as detailed in the target article). Applying questionnaires to determine how participants evaluate and interpret the stimuli is also recommended if stimuli do not have homophones.

In summary, I see no alternative to testing brain models of single word processing in experiments using well-matched groups of single words. It is important to investigate brain responses to words presented in different modalities and in different tasks. Clearly, variation of task and modality will change overall brain responses (**Elbert et al., Posner & DiGirolamo, Skrandies**), but topographical differences between word groups should persist.

R2.3. Artifacts. Both **Tucker** and **Urbach et al.** mention possible artifacts that may have occurred in some of the studies summarized. Tucker states that more electrodes are needed for current source density analyses than were available in the earliest studies of high-frequency responses to words and pseudowords (Lutzenberger et al. 1994; Pulvermüller et al. 1994). I should emphasize, however, that more recent studies using 32 recording sites and more led to similar findings (Eulitz et al. 1996; Pulvermüller et al. 1996a; 1996b). Thus, this possible source of artifacts was probably not crucial for achieving the earlier results.

Urbach et al. hypothesize that differences in the latency jitter of high-frequency (HF) responses may account in part for the differences in average 30 Hz-power to words and pseudowords. They propose that words and pseudowords evoke equally strong HF responses but with different latencies: word HF responses would always follow at a certain point, whereas pseudoword responses would exhibit more jitter. If Urbach et al. are right, the time interval during which average 30 Hz-power following words is stronger than it is for pseudowords must be preceded and/or followed by an interval during which the opposite is the case (cf. their Fig. 1B). However, there was no indication of stronger HF responses to pseudowords than to words at the relevant recording sites (see, for example, Pulvermüller et al. 1995b). Also, in some of the studies averages were calculated for rather long intervals (300–500 msec, or 400–800 msec), which confirmed the differences in HF responses. This argues against Urbach et al.'s hypothesis.

R3. Word physiology

R3.1. Content and function words. According to **Osterhout & Bersick,** physiological differences between content and function words are inconsistent over experiments. I would agree if they had said "different" instead of "inconsistent." As pointed out in the target article, there are differences, but also important similarities, and I did my best to relate the differences to differences in the paradigms applied and the stimuli presented. These commentators also propose that in the earliest study addressing the physiological distinction of vocabulary types (Garnsey 1985), no word-class differences were found. This is contradicted by **Chapman,** who provides a precise description of the same results. Importantly, this classical EEG study provides evidence for differential laterality of content and function word responses as well.

Chapman calls attention to the extreme effort and solicitude expended on stimulus selection in the Garnsey (1985) study. This study sets a standard for brain imaging work on language; much of the discussion in section 4 of the target article relates to the insights that led to this kind of experiment. It is accordingly important to emphasize that this work led to a result quite similar to the one confirmed later by Neville et al. (1992), Nobre and MacCarthy (1994), and other studies (among them our own, Pulvermüller et al. 1995a), namely, the differences in laterality of event-related potentials elicited by the major word categories.

As pointed out by **Chapman,** however, there was also an important difference between Garnsey's results and our own. Vocabulary differences in the EEG occurred early (starting at 150 msec after stimulus onset) in our study, whereas they were observed late (around 550 msec) in Garnsey's work. This difference calls for explanation. It is unlikely that the slight difference in response times between our content and function words was relevant, because the early responses elicited by the two word classes were similar except for a difference in amplitude of an early component (an N2 or mismatch-negativity-like effect). Exact stimulus-matching for word frequency and length was also performed in both studies, but there was a difference in the variance of both variables. Whereas variability was

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high in the Garnsey-study (ranges of word length: 3–10 letters, and of log frequencies: 0.5–3.1), it was substantially lower in our study (length: 4–7 letters; log frequencies: 1.8–3.0). If latencies of word-evoked components indeed covary with frequency and length, as suggested by Osterhout et al. (1997) and King and Kutas (1995), it may well be that high variance in these parameters leads to smearing and therefore to either the disappearance or delay in the electrocortical difference (see discussion in "method" above). Hence, the results support differential laterality of content and function word processing, whereas differences in latencies may be related to the factors word frequency and length, and to their variance.

R3.2. Nouns and verbs. It was not mentioned by the commentators that around the time the target article was written, two studies appeared that failed to reveal the postulated topographic differences in cortical activity elicited by nouns and verbs. However, in one of these studies (Warburton et al. 1996) no stimulus matching was performed (because a generation task was the focus of interest), and in the other (Gomes et al. 1997), matching was for word frequency but not length. In addition, the target article suggests that it is semantic word properties (rather than their lexical category) that are relevant for differences in the brain-internal processing. In neither study were stimuli evaluated with regard to their meaning. Hence these results do not weaken the conclusions drawn in the target article.

R3.3. Affective meaning. The target article focuses on one type of meaning, which can be called cognitive or, more precisely, referential. **Chapman** and **Skrandies** emphasize that there are also other types of semantic meaning. One has been called *affective or connotative meaning* (Osgood et al. 1957), which can be broken down into three dimensions, activity (active vs. passive), evaluation (positive vs. negative), and potency (strong vs. weak). In the target article, different but related terms (Lang 1979) were used for two of these dimensions (*arousal* instead of activity, *valence* instead of evaluation). Arousal/activity and valence/evaluation were focussed on because most pronounced differences in word-evoked potentials have been reported for these variables (e.g., see Dietrich et al. 1997; Naumann et al. 1992). Quite recently, Skrandies (1998) reported that all three dimensions of emotional meaning have an effect on latencies and topographies of evoked potentials from about 80 msec after onset of word stimuli presented visually. This new and important finding makes it desirable not only to evaluate stimulus words carefully along the dimensions of arousal and valence (as proposed in the target article), but to evaluate their potency (i.e., whether the entity they refer to is considered strong or weak). This may help disentangle the contributions of affective and referential meaning to word-induced brain responses. On the other hand, it appears worthwhile to investigate whether differences attributed to affective meaning can actually be related to referential word properties.

Skrandies's recent data accord with the studies discussed in the target article, further confirming that brain activity related to the processing of word meanings occurs considerably before brain components that are probably related to the computation of sentence meaning. Important open questions raised by Skrandies's results concern (1) why activity changes related to affective meaning may primarily occur in the occipital lobes, and (2) why they occur so early, even earlier than the word-category differences discussed in the target article. One possibility is that affective or emotional meaning is related to early subcortical processes based on pathways through the amygdala (as proposed by LeDoux 1992), which reach visual cortices.

R4. Neuropsychology

R4.1. The relevance of neuropsychological data. The importance of data from patients with focal brain lesions for neurobiological models of language is stressed by **Tranel & Damasio**. The "lion's share" of the relevant evidence is indeed from neuropsychology (Saffran & Schwartz 1994). However, a model of language processing should not account only for neurological cases. It is best to have a model explaining both neuropsychological syndromes and the behavioral and activity patterns in healthy individuals (Levelt et al. 1991).

Tranel & Damasio also propose that dissociations are easier to find in neurological patients than in imaging studies. There are important differences, however, between the conclusions suggested by neuropsychological and neuroimaging studies. One of these concerns language laterality: some imaging results implicate the right hemisphere in language, whereas most cases of aphasia would not support this conclusion, at least as far as word processing is concerned (**Kalbe & Thiel**). A possible resolution of this paradox (Pulvermüller 1996a) is that the contributions of cortical areas to language (and other cognitive) processes are gradual, with overt neuropsychological syndromes occurring only if an area with a strong role in a particular process is lesioned. Minor processing deficits not significantly affecting performance on standard clinical tasks such as naming and word comprehension may nevertheless be present if an area with a minor contribution to a process is lesioned. For detecting such minor impairments, sophisticated experiments may become necessary; it may be difficult to obtain this kind of evidence in neuropsychological studies without introducing sensible performance measures or neuroimaging. We have recently found a specific increase in error rates when action words had to be processed in patients with lesions involving the motor cortices of the right nondominant hemisphere; processing of other word groups was affected significantly less. Notice that this result supports another prediction of the CA model. These word-class-specific deficits did not surface on clinical tests (Pulvermüller et al. 1998).

Haase & Rothe-Neves think the target article supports modular theoretical notions. I do not see why they harbor this suspicion. Acoustic, articulatory, and semantic aspects of a word are thought to be bound together in one functional unit whose parts are proposed to ignite almost synchronously. What would this have to do with modularity as conceived, for example, by Fodor where these aspects would be thought to be kept separate in different modules? [See also multiple book review of Fodor's *The Modularity of Mind* BBS 18(1) 1985.]

R4.2. Explaining double dissociations. Grossi postulates and **Posner & DiGirolamo** suggest that the CA model cannot explain the neuropsychological double dissociations seen in many cases of aphasia, for example, language com-

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prehension deficits without production impairment, or phonological deficits with intact semantics. The explanation of neuropsychological syndromes and double dissociations is an important issue for any model of brain function; hence a brief excursus is necessary here on our own work (Braitenberg & Pulvermüller 1992; Pulvermüller 1992; 1995a; 1998; Pulvermüller & Preissl 1991; Pulvermüller et al. 1996c; 1998), in which it was argued that an important advantage of a CA model of language is that it provides an explanation of the *syndromes* of aphasia, double dissociations included, and that it should therefore be preferred to modular models.

Let me briefly specify how brain lesions can change the function of cell assemblies. If one neuron in an assembly is lesioned, this may have no effect at all. However, if a certain percentage of its neurons has been removed, the assembly will become unable to serve its functional role in cerebral life, so that it becomes inappropriate to speak about "full" activation or ignition when the remaining neurons are active. The smallest percentage of active neurons (of the intact assembly) necessary for speaking about an ignition can be called the "ignition threshold." If the number of assembly neurons surviving a lesion is smaller than this threshold, the assembly cannot ignite after stimulation, and will therefore be called "destroyed." Clearly, not every lesion leads to the destruction of all affected assemblies. If the damage is moderate, the assemblies will still ignite after appropriate stimulation, but the time needed for the ignition to take place will be longer. This can be illustrated by neural network simulations. Figure R2 gives average ignition times (t∅), cf. Figure 1, and percentage of destroyed assemblies (d) as a function of lesion size (l). The ignition threshold has been set to 70%. It is important that the assemblies tolerate lesions of a substantial percentage of their neurons with only minor ignition delays. However, after a certain critical amount of tissue damage has been reached, the performance very rapidly deteriorates with any further increase of the lesion. The illustrated mechanisms can therefore explain why small lesions, even in the perisylvian core, sometimes do not lead to overt language deficits; they also have obvious implications for progressive neurocognitive impairments. In the context of the present discussion, the simulation indicates that there is an alternative to simulating lesion effects by changing decay constants of neural units, as mentioned by **Code.** Much earlier processes may be delayed or otherwise impaired functionally.

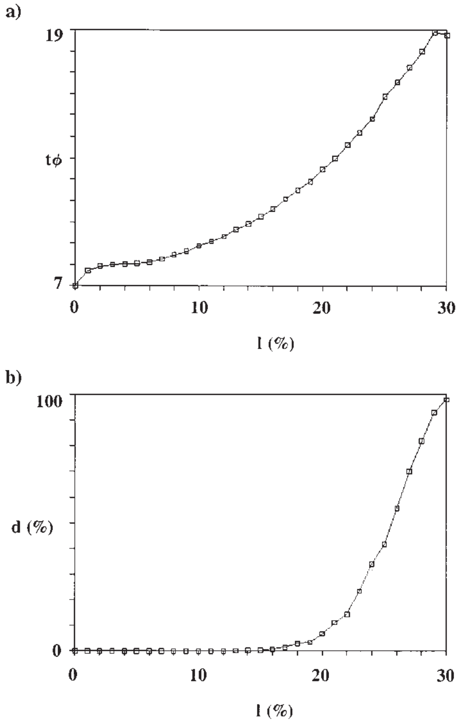

Figure R2. The effects of lesions (l) of different sizes on artificial cell assemblies each including 100 neurons. The ignition threshold was set to 70%, that is, the assembly was called "ignited" if 70 of the 100 neurons were active. As a function of lesion size, the average time t_T needed for an ignition, and the percentage d of destroyed assemblies (which could not ignite anymore) increased. Small lesions did not have a strong effect. In contrast, after removal of some 20% of the neurons, further increase of the lesion caused dramatic dysfunction. Reprinted from Pulvermüller & Preissl (1991).

What would be the effect of a lesion if more specific properties of cell assemblies involved in language processing were considered? Again, the idea is that acoustic, articulatory, semantic, and perhaps other aspects of words are bound together in *functional units* that exhibit specific cortical topographies. This means that these aspects are not functionally separate, although they are primarily related to separate brain areas. **Grossi** seems to have overlooked the second part of this statement. As elaborated in the target article, before learning, articulatory programs are controlled by neurons in the prefrontal, premotor, and primary motor cortex, acoustic properties relate to neurons in the superior temporal lobe stimulated by distinctive features of speech sounds, and input related to word semantics (reference) is exclusively processed in additional brain areas. However, after word learning, that is, after formation of the assembly, all (or most) of these neurons are activated together during comprehension, articulation, and semantic processing. Clearly, as they were functionally separate before learning, the cell groups may as well be functionally separate after their strong linkages have been cut by a lesion, or after part of the assembly has been destroyed.

An intact assembly includes efferent neurons, which control articulatory movements, afferent neurons stimulated by acoustic input, and perhaps additional afferent neurons related to word semantics. These groups can be considered to lie in the *periphery* of the assembly. In the *center* are neurons in various association cortices whose primary purpose is to bind information. Binding sites can themselves be connected to other such sites. Figure R3 shows a network of several partly overlapping assemblies and the way their elements (local neuron clusters) may be distributed over perisylvian cortices.[4] This is of course, a very rough sketch based on several simplifying assumptions. Notice that the equivalent of areas in the temporal lobe are represented at the top and those of the inferior frontal cortex at the bottom. Only the upper- and lowermost neurons in the periphery (upper- or lowermost layers) have efferent or afferent connections.

The problems **Grossi** sees can now be removed by considering the putative neuronal processes caused by lesions. Each lesion in one of the "areas" of the model, either in the center or the periphery, destroys assembly neurons. However, lesions in the periphery lead to additional disconnection of the assembly from its input or output. A moderate le-

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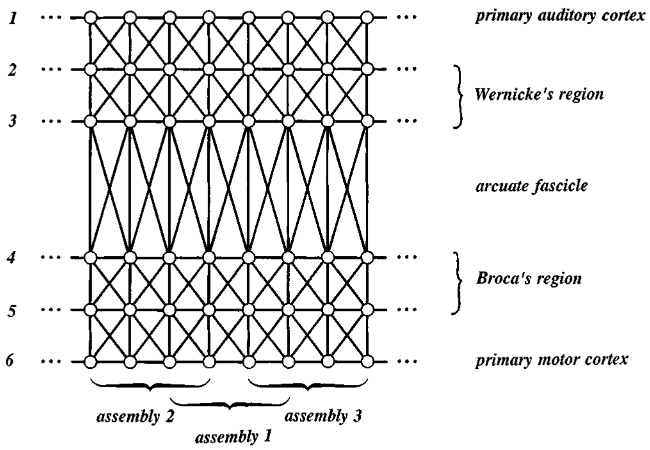

Figure R3. Structure of a network used for simulating the effect of local lesions in the perisylvian cortex. The artificial "assemblies" included neurons in the network-correlates of primary and higher-order perisylvian areas. Lesions in one of the "peripheral" parts of the assemblies (uppermost input or lowermost output layers) led to unimodal processing deficits in the simulation (either "word production" or "word perception"). Lesions in the middle (the network equivalent of Broca's and Wernicke's areas) caused multimodal deficits. Reprinted from Pulvermüller & Preissl (1991).

sion in the uppermost layer may therefore cause only a mild increase of ignition times (if stimulation comes through cortico-cortical input), leaving the assembly largely "intact," but this same lesion may make it impossible to ignite the assembly through its afferent fibers. This impossibility does not necessarily imply that all the assembly's afferent connections have been cut or that all neurons in the auditory input layer have been destroyed. Even removing a few peripheral neurons in the assemblies illustrated in the model can slightly delay their ignitions so that their neighbors, which happen to be affected less by the lesion, can take over and ignite in place of the stimulated assembly. This process corresponds to a failure or error in activating a word-specific assembly, that is, a failure or error in lexical access.

As illustrated by this example, unimodal processing deficits can be explained quite naturally in a CA model. What has been said about auditory lexical access – the process primarily affected in word-form deafness – can be generalized to unimodal production deficit on the motor side. Thus, **Grossi** is wrong in stating that this kind of dissociation "is not predicted by Pulvermüller's word-form model." The relevant arguments have been discussed in great detail in earlier publications (e.g., Pulvermüller 1992; Pulvermüller & Preissl 1991).

Much more important than the explanation of rare cases of unimodal deficits is the fact that most aphasias are multimodal and affect all language modalities, but to different degrees (as correctly noted by **Grossi**). Of particular relevance is the fact that our lesion simulations using cell assembly networks suggest that the closer a lesion is to the periphery of assemblies, the more "asymmetrical" the disturbance will be. Whereas a lesion in the periphery (i.e., input or output layer) leads to a unimodal deficit, a lesion in the next layer causes a multimodal but asymmetric disturbance (strong comprehension deficit but minor production impairment or vice versa), and a lesion in the layers in the middle causes an almost symmetrical pattern of errors. More details about this kind of model can be found in the cited publications, which also explain the difference in production errors between Broca's and Wernicke's aphasia. In providing explanations for typical neuropsychological syndromes, that is, symptom sets, the CA model appears to be superior to modular approaches according to which aphasia syndromes can only be modelled by proposing deterioration of several discontinuous modules (see Pulvermüller & Preissl 1991). The same point has also been made for other types of neural network simulations (Plaut et al. 1996).

Even more interesting explanations of neuropsychological double dissociations can be based on the assumption that cell assemblies have distinct cortical topographies. There are two types of explanation: One is based on the center-periphery argument, the other on different assembly topographies. Based on the latter the double dissociation between agrammatism (function word impairment, perisylvian lesion) and anomia (content word impairment, extra-perisylvian lesion) has been discussed in great detail (Pulvermüller 1995a); other word-category dissociations may well be explained along the same lines. For example, **Shillcock & Monaghan** mention an interesting explanation of why abstract words are misread as concrete words by deep dyslexics. Clearly, these explanations are rooted in cognitive models (for example, Coltheart 1980), but spelling them out in the language of neurons may help to improve our understanding of the relevant mechanisms.

R4.3. Reassembling assemblies. **Code** asks which processes are likely to underlie recovery of function in aphasia. As detailed above, a lesion in an assembly increases the time it takes for an ignition and may reduce the likelihood it will ignite at all. A possible later effect is that the deactivation slope is steeper. For recovery, one option may be to coactivate the rest of the assembly frequently, so that connections strengthen further and perhaps additional neurons can be included. For example, after large left-sided perisylvian lesions, it may be possible to connect the right-hemisphere's assembly-fragments more strongly through intense and frequent stimulation (see Pulvermüller & Schönle 1993). Here the frequency with which training is applied is important. Considering that infants babble several hours a day for several months, one hour of practice daily for a few weeks may not be enough for an aphasic to (re)establish the relevant connections. A second option may be to try to activate critical unimpaired areas that have been shown to be relevant for language. This may be possible using operant conditioning of brain responses recorded in the EEG (Mohr et al. 1998).

An explanation of the complex error pattern of the patient described by **Code** would require some discussion. The summarized simulations by Dell and colleagues emphasizing the role of memory mechanisms can clearly contribute to a better understanding of neurological language disorders. However, my feeling is that an alternative explanation is possible based on the assumption that errors result from an interaction of the effects of the lesion and the pattern of cortical facilitation related to different word processing tasks.

A last remark on **Code**'s comment: There does not seem to be a principled incompatibility between connectionist modelling and the CA approach. Various kinds of networks can be used to model aspects of the neuronal substrate re-

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alizing language, and different models may reflect important aspects of the truth. Clearly, if favoring a CA approach one should not deny seriality: First, information about an articulation enters the assembly at its Wernicke end (uppermost layer in Fig. R2) and then spreads throughout the rest of it. The point is that this ignition is supposed to be an almost instantaneous process, probably taking not much more than 10 milliseconds. Second, there needs to be an internal structure of the assembly determining the sequence of activations of efferent neurons. Without this assumption it would be difficult to explain how an assembly can control the articulation of a word, including well-defined delays between articulators (which may nevertheless vary with the speed of speaking). Third, assemblies can be assumed to ignite in a serial order determined by their mutual connections and internal activity dynamics. Modelling language in the CA framework requires serial mechanisms at various levels.

R5. Behavioral experiments

Spivey et al. and **Greenberg & Nisslein** make a strong point that in addition to imaging evidence (and neuropsychological data), the results of behavioral studies need to be considered when evaluating language models. I fully agree and call attention to the behavioral studies (e.g., those on interhemispheric interaction) mentioned above. Spivey et al. also discuss their own data on eye movement evidence during language processing. This is an interesting approach and the data, which appear supportive of the present proposals, are most welcome. Although behavioral results are usually not interpreted in terms of brain mechanisms at present, such interpretation can be important for further developing neuroscientific models.

R6. Sign language

Dubé & Cohen make a strong point that evidence from native speakers of sign languages is inconsistent with the CA model, according to which areas are superior to the perisylvian region involved in processing signs, because hand movements and visual input are crucial. These authors state that the available evidence fails to support this.

If no cortex dorsal to Broca's area were involved in the processing of sign language, a "pure" associationist account would need to be modified. Such modification could specify anatomical and physiological properties of the neuronal substrate in Broca's region relevant for its primary involvement in processing language, regardless of the input or output modality.

Neuropsychological data show that large left-perisylvian lesions cause aphasia in signers, too, as reported by Poizner et al. (1987). Because these lesions affect both the perisylvian core and the more dorsal areas controlling hand movements, they cannot help decide the issue. However, the case of Karen L. is reported by these authors. She suffered from a relatively small lesion dorsal to Broca's area but extending into the supramarginal and angular gyri. This may provide partial support for the present proposal. Poizner et al. emphasize that a lesion of this kind does not usually lead to persistent aphasia including comprehension deficits, and attribute this patient's aphasia to the posterior areas affected. However, it is likewise possible to relate the deficit to the anterior part of the lesion dorsal to Broca's region. Although this would be compatible with the proposed model, stronger data are of course needed.

These may come from imaging studies. Here, **Dubé & Cohen** state that the regions activated during the processing of sign language are the same as those activated by spoken language. Closer examination of some recent data, however, suggests that areas dorsal to the perisylvian core are activated when signs are being processed by native speakers of sign languages. For example, McGuire et al. (1997) report activation in the middle frontal gyrus of the left hemisphere (area 9 and 46) in a PET study, and Neville and colleagues (1998) also found activation for areas dorsal to Broca's region and the mouth area using fMRI. In the latter study, this activation was absent when native speakers of English processed written language. These results suggest that processing sign language may activate additional areas superior to the perisylvian core. This would be consistent with the cell assembly approach. The evidence that right-hemispheric processes are more strongly involved in the processing of sign language (Neville et al. 1998) is also in agreement with the present model. Meaningful gestures – the words or morphemes of a sign language – are typically performed with both hands (plus face and head), so that there is even more reason to assume bilateral activation than in the case of spoken language.

R7. Future perspectives

The CA model "might not be sufficient to explain brain functioning" (**Elbert et al.**). This would probably be too high an expectation. It is difficult enough to specify even a few of its aspects. However, one may ask whether the present approach is on the right track for achieving such an explanation. **Bierwisch** would probably doubt this, because various linguistic phenomena are not addressed, but please recall that the target article is on word processing and focusses on the questions of where and how words are represented and processed in the brain, why this is so, and what neuroimaging data are available to test the theoretical ideas. It does not seem fair to demand an explanation of a wide range of linguistic phenomena in such a paper, although the approach may be capable of handling them. The following paragraphs are intended to give some hints about where it may be fruitful to expand the model. (Further extensions have been reviewed in sect. R1 of this Response.)

R7.1. Neural networks. The suggestions by **Culicover & Nowak, Jorion, Spivey et al.** and **van der Velde** to examine further the possible properties of the cell-assembly machinery by using neural network simulations are extremely important. Such simulations may illustrate the theoretical framework and may allow detailed exploration of its explanatory capacity. Standard associative networks clearly have their limits in this regard because so many special properties are built into the brain structures relevant for language. It may therefore be better to use neural networks that mirror these neuroanatomical properties (see, for example Pulvermüller 1998 and Pulvermüller & Preissl 1991).

Culicover & Nowak and **van der Velde** advocate attractor neural networks, the former authors being rather

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specific about how such a network including a syntactic and a semantic component could function. As Culicover & Nowak point out, CA activity could be represented in a multi-dimensional space where each neuron (or neuron group) would correspond to one axis. In this state space, an active cell assembly would be represented as a vector or dot. If ignition states differ slightly, a cloud of dots could represent them. The reverberation and gradual decline of activity in an assembly can be represented as a set of trajectories starting in this cloud. I am not sure about how several simultaneously active assemblies reverberating at different activity levels (Fig. 10, target article) would be modelled. However, syntactic and semantic similarity can be represented by the similarity of the vectors representing the ignition of two word-related assemblies (e.g., the Euclidian distance between the vectors), and a trajectory through state space would denote a sequence of cell-assembly ignitions, as argued by Culicover & Nowak. I agree fully with these authors that a dynamical systems perspective provides important insights into the mechanisms of serial order.

Haase & Rothe-Neves argue that feedforward and feedback connections are necessary in a network designed to handle word strings (this appears to be meant as a criticism of my proposal). These authors should be reminded that the cell-assembly framework is based on the assumption that the cortex is an associative memory exhibiting multiple reciprocal connections between areas and neuron populations. Even a single-cell assembly, as conceptualized in the target article, is a dynamical system (**Culicover & Nowak**) and a neuron set, each part of which is reciprocally connected to the rest (Braitenberg 1978b).

R7.2. Syntax. I should thank **Bierwisch** and **Turnbull & Carpendale** for taking the time to point out linguistic phenomena that would need to be modelled in a neurobiological theory of language. Bierwisch states, however, that the present neurobiological approach is "inadequate . . . for absolutely principled reasons," an opinion I cannot share. According to Bierwisch's reading, the model cannot provide a perspective on modelling syntactic mechanisms such as lexical categorization of words. This is incorrect. It was stated in my target article that "the representation of grammatical properties of words does not . . . require separate cortical neurons or areas exclusively devoted to the storage of grammatical information "(sect. 7, para. 6). This does not imply that syntactic information (information about lexical (sub)categorization included) does not manifest itself in the network. It may well be represented in another way, also specified in the target article, namely, by connections between the assembly representing a word and sets of other assemblies. Suppose a word representation is connected to two such sets exhibiting mutual inhibition. In this case, the lexical categorization of the word would depend on which of these sets becomes active after the word assembly ignites. It is correct that these mechanisms are not specified in detail, but "the very model under consideration" clearly offers ways of doing so. The proposed neuronal push-down mechanism is not the only mechanism that may be relevant for determining word order in sentences. Why would Bierwisch ignore this?

Antipathy to associationist accounts surface in the statement by **Haase & Rothe-Neves** that a purely associative device cannot be used to explain serial order, and by **Osterhout & Bersick** that some of the results have "more to do with associative memory than with language." Well, what if language had a lot to do with associative memory in a genetically preprogrammed device? One of the *linguistic universals* determined by the genetic code is that word-object correlations in the input can be easily stored and retrieved around the end of the first year of life and later.

Between-assembly associations may underlie complex words consisting of two morphemes, one of which would be from the group of content words – or better, items – and the other from the function vocabulary (**Greenberg & Nisslein**). The target article deals only with simple words including only one morpheme (meaning unit), but now it is necessary to distinguish one-morpheme words, which would correspond to one assembly, from complex words including two or more morphemes modelled by connected assemblies. A regular verb in the past tense can accordingly be realized as two assemblies connected in sequence. On the basis of the elaborate discussion between connectionists and linguists on this topic, this may sound like a strong statement. However, it seems straightforward if the connections linking various regular stem representations to the past tense morpheme are assumed to be somewhat special. How simple linguistic rules (such as those involved in the formation of past tense) may be laid down in the cortex has been discussed recently (Pulvermüller 1998) and will not be elaborated here. In the target article, I focus on a more complex principle (sect. 8).

Haase & Rothe-Neves doubt whether center embedding is a universal property of languages and cite evidence that many errors are made with center embedded sentences. Most linguists, however, would probably attribute these errors to processing limitations irrelevant to linguistic theory (Chomsky 1980). Hence, these data would not argue against its being a universal.

Bierwisch calls attention to syntactic structures that cannot be explained by a push-down mechanism, or would be very difficult to account for if only one push-down storage and no other kind of memory were available. Other determinants of serial order are clearly necessary. One perspective is to assume that only larger constituents of sentences can become subject to push-down storage and that the local serial order within a phrase is primarily determined by between-assembly connections. In this case, the free placement of the verb particle after the verb ("she switched on her TV," "she switched her TV on") can be explained by the assumption that "switch" primes "on" (which reverberates subsequently) and sequential order depends on the activity level of the likewise primed noun phrase ("her TV") (whichever happens to be at the higher activity level will ignite first) (Pulvermüller 1993; 1994b). The learning of simple idioms (**Bierwisch, Ivancich et al.**) can be modelled along the same lines. These speculations are intended to illustrate perspectives of a CA approach that uses both between-assembly connections and dynamics of assemblies to achieve serial order of word strings. Additional mechanisms may also become relevant. A more elaborate description of a neuronal grammar based on the CA notion has been developed recently (Pulvermüller 1999b).

Bierwisch's remark about the two German words "umstellen," distinguished by their pronunciation pattern, calls for an extension of the proposal in which syllable accents are also represented, but it does not appear to challenge the model.

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Van der Velde makes an important point regarding the processing of repeated words. Most processing models, including the present one, assume representations of word types but not tokens. This is not sufficient to account for the repeated use of one word in a sentence. To solve this problem, one may postulate multiple representations of linguistic elements (Shastri & Ajjanagadde 1993). This is not fully convincing, however, because there is no reason different representations for the same word or phrase should develop. A possible solution within a CA framework is to assume that different activity states in one assembly represent how frequently the item occurs. Because this would interact with the proposed push-down store, it must be assumed that activity states of assemblies can vary in more than one dimension (Pulvermüller 1999b). Van der Velde's idea of representing "context-sensitive words," so to speak, is another attractive possibility.

R7.3. Meaning. The topic of word semantics was addressed at several places in this Response. For future perspective, the empirical questions raised in the commentaries by **Fuster, Miller, Posner & DiGirolamo, Skrandies,** and **Tranel & Damasio** may turn out to be particularly fruitful. Let me focus here on where the proposal needs to be extended.

Bierwisch correctly points out that word pairs such as buy/sell and come/go are identical regarding the actions they refer to, but that they nevertheless have different meanings. The common referents do not imply that the assemblies representing the words are identical, but rather that they are distributed over the same areas and strongly overlap. Their distinctive neurons probably represent additional semantic features and are connected to other assemblies involved in determining serial order. Here, further extensions are necessary. One perspective is offered by cognitive grammar (Langacker 1991).

Turnbull & Carpendale make the important point that function words can be used in different ways ("what" can be used to signal that one did not understand, and to ask somebody for information). Their example is interesting, illustrating not only a weak point of the model, but also that single words can be used to perform a full speech act. The same objections can therefore be raised against single-word presentation and isolated presentation of sentences in psychological experiments. In both kinds of experiments, language does not have its normal communicative function. However, one must make compromises regarding this if the aim is to investigate brain mechanisms.

Again, **Turnbull & Carpendale**'s point about different uses of function words is an important one. It challenges the model presented in the target article and calls for an elaboration. Function words, such as "what," can be used under different circumstances, to communicate different things. These circumstances would include not only nonlinguistic stimuli surrounding the communication partners (which may be quite variable), but also the assumptions and commitments they make when producing the particular word, the speech acts they performed before using it, and those they are about to perform. These assumptions and actions are, without any doubt, represented in the brain, and the "meaning" or use of a function word may be precisely the set of neuronal representations of assumptions and actions it primes (and is primed by) through connections of its assembly. If a function word, such as "what" has two or more uses, two or more sets of associated representations need to be postulated that inhibit each other, as suggested above for the representation of lexical subcategorization (sect. R7.2). Spelling out the relevant mechanisms in brain terms was not the aim of the target article but is highly important.

R7.4. Attention. The remarks on attention mechanisms in two commentaries, **Elbert et al.** and **Posner & DiGirolamo,** seem to be of utmost importance. The target article made the simplifying assumption that sufficiently high arousal and attention levels are present in the entire brain during word learning and use (cf. sect. 3). This is not true for all situations in real life. In some situations, special attention is paid to visual input, or even to a small part of the visual field. In others, different modalities may be the focus of attention. Moreover, there is the possibility that the general arousal level is so low that it affects cognitive processes. Brain theoreticians of attention have long realized this (Posner et al. 1997; Posner & Raichle 1994; Scheibel 1981; Skinner & Yingling 1976). Although the machinery underlying the control of attention probably involves various cortical and subcortical structures (including areas in prefrontal and parietal cortex and in the nucleus reticularis thalami and other thalamic structures; see Posner & Raichle 1994), the increase or reduction of background activity in either a large part of the cortex, in an area, or in an even smaller zone is a likely correlate of variations in attention. It is clearly important to combine the model of distributed cortical representations with a theory of attention. The result may be a theory that can not only explain (predict) (1) word-class differences in brain activity when word forms with different properties are processed in the same task, or (2) between-condition differences when the same set of words or sentences is processed in different tasks, but also (3) interactions of the word-class and task variables. Such a theory may specify, for example, the additional cell populations activated by the ignition of a CA when one of the areas over which it is distributed is preactivated by an attention process. The differences between tasks reported by Elbert et al. could be grounded in a mechanism by which the left perisylvian areas have a high preactivation level during phonological tasks and the entire cortex is under additional attention-related amplification during semantic tasks.

R7.5. Final remarks. Other questions, I must confess, I am unable to answer. Among them is **Kurthen**'s. What makes an assembly a concept? How would a group of neurons develop "aboutness"? Why do I consciously experience a certain association when hearing the word "mouse"? I believe these questions cannot be answered, and popular statements that consciousness starts at 5 μV (as Libet's 1985 results suggest) or is apparent in 40 Hz activity (Crick & Koch 1990; Koch & Crick 1994) are somewhat unsatisfactory, because the question can be iterated: Why should strong electrocortical potentials and high-frequency spatio-temporal patterns make me experience consciously? The activation of large (and strongly linked?) cortical neuron populations is the physical basis of consciousness. Further questions will probably lead to nothing but confusion.

I hope the target article and this discussion have shown that it makes sense to theorize about brain mechanisms of language. No future time need be awaited in which our un-

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derstanding of the brain will have reached a more satisfactory stage. Such a point can only be reached if language and other highly complex domains of performance are used to validate theories of brain function, as Lashley (1951) argued. "If there exist, in human cerebral action, processes that seem fundamentally different or inexplicable in terms of our present construct of the elementary physiology of integration, then it is probable that the construct is incomplete or mistaken, even for the levels of behavior to which it is applied" (pp. 134–35). Because "language presents in a most striking form the integrative functions that are characteristic of the cerebral cortex" (p. 113), it is necessary to look at language to improve our understanding of the brain. The target article tried to show that the Hebbian perspective can, with slight modification and some extension, explain a few relevant aspects of language and can thereby help bridge the gap between language theory and brain functioning. The model is still incomplete, clearly, although I have done my best to point out ways to incorporate further syntactic, semantic, and attentional mechanisms. In the best case, it may nevertheless aid our brains to better understand their own language.

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NOTES

1. Of course, structure (anatomy) and function (physiology) include the micro-levels of pharmacological, chemical, and molecular structures and processes.

2. I am grateful to Werner Lutzenberger who recently explained this argument to me. I am solely responsible for any inappropriateness of this description, however.

3. To be appropriate, these baselines need to be identical over conditions, an assumption that appears unproblematic if trials are randomized (or pseudo-randomized).

4. This has been dubbed the "cathedral model" by a colleague, Thomas Becker, who called attention to the fact that the network structure resembles the layout plan of a Gothic cathedral.

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Letters "a" and "r" appearing before authors' initials refer to target article and response, respectively.

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