BEHAVIORAL AND BRAIN SCIENCES (1999) **22,** 661–721
Printed in the United States of America

A model of saccade generation based on parallel processing and competitive inhibition

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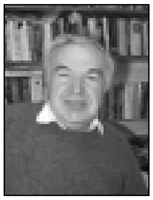
Abstract: During active vision, the eyes continually scan the visual environment using saccadic scanning movements. This target article presents an information processing model for the control of these movements, with some close parallels to established physiological processes in the oculomotor system. Two separate pathways are concerned with the spatial and the temporal programming of the movement. In the temporal pathway there is spatially distributed coding and the saccade target is selected from a "salience map." Both pathways descend through a hierarchy of levels, the lower ones operating automatically. Visual onsets have automatic access to the eye control system via the lower levels. Various centres in each pathway are interconnected via reciprocal inhibition. The model accounts for a number of well-established phenomena in target-elicited saccades: the gap effect, express saccades, the remote distractor effect, and the global effect. High-level control of the pathways in tasks such as visual search and reading is discussed; it operates through spatial selection and search selection, which generally combine in an automated way. The model is examined in relation to data from patients with unilateral neglect.

Keywords: competitive interaction; fixation; latency; model; reciprocal inhibition; saccade; salience; search selection; spatial selection; visual attention

1. Introduction

Active human visual behaviour is dependent on saccadic eye movements, or *saccades*, rapid jerk-like movements of the eyes that direct the gaze to a new location and redeploy the region of high visual acuity centred on the fovea. These movements are made several times each second during active scanning. They are ballistic movements in the sense that their duration is too short for new visual information to be used during their trajectory. Saccades are regarded as voluntary movements but are generally produced with highly automated routines. They are used in a great variety of ways in human behaviour. Saccades are used in the process of obtaining information about the visual environment and seeking new sources of stimulation. Saccades are used when searching visually for a particular target. Saccades are used in ordered scanning, such as human text reading. Finally, saccades are used to orient to salient new events in the visual field. Such orienting saccades have a reflex-like quality, and much of our knowledge about the saccadic system comes from study of the *stimulus-elicited* saccade in which a subject is asked to make a saccadic orienting response to a new target appearing in the visual field.

This target article presents a framework for understanding human saccadic eye movement generation. We emphasise parallel processing of command signals for the movement and also processes of conflict resolution by competitive inhibition, which occur at various levels. We believe that conflict resolution is the important, time-consuming process



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0140-525X/99 $12.50

even for simple orienting responses. Experimental studies on saccadic eye movements have generated a considerable body of data. In the case of eye movements elicited by specific visual targets, the significant measures are the *metrics* of the saccade (direction and amplitude) and the *latency*, that is, the time from target appearance to the initiation of the movement. These measures provide a full specification of the movement since saccade trajectory and dynamics are generally constant for movements with a specified metric. We discuss the programming of both measures in the paper. Our framework is able to account for a number of robust effects that have been observed in research studies with stimulus-elicited saccades, among them the *gap effect, express saccades,* the *remote distractor effect,* and the *global effect.* Although our main focus is processes that operate in a stereotyped automatic fashion, we also indicate how the framework is "upward-compatible" to allow more cognitive influences to be incorporated.

We present the framework in section 2 in the form of an information flow model. We shall frequently refer to the framework as a "model," although we recognise that it does not at present satisfy the formal requirements of a quantitatively testable model. Section 3 discusses how the framework relates to existing work. In section 4, we show how existing data can be interpreted and indicate a number of instances where the approach makes predictions different from those of other existing models.

The framework is described in functional terms but has been considerably influenced by work in oculomotor neurophysiology. Possible correspondences are discussed, particularly in section 3.2. Our framework describes information and control flow in a conceptual neural network. However, we are interested in performance rather than learning so although we recognise that such a network has a capacity for learning, we are not concerned here with this plasticity and the important adaptational processes operative in connection with saccades (Deubel 1987; 1995). Neither do we explore the converse problem of how the visual system takes account of changes produced by saccadic eye movements. New perspectives on this traditional theme have recently emerged (e.g., Bridgeman et al. 1994). Another limitation is that we shall ignore the third dimension of the visual world – depth – and retain the traditional account of saccades as conjugate eye movements. This account must be recognised as only an approximation (Enright 1984; 1992; Erkelens et al. 1989).

We hope that our proposal will be of interest to a broad spectrum of neuroscientists and cognitive scientists, including oculomotor physiologists, specialists in visual cognition, and workers in clinical areas who are attracted by the simplicity and elegance of eye-movement control for investigative and diagnostic purposes.

2. The model

2.1. Overview

The model is shown in diagrammatic form in Figure 1, in which two parallel information and command streams run vertically through a hierarchy of processing levels. Information in the right-hand (WHERE) stream is transmitted in spatially mapped pathways (see sect. 2.2.3), whereas in the left-hand (WHEN) stream, a single nonspatial signal is involved. The distinction is shown symbolically with circular "map" symbols and rectangular "gate" symbols, respectively.

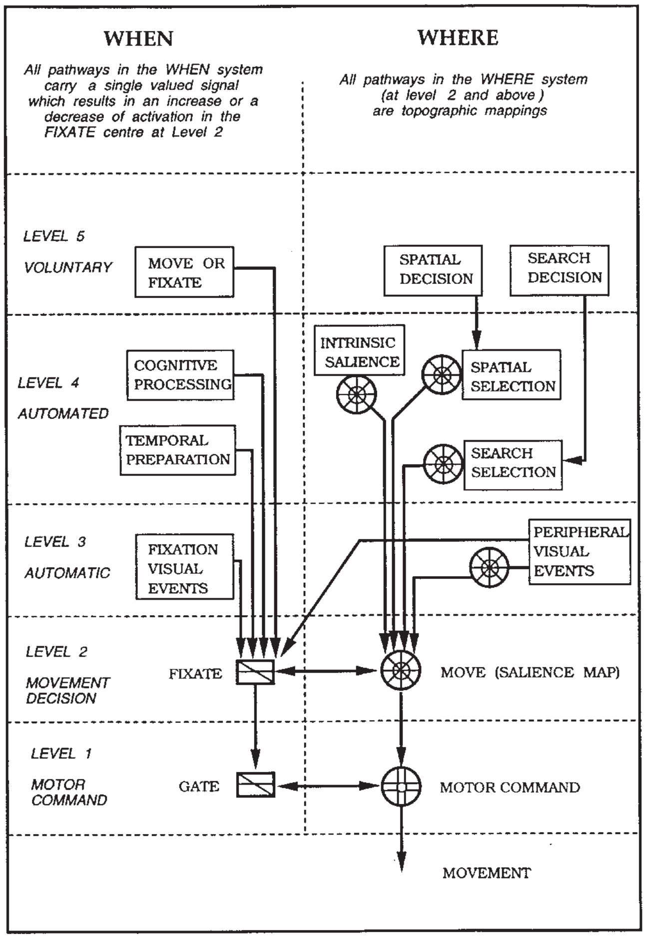

Figure 1. Diagram indicating the information flow routes and competitive pathways in saccade generation

Competitive interaction occurs when two centres, or two regions within a centre, are cross-connected with reciprocal inhibitory links. Such a pattern of cross-connections will mean that increased activity in one of the centres will tend to reduce activity in the other and vice versa. This is a push-pull situation and, apart from brief periods of dynamic nonequilibrium, either one centre or the other will become active in a winner-take-all manner. We identify three points where competitive interaction occurs during the process of saccade generation. The first two are between the WHEN and the WHERE streams. The third instance is when competition between potential targets arises in the WHERE pathway.

2.2. Model details

Of the five levels, we suggest that, at least for the range of phenomena and time scales discussed in connection with the model, the processes in levels 1, 2, and 3 operate in a stereotyped way that is not modifiable by cognitive influences other than through the descending pathways of the model. In other words, at these levels, the processes are effectively automatic and hard wired. So, for example, the automatic access of visual onsets means that when saccades are made, visual onsets cannot be totally "ignored." This does *not* of course entail that visual onsets will automatically result in saccadic orienting.

2.2.1. Level 1: Motor command (immediate pre-motor stage). There are three pairs of oculomotor muscles that rotate each eye. The motor command to these muscles is produced at level 1. Saccadic movements occur when a trigger signal opens a gate in the WHEN pathway at this level. This leads to a spatially coded motor command being generated by the final stages of the WHERE pathway. Coding is here in terms of muscle activation, shown schematically by a symbol representing four recti. The processes at this level ensure that the eyes move with optimum speed and efficiency when a command signal is received, but otherwise remain immobile.

This level reflects, in a highly oversimplified way, the brainstem circuitry of omnipause cells and pre-motor burst cells (see sect. 3.2.1). An important feature is the separation of two processes at this level and two routes to these processes descending from higher levels of the WHEN and WHERE systems. Because of operations at level 2, the signals travelling down these pathways have been prepackaged in a suitable form to produce a saccade. For example, we suggest that, as a result of level 2 processes, the signal conveying the spatial characteristics of the saccade will in general have a constant value rather than being dynamically changing. Level 1 processes are, apart from the signals reaching them along these two routes, effectively immune to other, higher-level influences resulting in the stereotyped nature of saccade trajectories (see sect. 3.3.2).

2.2.2. Level 2a: The fixate/move balance. Competitive push-pull interaction is also a critical aspect of the processing at level 2. The major form of competition in this case is between the *fixate centre* and the *move centre*. Whereas at the motor command level the push-pull interaction served to shape a rapid movement, the operation at level 2 is more concerned with integrating the various competing information signals to decide whether and where a saccade should be made. It is suggested that this conflict resolution process involves a relatively slow buildup of activation in one centre with a decline in the other. Moreover, it is this time-consuming process that determines the exact point in time at which the saccade is initiated. Saccades are generated when the activity in the fixate centre falls below a certain threshold level, at which point the level 1 gate is opened. Reduction in fixate centre activity may be termed disengagement. Any increased activity in the move centre will promote disengagement through the reciprocal inhibitory connections, and disengagement can also occur via descending influences to level 2. The fixate centre is part of the WHEN pathway and thus operates as a single unit. However, as discussed in section 2.3, it can be directly influenced by events in the visual periphery as well as those at fixation.

2.2.3. Level 2b: The move centre and the salience map. The move centre forms part of the WHERE pathway and carries a spatial code. We envisage it as a two-dimensional map formed by a neural network with each point on the map coding a different visual direction. In contrast to the coding at the motor command stage, the coding at this stage is spatiotopic, although in a highly distributed manner (sect. 2.2.4). This map is subject to descending influences from higher stages. The routes carrying these influences carry a topographic mapping and some of these routes arise, directly or indirectly, from retinotopically mapped visual sensory areas.

At any instant, each point on the map registers an activity value. We term this the *salience map*. We postulate that, when a saccade is triggered, the point of current maximum salience determines its metrics. This deceptively simple statement will receive further elaboration and justification subsequently (sect. 3.3.3). The activity in the salience map is in competitive interaction with activity in the fixate centre as discussed previously. A further set of conflict resolution processes can occur *within* the move centre. We postulate multiple inhibitory cross-links between the various different regions of the map. These operate to ensure that activity in the network tends toward a winner-take-all state with a single salience peak. Conflict resolution between multiple potential saccade targets occurs in this way. Once this occurs, the single peak dominates and has the potential to shift the fixation-move balance in favour of a movement. We envision the processes at this stage operating like a sample-and-hold system so that in general saccade trajectories are not subject to influence from the continuously changing activity at higher levels.

2.2.4. Level 2c: Distributed mapping and the calculation of saccade metrics. An important characteristic of the salience map is the use of spatially distributed coding, alternatively termed "population coding" or "ensemble coding." Spatially distributed coding maps a topographic spatial map with divergent and overlapping connections (i.e., through large and overlapping receptive fields). Distributed coding ensures that the salience landscape is one of smoothly changing contours rather than of multiple, isolated peaks. This simplifies the conflict resolution process. It might appear that distributed coding results in a loss of accuracy in the spatial representation. However, if just a single target is involved, this is not the case (Hinton et al. 1986). The disadvantage of distributed coding is the lack of ability to code two simultaneous targets.

2.2.5. Level 3: Direct visual influences. At the next level in the hierarchy, we identify routes by which visual stimulation influences the fixate-move system. The separate level for these influences indicates that these routes directly influence level 2 processes, resulting in effects that are not subject to cognitive influences. Our model postulates that stimulus change, in particular onset and offset of visual stimulation, has automatic effects on both processing streams as described in the next paragraph.

Central visual events at the currently fixated location have a direct effect on the fixate centre. Offset of central stimulation promotes disengagement, whereas onset increases activity in the fixate centre. Peripheral visual events occurring away from fixation generate effects in *both* the fixate and the move centres. The effect on the move centre is to stimulate activity in the salience map at the point corresponding to the event location. This will frequently determine or influence the choice of saccade target. This increase in activity in the move centre will render saccade triggering more likely. However, there is also a direct effect of a peripheral event on the fixate centre. Visual onsets, even in the periphery, act to enhance fixation centre activity. This paradoxical route is required to account for the findings of Walker et al. (1997) discussed in section

4.1.2 and is also consistent with the physiological data of Gandhi and Keller (1997) described in section 3.2.2.

2.2.6. Levels 4 and 5: Automated effects and habits of cognitive control. In levels 4 and 5, we attempt to sketch the way in which our model is capable of integrating high-level influences. Level 5 reflects the self-evident point that, at least for normal individuals, all lower-level processes can be overridden and an individual can either suppress saccades and maintain fixation, or can move the eyes voluntarily. Such considered actions are unusual. Normally, saccade control occurs at level 4, and the term *automated* has been chosen to describe the operative processes. This term both indicates that the processes operate below the level of conscious awareness and provides a marker that implicit learning and memory may be expected to play a significant role in the level 4 stages (Lambert & Sumich 1996; Maljkovic & Nakayama 1994).

The multiplicity of uses of saccades was mentioned in the introductory paragraph of this paper. This multiplicity gives rise to the problem of coordination of different sources and streams of information, echoing in a miniature way a general feature of human activity – frequent multitasking and task switching (Norman & Draper 1986). Situations often arise in which more than one target could be selected for gaze redirection. The eye can of course only move to one at a time. How is conflict between the potential targets resolved? The salience map introduced in section 2.2.3 is a two-dimensional, contoured surface, with the two spatial dimensions representing visual directions and "depth" representing salience. There are multiple inputs integrated into this salience map. We propose that the point of highest salience in the map becomes the target for the saccade. The architecture of the move centre provides for some implicit conflict resolution to enhance the high salience point. We propose that conflict resolution is *only* resolved in this implicit way with no overriding supervisory decisions or more elaborate processing.

2.2.7. Influences in the WHERE pathway. We believe that two forms of cognitive control of saccade metrics can be identified. *Spatial selection* works by modifying the salience map in specific regions, in either a potentiating or an inhibitory manner. Thus selecting a particular region of the visual field will take the form of a potentiated spatial window. This window will always be quite extensive, because of the constraints of the distributed coding at level 2. Following such selection, saccades will be directed to a location constrained by the window, although the exact landing position may be determined by the specific details of the visual stimulation within the window. The phenomenon of *inhibition of return* (Rafal et al. 1989) is another spatial-selection influence. Inhibition of return refers to an increased difficulty of orienting to a location to which attention has previously been directed. This possibly ensures that fixations are less likely to return to a previous point of high salience (Klein 1988).

The second form of control, which may operate together with the first, is referred to as *search selection* in Figure 1 and promotes saccades to particular visual features wherever in the visual field they may occur. Search selection is assumed to operate within the visual processing areas of the brain. If search selection is not active, then the visual input to level 2 is a general visual map. Search selection allows selected features to have preferential access to Level 2.

The final factor operative at level 4 has been denoted *intrinsic salience.* It seems plausible to suggest that visual contours and high-contrast areas of the visual field are intrinsically salient. We suggest also that long- and medium-term learning and adaptive processes may also modify the salience of visual information. For example, Beauvillain et al. (1996) have shown that unusual orthographic patterns can attract saccades during reading. Also carry-over effects noted in experiments on visual search suggest that the target item used in an earlier search retains salience when the task changes to require a different search target (Findlay 1997; Maljkovic & Nakayama 1994).

2.2.8. Influences on the WHEN pathway. We identify two routes whereby higher-level influences can affect the WHEN pathway. The first concerns temporal preparation. We suggest that disengagement at level 2 can be promoted by suitable temporal preparation, such as is produced by warning signals or predictable timing of the target onset. The second descending route is from ongoing cognitive and perceptual processing. When engaged in a complex perceptual activity, such as text reading, the saccadic system must be able to sequence movements to enable visual information uptake to occur smoothly. Too brief a fixation would not allow visual information to be taken in adequately, whereas too long a fixation would be time-consuming. Remarkably, human visual scanning seems to be able to control this balance very effectively. We suggest that this is because the level 2 fixate centre can be influenced directly and rapidly from centres of cognitive processing.

3. Relation to other work

3.1. Antecedents of the model

In this section we acknowledge specific work that has influenced our thinking.

The idea of separate control for the temporal and spatial decision in connection with saccades emerged in the late 1970s. Becker and Jürgens (1979), in a classic article, proposed a model in which a triggering process controlled the occurrence of a saccade as well as the choice of direction, whereas a separate computational process determined its amplitude. Our model can in some ways be regarded as an extension of their thinking. Workers of a more cognitive persuasion (Rayner & McConkie 1976) also noticed that in tasks such as reading, there appeared to be separate control of temporal parameters (fixation duration) and spatial parameters (saccade size).

The emphasis on competitive interaction in saccade generation can be found in much physiological thinking (see sect. 3.2) and has also been promoted by Carpenter (1981; Carpenter & Williams 1995). The potential of a distributed spatial code has long been recognised (Erickson 1968; McIlwain 1976) and has formed one of the distinctive features of modern neural network theory. The suggestion that the goal for visual attention capture might be determined by the point of highest salience on a map representation of visual space has been frequently suggested in the context of visual attention and visual search (Henderson 1992; Koch & Ullman 1985; Treisman & Sato 1990; Wolfe 1994).

We believe that our discussion of the direct effects of visual stimulation has some original features, although we acknowledge similarity between it and concepts such as the "ocular disengagement" of Tam and Stelmach (1993). We also sense a convergence with work on visual attention in human experimental psychology (Egeth & Yantis 1997), which has also recognised the compelling nature of sudden visual onsets (Jonides & Yantis 1988). It is possible that a novelty detection system somewhat more sophisticated than simple detection of transients exists (Nakayama & Mackeben 1989; Yantis & Hillstrom 1994), but this detail will not be developed further here.

The discussion of spatial selection and search selection owes much to current work in visual attention and search, as well as some specific suggestions (e.g., Kowler 1990) by oculomotor workers. Ideas about covert visual attention have included spotlight and zoom-lens models (Eriksen & St. James 1986; Posner & Cohen 1984; Posner & Petersen 1990). Work in visual search has shown how excitatory and inhibitory processes could achieve search filtering (Desimone & Duncan 1995; Schall & Hanes 1993). A specific suggestion that has close affinity to ours is that of Duncan (1995), who has used the term *competitive interaction* to describe how visual search might occur. Competitive interaction works within feature maps to select a desired feature as well as across spatial maps to enable object selection. It has obvious similarities to our competitive inhibition.

3.2. Physiological background

3.2.1. Brainstem processes. The immediate saccadic premotor circuitry in the brainstem has been investigated in considerable detail, and our level of understanding of it is high. Convenient summaries are given by Fuchs et al. (1985), Moschovakis and Highstein (1994), and Wurtz and Goldberg (1989). Level 1 of our model is explicitly based on brainstem processes. For our purposes, the essential programming feature is the flip-flop-like switching between pause cells and burst cells in the brain stem. Pause cells, or omnipause cells, normally fire at a high rate but cease activity for the duration of each saccade made (the pause of activity precedes the actual saccadic movement by 5 to 15 msec). Burst cells show just the opposite pattern of activity; their rate of firing increases dramatically during appropriate saccades. The omnipause cells show no specificity and cease firing for each saccade made, whereas the activity of the burst cells is coded in terms of the spatial metrics of the saccade. To account for this specificity difference, it is necessary to postulate at least two descending pathways, one carrying spatially coded information and the other acting merely to convey a trigger signal. The WHERE and WHEN terminology appears to have been first introduced by oculomotor neurophysiologists (Van Gisbergen et al. 1981).

The above brief account enormously simplifies the brain stem system, ignoring (1) the neural integrator circuit, which ensures that the eye is held stable in the new position following the end of the saccade; (2) the separation of the burst cell regions for horizontal movement and vertical movement; (3) the routing circuitry, which ensures that the correct muscle pairs of each eye are given appropriate signals; (4) the feedback pathways (see sect. 3.3.1) that enable accurate saccades to be made to visual and remembered targets; and (5) long-term adaptive processes that maintain the accuracy of the system.

3.2.2. Fixate/move competition. Recent work by Munoz, Guitton, Wurtz, and collaborators (Munoz & Guitton 1991; Munoz & Wurtz 1992; 1993a; 1993b; Wurtz 1996) has achieved a major breakthrough in our understanding of the neurophysiology of saccade control. Their work has concerned the rostral pole region of the superior colliculus, which carries the representation of the fovea in the visual and motor maps and appears to be directly connected to the omnipause neurons of the brain cell (Paré & Guitton 1994). Munoz and collaborators have shown that the term "fixation centre" can be used appropriately to describe the function of the region in both cats and monkeys.

In monkeys, cells in the region are active whenever the animal is fixating and pause during saccadic eye movements (Munoz & Wurtz 1993a). The region is GABA-sensitive (Munoz & Wurtz 1993b). Injection of the GABA agonist muscimol into the region increases saccadic activity, leading to difficulties in maintaining fixation and reducing the latency of target-elicited saccades. Conversely, injection of the GABA antagonist bicuculline into the region has the opposite effects and saccade latencies are increased.

Munoz and Wurtz (1993b) suggest that the evidence supports a push-pull relationship between the cells in the fixation region of the rostral pole and the cells in the remainder of the deep layers of the colliculus, known to code saccade metrics as a "motor map." Their stated hypothesis is that "activation of fixation related cells of the rostral superior colliculus is necessary to maintain visual fixation; whereas a pause in the discharge of these cells is a prerequisite for the initiation of a saccade" (p. 585). This viewpoint is reinforced by the demonstration that, when monkeys are tested in the gap paradigm (sect. 4.1.1), fixation cell activity is attenuated during the gap period, with activity in buildup neurons increasing in reciprocal fashion (Dorris & Munoz 1995; Dorris et al. 1997).

An issue that is still unresolved is the spatial size of the fixation centre. As described by Munoz and Wurtz (1992; 1993a), the centre was located in the rostral pole of the colliculus, corresponding to about the central 2 degrees of the visual field. However, other work (Gandhi & Keller 1997) has reported that cells with the appropriate properties for fixation neurons can be found in a more extensive region of the colliculus (extending over at least the central 10 degrees). A further puzzle relates to the issue of whether the fixation centre operates as a single unified system. The collicular fixation system shows a degree of directional (left/right) specificity that we have not included (see sect. 4.7).

We thus believe that there is strong evidence that the fixation system in the superior colliculus operates in a way that is compatible with the fixate system of our level 2. However, we do not wish to imply that our model shows total physiological isomorphism with this system. In particular, we wish to leave open the possibility that the fixate system may be more widely distributed than the collicular fixation system. Neurons with properties similar to those of the collicular fixation system are also found in parietal and frontal cortex (Goldberg & Segraves 1989; Hyvarinen 1982; Sakata et al. 1980), and a direct pathway exists between the frontal eye fields and the oculomotor centres (Segraves 1992). Hanes and Schall (1996) recently reported an impressive correlation between rate of activity in frontal eye field neurons and saccade latencies. We have chosen a terminology (fixate rather than fixation) different from that used by most physiologists to make clear that our model is functional rather than physiological.

3.2.3. Distributed processing. Distributed coding is a notable feature of the superior colliculus. Visual cells have large and overlapping receptive fields and, moreover, the colliculus is a layered structure in which field size increases systematically with depth (Sparks 1986; Sparks & Hartwich-Young 1989). As a consequence, any particular point in the collicular motor map can be stimulated by visual input from a wide region of visual space, and stimulation from a punctate peripheral source generates activity over a wide region of the colliculus. The potential importance of this distributed coding for the conversion of the spatial visual code to a suitable oculomotor code was first appreciated by McIlwain (1976) and has been the basis of subsequent physiological work and quantitative modelling (Lee et al. 1988; McIlwain 1991; Van Gisbergen 1989; Wurtz 1996).

3.2.4. Competitive interaction within the salience map. In section 2.2.3, we suggested that processes of competitive interaction operate within the salience map to promote the selection of a unique saccade goal. We believe a plausible physiological substrate for this conflict resolution involves the system of reciprocal inhibitory connections between different regions within each colliculus (intracollicular inhibition) and further inhibitory cross-connections between the colliculi (intercollicular inhibition). Early work in cats found evidence for both forms of inhibition (Rizzolatti et al. 1974; Sprague 1966) and similar findings were later reported in the monkey (Wurtz et al. 1980). Koch and Ullman (1985) showed how a neural network might be implemented in this way to determine the locus of maximum salience.

More recently, a number of physiological studies (reviewed by Desimone & Duncan 1995) have shown how the processes of target selection for the oculomotor system might work at the detailed level through a similar interplay of excitation and inhibition. For example, Schlag-Rey et al. (1992) have considered how target selection might occur in a situation demanding conflict resolution. They showed, in monkeys, that electrical stimulation of the frontal eye fields of a strength to potentially evoke a saccade has a dual effect on neurons in intermediate layers of the superior colliculus. In regions whose movement fields correspond to the direction of the elicited saccade, excitation occurred. However, in other regions, an inhibition of neural activity was found. Schlag-Rey et al. noted that surround inhibition in the colliculus plays an important role and suggested that the inhibitory effects arose through collicular cross-connections.

This principle, moreover, can extend to search selection (Duncan 1995). Schall and Hanes (1993) studied responses of frontal eye field neurons in monkeys performing a simple colour search task. Neurons responsive to the spatial region of the target showed an activation enhancement around 50 msec prior to the monkey making a saccade to it. Conversely, neurons responsive to neighbouring regions where there was a distractor stimulus of the wrong colour showed a marked diminution of activity prior to the saccade. A similar result for cells in inferotemporal cortex has been reported by Chelazzi et al. (1993). Furthermore, these spatial patterns of enhanced and diminished activity are maintained during periods in which the animal is required to delay responding, thus forming a short-term spatial memory (Chelazzi et al. 1993; Glimcher & Sparks 1992).

3.3. Contrasts with other work

In this section we consider some points of contact between our framework and other work in saccade modelling from an oculomotor standpoint.

3.3.1. Feedback processes in saccade generation. Twenty years ago, Robinson (1975) suggested a model of saccade generation that has been very influential. There were two novel aspects to this model. Robinson argued first that, although saccadic eye movements were ballistic from an overall functional standpoint, the neural mechanisms generating saccades employed a feedback process driven by some internal representation of the movement goal. His second suggestion was that the movement goal consisted of a representation of the target position in head-centred, rather than eye-centred, space.

There has been strong support for Robinson's first postulate. Under some conditions, the trajectories of saccades show the existence of a corrective process operative during movement generation (Jürgens et al. 1981; Zee et al. 1976). Furthermore, Mays and Sparks (1980) showed that if, during the course of preparation of a visually elicited saccade, a movement of the eye was induced by electrical stimulation of the superior colliculus, then the visually elicited saccade showed compensation for the perturbation even though the visual target was no longer visible. These and other results show that during the process of saccade generation, some reference signal about the saccade goal is available.

The second part of Robinson's suggestion has received less support. Although considerable effort has been devoted to discovering a signal in neural centres devoted to saccadic eye movements in which the coding is not oculocentric, no compelling evidence for such a signal has emerged (Moschovakis & Highstein 1994). Furthermore, more subtle tests looking for effects relating to saccadic eye movements that might suggest evidence of a signal specific to target position have also given negative results (Rohrer & Sparks 1993). Andersen et al. (1985) discovered cells in the posterior parietal cortex whose responses were modulated by eye position. In principle, such cells could be used to obtain a head-centred representation of the target (Zipser & Andersen 1988). Such a representation is of undoubted importance in visually coordinated behaviour but is not necessarily involved in the generation of visually elicited saccades.

We have not included the feedback process in our model because, at a functional level, our model merely requires the conversion of a spatial signal into an appropriate motor command signal. There are several current suggestions about how this could be accomplished without using a head- or body-centred coordinate system (Arai et al. 1994; Moschovakis & Highstein 1994; Van Opstal & Van Gisbergen 1989). An alternative approach suggests that the feedback process operates on motor error (Sparks 1986). Motor output uniquely codes eye position (Wurtz & Goldberg 1989), and thus motor error is equivalent to eye position error. Moschovakis and Highstein (1994) have suggested a feedback control process working on eye position error that is compatible with current physiology. This approach has the advantage that the stored representation involved in the feedback loop is interpretable as the memory of desired eye position to acquire the target. It has been previously suggested (Droulez & Berthoz 1990; 1991) that the results of

Mays and Sparks (1980) could be interpreted in terms of visual or oculomotor memory.

3.3.2. Saccade trajectories: Selection from the salience map. In our model, saccade production requires the opening of gates in the WHEN pathway to allow the control signals to be generated for the eye muscles. These gates must be opened for a period that corresponds at least roughly to the duration of the saccade. If the input signal changed during the period the gate is open, the motor output would be influenced by the change and saccade trajectories would vary in a manner reflecting this changing stimulation, rather than being stereotyped for saccades of a given size.

Several studies have examined saccade trajectories to discover whether a changing saccade goal can result in online modification of saccade trajectory. Large saccades (40 degrees) recorded in a double-step paradigm frequently show trajectory shifts in which the saccade goal appears to be updated during the course of the trajectory (Van Gisbergen et al. 1987a). However, with only very rare exceptions, smaller saccades (up to 10 degrees) show no major systematic variability of trajectory (Findlay & Harris 1984; Hou & Fender 1979), although detailed analysis reveals small but systematic effects of higher processes on trajectories (Rizzolatti et al. 1994). This suggests that for the small saccades typical of everyday viewing, the system operates with a unique spatial goal and thus circumvents the problems of dynamic update. In the next section we make a speculative suggestion about how this could be achieved.

3.3.3. Selection of the salience peak. We proposed in section 2.2.3 that the metrics of the saccade are determined by the location of a peak in the salience map. We argue that this takes place through a winner-take-all process within the underlying salience map. Koch and Ullman (1985) demonstrated the computational plausibility of such a process, and there is currently considerable interest among workers in computational vision for implementing such networks (Tsotsos et al. 1995). We recognise that our own suggestions for implementation are relatively sketchy but believe that they provide an account that will eventually yield to full quantitative modelling.

We propose that a winner-take-all process selects the salience peak at a particular instant in time so that, when this selection occurs, the saccade is directed to the location on the salience map represented by the peak. We suggest that the metrics are based on the *location of the activity peak* rather than on integrated neural activity. This requires an implicit "sample and hold" process quite similar to that of the classic early model of Young and Stark (1963), except that the signal sampled arises from the salience map rather than the direct retinal input. Once the location of the activity peak is selected, a nonlinear triggering process occurs that results in a *fixed* and *stereotyped* burst of activity localised at this peak.

An attractive feature of this proposal is that it can also achieve the solution of a further problem that has taxed modellers of the saccadic system. The problem is ensuring that the response is characteristic only of the *location* of the target and independent of other target characteristics, in particular stimulus intensity. This may be termed the "normalization problem." In one of the most fully formulated models of saccade metrics using distributed processing, Van Gisbergen et al. (1987b) showed quantitatively how saccade metrics could be accurately generated. Their model used linear vector addition over a stimulated region of a hypothetical collicular map. Nevertheless, this model was unable to explain such phenomena as the global effect (sect. 4.2.2), essentially because metrics were calculated on the basis of a vector sum of input activity. A subsequent modification (Van Opstal & Van Gisbergen 1989; cf. Lee et al. 1988) overcame these deficiencies by introducing nonlinear lateral spatial interactions to provide normalization; our proposal is an alternative nonlinear solution of the normalization problem.

We believe this suggestion is plausible in the light of recent discoveries about collicular processing. Munoz and Wurtz (1995a; 1995b) have reported two categories of cells – buildup cells and burst cells – involved at the level of the collicular map. Buildup cells and burst cells were located throughout the collicular map except at the rostral pole where the fixation cells formed a rostral extension of the buildup cells. Buildup cells showed a gradual rise in activity following the onset of a peripheral saccade target that was reciprocally related to activity in fixation cells; buildup cell activity increased as fixation cell activity decreased. In contrast, burst cells showed a sudden burst of activity just before saccade onset. Burst cell activity extended over a region of the colliculus, the location of which, but not the extent of which, depended on the saccade size. Burst cell activity did not spread spatially from this region. Munoz and Wurtz suggest that the buildup cells are involved in the "preparation to make a saccade," whereas burst cells may encode the metrics of the desired movement (see also Wurtz 1996).

We suggest that processing in the buildup cells leads to the selection of an unequivocal activity peak, perhaps by competitive inhibition between different potential peaks. The burst cells only operate once a peak has emerged and, in addition, operate subsequently in an all-or-none manner to give a stereotyped burst in a restricted region of the map around the selected peak. Such a process could provide a solution to the normalization problem because the burst would depend only on the location of the peak and not on its other characteristics. This suggestion is obviously speculative but still seems plausible.

4. Behavioural data

This section reviews experimental studies of human saccadic movements and suggests how the data can be explained using the model. Sections 4.1 and 4.2 consider a number of experimental findings obtained with the target-elicited saccade paradigm. Sections 4.3 to 4.5 deal with saccades where higher level influences play more of a role. Section 4.6. relates our work to attentional theory and, in conclusion, section 4.7 considers some results from eye movement studies in the neuropsychological disorder of hemispatial neglect as an example of how the model might be applied. In this section, we also contrast predictions of our model with other extant models (see particularly sects. 4.1.3, 4.2.2, 4.4.1, 4.5.1, and 4.6)

4.1. Target elicited saccades: Latencies

4.1.1. The gap effect. The gap effect describes how visual events at the fixation location have a substantial effect on saccade latency. In particular, if a fixated stimulus disappears slightly before the target appears, saccades have very short latencies. The effect is robust and is independent of advance knowledge of the location of the saccade target (Kingstone & Klein 1993a; Walker et al. 1995). The effect shows that some of the processing for a saccade can occur with no foreknowledge of where it will be directed, thus supporting in a general way the proposal of parallel processing in WHEN and WHERE streams. The first report of this effect was by Saslow (1967a), who varied the point in time of fixation point offset relative to the onset of a saccade target. When the fixation disappeared 100 to 200 msec before the target onset (leaving a gap period with no stimulation visible), latencies to the onset of the target were much shorter than if the fixation point remained until target onset. If the fixation point remained on after target onset (overlap), latencies were further lengthened to become about 100 msec longer than in the gap condition.

Ross and Ross (1980; 1981) suggested that the fixation point offset might provide a warning signal that gives temporal information about the appearance of the target. As shown in earlier work (Cohen & Ross 1977), saccadic latencies can be reduced by temporal warning signals. Ross and Ross reasoned that any event at the fixation point (such as brightening or change) might also reduce saccade latencies. They showed this to be the case. Nevertheless, the latency reduction was considerably stronger when the fixation point was extinguished. Moreover, visual onsets at fixation simultaneous with, or slightly following, the target onset produced a substantial latency increase. They concluded that the gap effect resulted from two components, a warning signal effect and an effect specific to visual offset. Several recent studies (Forbes & Klein 1996; Kingstone & Klein 1993a; Reuter-Lorenz et al. 1991; 1995) have confirmed the suggestion that the gap effect has two components. The warning-signal-like component effect is also found with manual reactions (Tam & Stelmach 1993), whereas the second effect is specific to saccade generation. This second effect has been called variously fixation offset, fixation release, fixation disengagement, or ocular disengagement.

In our model, the critical stage in determining saccade release is the resolution of the fixate/move conflict at level 2. The gap manipulation affects this conflict via two routes. Visual events at the fixation point have *direct* access (level 3) to the fixate system. Offset of a stimulus at the fixation point automatically reduces activity in the fixate centre and renders saccade triggering more likely. The second route involves the temporal preparation stage at level 4.

4.1.2. Simultaneous second stimulus: The remote distractor effect. Paradigms involving double stimuli have been very revealing in studies of saccades. If two stimuli are presented simultaneously in reasonably close proximity, the primary effects are on saccade metrics (sect. 4.2.2). However, if two widely separated simultaneous stimuli are presented, the saccade lands accurately on one of them but its latency is prolonged. The effect was first observed by Lévy-Schoen (1969) in a study attempting to establish what rules governed the choice of stimulus fixated under these circumstances. Lévy-Schoen presented two simultaneous targets and found that an accurate saccade was made to one or the other, with various biases influencing the one likely to be fixated – the strongest being proximity to the fovea (Findlay 1980; Lévy-Schoen 1969; 1974). The latencies of these saccades were greater than those for single-target controls, a finding that has been replicated in several studies (Findlay 1983; Weber & Fischer 1994).

Walker et al. (1995) showed that the latency increase occurs whether or not the subject has prior knowledge of target location. Moreover the effect is temporally specific to simultaneous or near-simultaneous stimulation (less than 100 msec offset between the two stimuli). Rafal et al. (1990) studied responses to bilateral target presentation in a group of patients with homonymous hemianopia as well as in a control group of normal subjects. They reported bilateral target slowing in the case when the bilateral distractor occurred in the blind temporal hemifield of the hemianopes but not when it was in the blind nasal hemifield. In contrast to the studies reviewed above, they reported no effect in control subjects. However, Figure 3 (p. 120) in their paper shows a small latency increase for bilateral presentations, albeit a possibly nonsignificant one, in the control subjects.

The above studies used exclusively two targets located on the horizontal axis and often at equal eccentricity. We have recently (Walker et al. 1997) examined the effects of distractor stimuli in different positions of the visual field. Our results show that the effect is a very widespread phenomenon and is neither specific to distractors on the opposite axis to, nor to those at the same eccentricity as the saccade target. Visual onset of a distractor results in a latency increase at any location remote from the target, including remote locations in the same visual field as the target. Moreover, the latency increase is dependent in a systematic way on the location of the remote distractor, being greatest when this is at the fixation point and reducing monotonically as the distractor is positioned more eccentrically. This pattern of results implicates strongly the nonspecific fixate system. If the effect depended on interactions within the salience map, then its magnitude would be expected to depend on the distance between distractor and target.

When the distractor is positioned at the fixation point, its effect is readily explicable in terms of direct activation of the fixate system (sect. 4.1.1). We suggest that the onset of a remote distractor at other locations also affects the fixate system. This postulate requires that the fixate system is accessed by stimulation from an extended central region of the visual field, a suggestion compatible with some physiological evidence from the collicular fixation system (Gandhi & Keller 1997). We suggest that events in the near visual periphery (out to at least 10 degrees) directly influence the fixate system with a strength of connection that depends on the degree of eccentricity. This direct influence increases activity in the fixate centre and thus slows the triggering process.

4.1.3. Express saccades. Fischer and Boch (1983) used the gap paradigm with trained monkeys and observed that target-directed saccades with extremely short latencies (80 to 100 msec) were frequently produced. They introduced the term *express saccade* to describe these movements and later reported them in human subjects (Fischer & Ramsperger 1984). Subsequent work has elaborated their properties and the conditions under which they occur (Fischer & Weber 1993). A striking finding is that under some circumstances there is a marked bimodality in the latencies with a short latency "express" population and a longer latency "regular" population (Jüttner & Wolf 1992; Nothdurft & Parlitz 1993), although this bimodality has not always been found (Reuter-Lorenz et al. 1991; Wenban-Smith & Findlay 1991).

We have already discussed in section 4.1.1. how saccades with short latencies might arise when the fixate system is disengaged. We believe our model might also account for bimodality in saccade distributions. Critical to our explanation is the spatially extended fixation region discussed in section 4.1.2. A consequence of this is that a peripheral visual target will affect *both* the move system and the fixate system. We suggest that, if the fixate system is already in a state of disengagement, it is possible that the triggering can occur immediately as a result of the increased stimulation in the move system. Such a state of disengagement would be likely in paradigms where target occurrence was highly predictable and also with trained subjects. These situations are indeed ones that render express saccades frequent (Fischer & Weber 1993; Paré & Munoz 1996). However if immediate triggering does not occur, the fixate system activation builds up through the direct pathway (level 3) and an extra time-consuming period is needed to overcome this target-generated activation. During this period the system is refractory and saccades are less likely to be triggered.

According to this account, express saccades should be rendered more likely in conditions in which the move system is activated by the target rather than fixate system. Hence it would be expected that express saccades should be more common with more eccentric stimuli, because activation of the fixate system increases with proximity to the fovea (sect. 4.1.2). Exactly this finding was made by Weber et al. (1992). They showed that express saccades occurred frequently when targets were at 4 degrees eccentricity, but their frequency decreased for targets at smaller eccentricities and they became absent at eccentricities below 1.5 degrees. Their account of this phenomenon is quite similar to the one presented here.

The earliest theoretical accounts of express saccades (Fischer 1987) suggested separate anatomical pathways. A quantitative model recently formulated by Fischer et al. (1995) envisions saccades being produced purely by the buildup of excitation to some threshold level. In contrast to our model, no role is assigned to inhibition. Other recent work has given more emphasis to processes such as attentional disengagement (Fischer & Weber 1993; Fischer et al. 1995) and gating of the fixation system (Cavegn 1996). This treatment in terms of processes is closer to our own thinking, although we argue in section 4.6 against the specific idea of *attentional* disengagement. Recent physiological work directed to understanding the neural substrate of express saccades (Dorris et al. 1997; Edelman & Keller 1996; Paré & Munoz 1996) supports an account in terms of fixation system activation, although Dorris et al. argue that, in addition, oculomotor preparation (involvement of the spatial selection system) is a requirement for express saccades.

4.1.4. Antisaccades. The "antisaccade paradigm" is one in which saccades are voluntarily directed away from a peripheral target. Hallett (1978) developed this technique and reported that antisaccades were characterised by longer latencies than reflexive saccades and showed more variable primary amplitude. On some trials, subjects were found to erroneously make saccades to the target ("prosaccade" errors). It was found that the latency of antisaccades was related to the latency of reflexive saccades (Hallett & Adams 1980), which was attributed to the sum of a constant delay (neural impulses) and a variable "goal redefinition" process. The goal redefinition process cancelled the primary reflexive saccade, and if it was delayed a reflexive "error" saccade would result. Although this account is appealing, it should be noted that a clear relationship between reflexive and antisaccade latency has not always been observed (Guitton et al. 1985).

A number of studies have examined the facilitatory effects of the gap condition on reflexive and antisaccade latencies. Although Reuter-Lorenz et al. (1991) failed to find a reduced latency for antisaccades in a gap condition, a latency reduction has been reported in subsequent studies (Fischer & Weber 1992; Reuter-Lorenz et al. 1995). The magnitude of the gap effect, however, is greater for reflexive saccades than for antisaccades (Forbes & Klein 1996; Reuter-Lorenz et al. 1995). Such a finding is consistent with the two-component explanation of the gap effect discussed in section 4.1.1. Antisaccades only benefit from the nonvisual (warning signal) component, since the suppression of the central fixation system necessary to prevent release of a reflexive saccade renders ineffective the activity reduction through fixation point offset.

Antisaccades involve the voluntary inhibition of a reflexive saccade and the cognitive manipulation of the spatial parameters to produce a saccade in the opposite direction. In our model, the ability to voluntarily suppress a saccade can be performed by the level 5 voluntary decision process connected to the central fixation system. This route enables reflexive saccades to be cancelled. The cognitive control over saccade metrics in Hallett's goal redefinition process must also depend on level 5 processes. These might work through controlling spatial selection but could also use search selection processes, the search target being a region of absence of stimulation.

Damage to the human frontal cortex is known to increase the number of prosaccade errors made in the antisaccade task (Guitton et al. 1985). One explanation of this increase in reflexive prosaccades is that the timing of the cancellation signal is altered. Antisaccade errors would be more likely to occur if the time taken for the voluntary inhibition was increased. (If the level 3 operations are completed before the cancellation signal is produced then a reflexive saccade would result.)

A recent alternative account has related antisaccade errors to so-called "executive processes," such as working memory, that are thought to be functions of the frontal lobe. Support for this view has come from Roberts et al. (1994), who studied antisaccade performance in normal subjects when performing a concurrent working memory task. They found that prosaccade error rates were greatest when the task with the highest working memory load was performed. Further support of a link between working memory processes and antisaccade error rates has been provided by a recent single case study of a patient with frontal lobe damage (Walker et al. 1998). The patient was unable to suppress his reflexive glances in the antisaccade task and also showed impairment on tests of working memory and executive function (involving the temporary suppression of a response). This suggests a link between higher level (level 5) processes and the generation of signals to suppress potent responses. Damage to this system can result in deficits both in working memory and in the antisaccade paradigm.

4.2. Target elicited saccades: Metrics

In our model, we follow the suggestion of Becker and Jürgens (1979) that the metrics of the saccade are programmed separately and subsequent to the decision to trigger a saccade. Following triggering, a saccade is made to the point of greatest salience in the salience map of the move system. Our model also incorporates the idea that the salience map codes spatial locations in a distributed way. Sections 4.2.1 and 4.2.2 show how the model explains results from the two-step and two-target paradigms.

4.2.1. The two-step paradigm. In the two-step situation, a subject is required to track a target that moves in steps. On some trials, two steps occur in rapid succession so that the second step occurs while the subject is preparing the response to the first step. In this situation a variety of types of eye-movement behaviour can occur. The subject may accurately track both steps with two separate saccades. The subject may make just one saccade to the final position of the target. The subject may also make a first saccadic response to an intermediate position between the two positions of the target and a second saccade to the final target position. Becker and Jürgens (1979) demonstrated that the critical parameter in determining the type of response made was the time interval between the second step and the commencement of the first saccade. This interval, which they termed "D," can be seen as the time available for the information from the second target step to modify the response to the first target step.

If D is small, there is no perturbing effect of the second step and the response goes to the first target position. Likewise, if D is large, the response goes to the second target position. However, Becker and Jürgens showed that there is an intermediate range of D values in which saccades of intermediate amplitude occur. If the positions of the two target steps are both in the same direction from fixation (e.g., both on the right at 5 degrees and 10 degrees), then a range of intermediate positions occur. The saccades show a characteristic *amplitude transition function* (ATF), with the average amplitude showing a systematic dependence on the value of D. If the target positions are more distant or if they are on opposite sides of the fovea, then such a transition function is absent or only minimally present (Ottes et al. 1984). The pattern found in these cases is of a set of saccades toward the position of the first target for small values of D and a set toward the second position for large values of D. There is an intermediate range of D values for which no saccades are found. This suggests that a finite time is required to cancel the saccade during preparation for the first target position and reprogram one for the second position. Becker and Jürgens used these results to develop their model of saccade control.

Subsequent work has confirmed this basic pattern and has extended investigations to remove the restriction to the horizontal meridian. If two steps occur between positions, which differ in *direction* from the fixation point with each having the same eccentricity, then similar transition functions can occur. If the two directions fall within a sector subtending less than about 45 degrees from the fixation point, a range of intermediate saccade directions occur in a systematic transition function (Findlay & Harris 1984; Ottes et al. 1984). This result holds even if the steps take the target across a horizontal or vertical meridian, requiring a change in direction of one component of the saccade.

Our model follows the ideas of Becker and Jürgens (1979) in explaining double-step results in terms of spatial and temporal integration of visual information within the salience map. Our model treats the triggering stage as entirely nonspatial, whereas in Becker and Jürgens's original model, this stage also produced the direction decision for the saccade. To account for the additional delays when the second target step takes the target to a position across the fovea (the "pulse overshoot" condition), we suggest that under these circumstances the second step operates as a remote distractor, producing direct activation in the fixate system (discussed in sect. 4.1.2). The magnitude of the extra delay in the pulse overshoot condition is comparable with that found in the remote distractor effect. In the pulse undershoot configuration, the second step is in a *neighbouring* position, producing input into the part of the move system that is already activated.

A critical question in saccade programming is whether direction and amplitude are in some sense programmed separately. Becker and Jürgens (1979) argued for separate programming because of the extra delays found when the second step of a double-step stimulus required a direction reversal. However, in view of the subsequent findings, it may be that factors other than the direction reversal per se contribute to the extra delay. In a subsequent review, Becker (1989) was indeed more cautious. Aslin and Shea (1987) carried out work with the double-step paradigm and found transition functions for both amplitude and direction. They also investigated situations in which the second step modified both amplitude and direction. They found transition functions but with differences in their time course and argued that direction and amplitude are separately programmed. It should be noted that the time course differences, although clear-cut, are relatively small and that the time relationships are not systematic. In some cases the changes in amplitude preceded the changes in direction, and in other cases the reverse order occurred. We discuss this issue more in section 4.4.1.

4.2.2. The two-target paradigm (global effect). Another elaboration from the single-target case is the study of saccades when more than one lone target is presented. If two stimuli are in reasonably close proximity in the visual field, a frequent finding is that the first saccade made to them goes to some intermediate location. This was first reported by Coren and Hoenig (1972) for voluntary saccades. It was later found to be a very characteristic feature of target-elicited saccades (Deubel et al. 1984; Findlay 1981b; 1982; Ottes et al. 1984). The result has been termed the *centre of gravity* or *global* effect. The saccade landing point is influenced by the relative visual properties of the two stimuli, such as size, luminance, or spatial frequency (Deubel et al. 1984; Findlay 1982; Findlay et al. 1993), suggesting that it results from spatial integration within the visual pathways.

He and Kowler (1989) pointed out that the global effect can be modulated by higher level factors such as expectancies and suggested that the effect might be entirely due to high-level strategies. However, we believe a more appropriate interpretation is that of Ottes et al. (1985), who suggested that the global effect represents a default option for the saccadic system that can be modified by higher level strategies but is manifest when no such influences are present. In our model the effect is a consequence of the distributed spatial coding in the salience map and pathways leading to it. The integration process occurs over all signals, which are feeding into the salience map in any particular situation. Thus, for example, global effects are seen in visual search when targets are present in neighbouring locations (Findlay 1997; Findlay & Gilchrist 1997).

4.3. Influence of higher processes on the WHEN system

Saccadic latencies show strong effects of prior information. As discussed in section 4.1, if accurate estimation of the time of the occurrence of the target can be made, latencies are shorter than in conditions of temporal uncertainty. These effects seem particularly powerful and the latency difference may be as large as 100 msec (Cohen & Ross 1977; Michard et al. 1974). In our model these effects are subsumed under the heading of Temporal Preparation. This powerful temporal preparation process has been little investigated. Becker et al. (1972), in a study of event-related potentials, showed that saccades are accompanied by a pre-motor positivity in a similar manner to that found with voluntary hand movements.

It has been repeatedly demonstrated that the decision about when a saccade should be made is directly related to the information being processed foveally. As reviewed, for example, in Rayner (1995), the relationship is indeed reliable enough to have given rise to a substantial body of work in which fixation durations are used as indicators of processing load. A particularly clear-cut demonstration of the effect of foveal information processing load occurred in a study by Gould (1973). Gould used a task of memory search, in which letters were scanned and a decision was required about whether or not the letters were members of a memorised target set. He found a substantial effect of memory set size on fixation durations. In this study the immediate visual stimulus was unaltered but its informational load was varied. This variation in informational load had a clear effect on fixation duration. Another example showing the effect of information load is from a study by Zingale and Kowler (1987). They showed that, if a subject is required to execute a preplanned sequence of saccades, the latency for the first saccade increases with the length of the sequence.

4.4. Influences of higher processes on the WHERE system: Spatial selection

The ability to direct the eyes voluntarily to a particular location is so familiar that its formal incorporation into a model of the saccadic system is unlikely to be questioned. Our proposal is that spatial selection operates by selection of a localised region within the topographically mapped WHERE system. This follows Kowler's (1990) idea that saccade metric selection is based on spatial integration of information within some selected region of the visual field. This suggestion appears to offer an approach to the way that cognitive and sensory influences can be combined. The selected region forms a window with the nonselected region outside subject to inhibition in the salience map so that visual stimulation is less effective, possibly to the extent of being totally gated out. The distributed nature of the spatial processing within the maps sets a limit to the minimum size region of visual space that can be selected and to the accuracy with which saccades can be made. Thus Kowler and Blaser (1995) showed that the precision of saccades to simple targets is very little affected by target size over a wide range of sizes.

4.4.1. Effect of spatial selection on saccade latencies. In the parallel processing account, spatial selection operates in the WHERE pathway and thus would be expected to produce an influence on saccade latencies only through modification of the fixate/move equilibrium. A strong prediction of the model is that the effects of such selection on latencies will then be small. This section examines the relevant evidence.

A number of studies have failed to find any effect of the number of potential target locations on saccade latencies (Heywood & Churcher 1980; Megaw & Armstrong 1973; Saslow 1967b). This result contrasts strongly with the well-known increase in latency for manual choice reaction times as the number of choices is increased. Several studies have looked at the question of whether prior knowledge of likely target position affects latency. Michard et al. (1974) found that prior knowledge of target position led to latencies that were about 40 msec shorter than when the target could appear in four alternative positions. It should be noted however that the targets eccentricities used in this study were rather large (20 and 40 degrees). Megaw and Armstrong (1973) found an advantage of about 18 msec for the prespecification of target direction. In contrast, Walker et al. (1995) found very small benefits for attentional precueing in comparison with a no-precueing condition, although precueing did result in costs (i.e., increased latencies to targets at uncued locations).

Abrams and Jonides (1988) developed a model of saccadic eye movement programming based on a study of precueing. Their model differs from ours in several respects and thus the supporting evidence is examined in some detail here.

Abrams and Jonides used a precueing paradigm in which subjects were given various types of advance information about the possible location or locations of a saccade target. The influence of this prior information on the latency for target-elicited saccades was measured. Four target locations were used, two on the left of fixation and two on the right, at 3 degrees and 6 degrees eccentricity, respectively. They were particularly concerned with the comparisons between precueing that specified direction (2 targets on the same side precued), amplitude (2 targets with the same eccentricity on left and right), and the mixed condition (2 targets but with neither direction nor amplitude uniquely specified). They found that the mixed condition resulted in latencies that were about 13 msec slower than if a single factor (direction or amplitude) was precued. This finding was used to argue for a model in which direction and amplitude are programmed separately, although not necessarily in a fixed serial order.

Although Abrams and Jonides's conclusions are logical given the framework adopted, some critical points can be made. First, the saccades in this study showed an abnormally high error rate (20% to 25%). Second, although the mixed condition resulted in saccades that were slower than in the single-dimension cueing conditions, mixed precueing nevertheless produced saccades that were about 30 msec faster than with no precueing – a puzzling result if components are separately programmed.

In general, there are small but reliable effects of prior spatial knowledge on saccade latencies. We do not feel that these are of sufficient magnitude to undermine our model, but rather that they indicate that processes within the WHERE stream can contribute to a small extent to the latency of saccades. Indeed we have suggested in section 2.2.3 that a set of conflict resolution processes occurs *within* the move centre. As we have indicated in the previous section, we believe it is misguided to think of saccade programming as a matter of parameter specification in a discrete way. We wish to place much more emphasis on location specification in a representational map of visual or motor space. Although at the brain stem level (sect. 3.2.1) saccadic eye movements are programmed in terms of muscular components, we are sceptical that this level is cognitively penetrable.

If both spatial and temporal predictability are high, then anticipatory saccades often occur. Saccades, which are initiated before the target appears, are clearly anticipatory rather than target-elicited. There is good reason to suppose also that any saccade with latency less than about 80 msec from target onset remains anticipatory with a quite abrupt transition at that time to stimulus-driven saccades. There are measurable differences in amplitude and in trajectory between the two types (Findlay 1981a; Smit & Van Gisbergen 1989). Moreover if two possible target positions exist, then saccades with latency less than 80 msec go to either position indiscriminately (Wenban-Smith & Findlay 1991), whereas saccades with longer latencies are almost invariably target directed.

4.5. Influences of higher processes on the WHERE system: Search selection

In visual search, saccadic eye movements are subject to cognitive control. A particular target is selected from a number of distractors, which differ from the target in some visual characteristic. Recent experimental work, both with humans and with monkeys, has elucidated these search processes.

We envision search selection as a natural mode of operation of the various retinotopically mapped areas, which map in turn onto the salience map in the move centre. The salience map may be activated in an excitatory manner by stimulus properties appropriate for the search target and in an inhibitory manner by other stimulus properties. The distributed nature of the salience map representation places limits on such a process. In an experiment by Ottes et al. (1985) subjects were presented with one red and one green stimulus, and the instruction was to saccade to the target of a particular colour. The task proved simple if the targets were in very different regions of the visual field, but if the targets were within the spatial averaging regions (sect. 2.2.4), then it was only possible to direct the first saccade to the target if its latency was abnormally prolonged; in other cases spatial averaging saccades occurred.

Search selection thus operates through competitive interactions, which can occur at various levels in the multiple different visual areas (see sect. 3.2.4). This view is elaborated elsewhere (Desimone & Duncan 1995; Findlay 1997). In principle, the search selection processes in our model allow complex information to affect saccade landing position *providing that* the processing of the information can be achieved rapidly enough to modify the salience map (sect. 4.5.1). The role of covert attention in the search process is discussed briefly in section 4.6.

4.5.1. Time course of the selection processes. An important issue to consider in the high level control of saccades is what type of information can influence saccades, in particular the relationship between saccade processes and visual object recognition. We do not feel that there is enough firm knowledge about visual processing speeds to provide more than tentative answers to such questions. It is possible that only relatively simple information can be made available with sufficient rapidity. In a recent study (Findlay & Gilchrist 1997), we showed that shape information (square versus circle) is available to influence long-latency saccades in a search task but not short-latency ones. This result shows the critical importance of processing speeds. These temporal constraints may also be accompanied by constraints resulting from the pattern of neural connectivity. For example, it might be expected that processes in the dorsal cortical stream would be able to influence saccades more readily than processes in the ventral stream as a consequence of the more direct connectivity from the parietal cortex.

Similar considerations will apply in text reading. A controversial issue in reading research has been whether high-level cognitive factors can influence saccade landing positions. There seems little doubt that low-level visual factors are the primary determiners of landing position, but evidence is accumulating for higher-level effects. Several studies have examined saccades to an isolated word target presented in parafoveal vision. If the saccades have short latencies, integration of purely visual information characteristic of the global effect is seen, and the global effect is thought to play some part in determining eye fixation positions in reading continuous text (Vitu 1991a). The saccades are influenced by visual factors such as relative contrast of letters (Beauvillain et al. 1996). If the initiation of the saccade is delayed, a more accurate saccade can occur to any desired position within the word (Coëffé & O'Regan 1987). Furthermore, careful analysis has demonstrated that some linguistic factors, such as unusual orthographic patterns (Beauvillain et al. 1996), can influence saccade landing positions.

We have suggested that transient visual information is processed automatically (level 3). In the situation of saccades to targets with transient onset, the onset transient will provide the dominant input to the salience map. However, if the subject delays a saccade, the saccade target may be more precisely selected (Findlay 1997; Lemij & Collewijn 1989; Ottes et al. 1985), reflecting the dynamic nature of the salience map. Moreover, any new transient stimulation arriving during a fixation will influence the subsequent saccade, and such influences are reliably found (Reingold & Stampe 1997).

4.6. Overt and covert attention

A theory of saccade programming is necessarily a theory of attentional deployment. However, in the discussion so far, little explicit reference has been made to attention. Much traditional theorising in the area of attention was predicated on the supposition of resource limitations or limited capacity. We have not found it necessary to make use of such concepts in our theory, although the time-consuming processes of competitive interaction do limit the speed with which saccadic eye movements can occur. Our model follows the admonishments of Allport (1993), who argued that there are a multiplicity of attentional mechanisms and thus workers should adopt goals in domain-specific areas.

Studies of costs and benefits in reaction times and in visual performance have repeatedly shown that a selective advantage can be conferred on restricted "attended" areas of the visual periphery when the eyes are held stationary. This covert visual attention contrasts with the overt attentional deployment of eye movements. Space limitations preclude a full discussion of the relationship between covert and overt attention (for recent work, see Findlay & Walker 1996; Rizzolatti et al. 1994; Walker et al. 1995), but our proposal of spatial selection has affinities with both spotlight and zoom lens models of spatial attention at the same time that it introduces the constraints imposed by distributed processing. We have argued that visual transient information has privileged access to the eye movement control system. In a similar way, most theorists of visual attention accept the idea that attention is captured in a reflexive, or exogenous, way by peripheral events (Egeth & Yantis 1997). We believe that there are close general affinities between our work and research derived from more traditional attentional viewpoints, although we note some contentious points below.

An early theory of visual search (Treisman & Gelade 1980) emphasized scanning with covert attention, assigning minimal role to eye movements. Our model, in contrast, has no role for an internal attentional scanning process. Indeed our model would be invalidated if it could be demonstrated that a fast covert attentional scan over a number of locations was possible in the preparation period before a saccadic movement. However, recent estimates of the rate of covert attentional scanning are at least as slow as those for overt eye movements (Findlay 1997; Sperling & Weichselgartner 1995; Ward et al. 1996). As elaborated elsewhere (Findlay & Gilchrist 1998), saccadic eye movements are rapid, easy to produce, and serve to direct the high resolution foveal region to the location of interest. We question whether covert attention plays any role in normal visual scanning.

An influential attention theory, which has relevance to oculomotor control, has been developed by Posner and colleagues (Posner & Peterson 1990). As described by Posner et al. (1984, p. 1864), "One can consider the act of orienting attention toward the target in terms of three mental operations: disengaging from the current focus of attention, moving attention to the location of the target and engaging the target." This theory was first formulated from consideration of neuropsychological deficits. We argue that, at least as applied to saccadic eye movements, the concept is flawed. In our model, processes equivalent to disengagement and attentional allocation both occur but we entirely reject the idea that the same process is involved in each case, in other words, the idea that whatever is disengaged is the same as what is moved. In our view, disengagement occurs in the channel, which is not spatially specific and so is not connected with the spatial aspect of attentional allocation. In support of this position, the magnitude of the gap effect is not affected by manipulations of spatial attention (Kingstone & Klein 1993a; Walker et al. 1995).

Henderson (1992; 1993) has advanced an attentional-based model to account for saccades during reading and scene scanning. According to this model, attention is initially allocated to the stimulus at the point of fixation. When the foveal stimulus is processed, attention is reallocated to some location in the periphery and the system begins to program a saccade to this new location. Thus attentional movements are primary and eye movements are secondary. This model recognises that perceptual and cognitive processing both affect saccade release, and subsequent work (Henderson & Ferreira 1993) has confirmed an earlier finding by Lévy-Schoen (1981) that only foveal, and not peripheral processing, has this effect. Henderson (1992) gives the following account of attentional allocation: "First, a preattentive map of likely stimulus locations is made available to the attention allocation system. Second, stimulus locations are weighted so that attention is allocated to the stimulus location with largest weight" (p. 264). This has evident similarities with the salience peak selection described in section 2.2.3. While Henderson's model has some parallels with our own, we are unclear what is gained by using attentional terminology since the properties assigned to attention mimic closely those of the eye itself (unique pointing direction; rapid movement from one location to the next).

4.7. Unilateral neglect

Space precludes any full discussion of the effects of brain damage on eye movements. We do, however, discuss here results from individuals with unilateral neglect because we believe that our model has the potential to throw some light on the attentional deficit present in this condition.

One consequence of unilateral parietal damage is visual neglect and visual extinction. These conditions are characterised by a failure to detect stimuli and objects located in the contralesional side of space. In addition to extinction and neglect, selective impairments in eye movement control are also observed in both monkeys (Lynch & McClaren 1989) and man (Girotti et al. 1983) following parietal lesions. The manifestations of extinction and neglect may be dissociated from the eye movement disorders and are typically regarded as reflecting higher-level disorders of visual attention (Posner et al. 1984; 1987) and visual awareness (Bisiach et al. 1979).

The eye movement deficits observed in patients with neglect have the following characteristics. Neglect patients are known to be generally able to make saccades following a verbal command (De Renzi 1982). Considering visually elicited saccades, there may in the most severe cases be a failure to initiate a saccade to a contralesional visual stimulus; if contralesional saccades are made these are of long latency and the amplitude is hypometric (Girotti et al. 1983; Ishiai et al. 1987; Walker & Findlay 1996; Walker et al. 1991). Patterns of small, contralesional, multistepping saccades are also observed to locate stimuli in the contralesional hemifield (Meienberg et al. 1986). In the monkey, a less severe deficit is observed. The animal can make saccades to a contralesional stimulus, but if two targets appear simultaneously in both hemifields then an ipsilesional saccade is always made (Lynch & McClaren 1989).

We have examined the saccades made by patients with unilateral parietal damage and visual neglect under fixation gap and overlap conditions (Walker & Findlay 1996). All of the patients showed the normal latency reduction (gap effect) for ipsilesional saccades, but none showed the normal latency increase (remote distractor effect) when a distractor appeared in their contralesional visual field. Two of the patients did not have a visual field defect and so the lack of a remote distractor latency increase cannot be attributed to a low-level, sensory-loss explanation. We also noted that neglect patients made more contralesional saccades under the gap condition than in the overlap condition (Walker & Findlay 1996; Walker et al. 1991). Although the increase in numbers of contralesional saccades in the gap condition appears consistent with Posner's deficit of attentional disengagement hypothesis, we have cautioned against this conclusion. A consistent finding in both studies was that patients also made more ipsilesional saccades in the gap condition than in the overlap condition. Furthermore, the amplitude of the contralesional saccades remained hypometric in the gap condition, and a pattern of multistepping indicative of a search strategy was also observed. Thus, the increase in contralesional saccades shown by some patients may be interpreted as reflecting an increase in a nonspatial attention caused by warning signal effects of fixation offset.

The saccadic abnormality observed in neglect can be accounted for in terms of our model with one extra assumption that at some level the spatial channels for L and R saccades are separate. Unilateral brain damage appears to result in an imbalance in the system that affects the level 3 automated processes in the spatial channel on the same side as the brain damage. More specifically, it is proposed that the ipsilesional automatic peripheral detection processes (involved in orienting to contralesional stimuli) remain permanently underactivated. The consequence of this underactivation is twofold. First, the salience map involved in coding saccade metrics remains permanently depressed, making it unlikely that a peak will occur on the contralesional side and that a contralesional movement will be generated. Any contralesional saccades that are made will be hypometric and of long latency, although such saccades are not precluded.

A further consequence of the unilateral underactivation of the peripheral detection processes is a low level of activation in the fixate system following the onset of a stimulus in the contralesional hemifield. When two targets appear simultaneously in both hemifields, the system will be biased to making a saccade in the ipsilesional direction by the intact movement channel. The latency of ipsilesional saccades will not be increased under bilateral target conditions due to the lack of automatic inhibitory effects, which would normally be produced by the connection to the fixate system. As the response of the ipsilesional movement channel remains underactivated, there is little activation of the fixate system following a contralesional input.

5. Summary and conclusion

In this article we have presented a framework for the understanding of the generation of individual saccadic eye movements. We have shown how this framework is consistent with known brain processes and how certain robust experimental results can be accommodated by the framework. In section 4, we highlighted points of difference between our framework and those of other workers.

We hope our presentation serves both to review past work and to provide pointers for future directions. We have concentrated on studies analysing visually elicited saccades, because a wealth of data has been obtained from these studies that we believe are well accounted for by the lower levels in our hierarchy. Our discussion of the upper levels of the hierarchy is more sketchy, but we expect understanding of the processes involved at these levels to develop rapidly. At the detailed level of neural computation, plausible accounts of spatial and search selection have been discussed and we expect these to become integrated with our increasing knowledge of the multiple cortical processing streams involved in visual analysis and saccade generation.

ACKNOWLEDGMENTS
Work on this paper was started during a visit made by the authors to the Max-Planck Institute of Psychological Research, Munich. We are grateful to the Max-Planck Foundation for financial support. We are also grateful for the constructive comments of H. Collewijn, D. Munoz, A. Wertheim, and other, anonymous referees.

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Change in motor plan with a change in the selection of the to-be-recognized word

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Abstract: New experimental evidence throws doubt on postulating no relationship between saccade control and visual object recognition. The control of saccades during reading depends on the perceptual system mediating object recognition.

The thorough analysis of human saccadic eye movements by Findlay & Walker (F&W) stands on its own without a discussion of the influences of perceptual processes in visuomotor coordination. Although their analysis is convincing, it does not exclude the possible use of perceptual information for achieving eye movement control. I take issue with the reason put forth by the authors for this exclusion (i.e., that "only relatively simple information can be made available without sufficient rapidity" to influence saccades, sect. 4.5.1). Growing evidence, from our laboratory and others, calls into question the idea that perceptual and visuomotor control rely on separate or different mechanisms. Such evidence is provided in reading performance when subjects intentionally scan a to-be-recognized stationary word. Such intentional saccades are internally triggered. Readers intentionally decide when to trigger a saccade and where to move the eyes into the word. When engaged in this perceptual activity, the saccadic system controls sequences of movements and fixations very effectively, enabling visual information uptake to occur with highly automated routines. Hence goal-directed movements are coordinated to some extent with the inner working of higher perceptual events. Conversely, the assumption that there is a direct relation between the observable eye and the mind's eye is quite controversial. In any case, a theory of saccade generation must be explicit about when and how perceptual processes and saccade programming are coordinated.

I hypothesize here that the When system is of vital importance for the metrics of the subsequent movement. This assumption is based on a new experimental finding that suggests that the metrical control of the saccades triggered after the first fixation in a word differs as a function of the selection of the saccade target – the same word or the next one. In these double eye movement experiments, subjects have to read a target sequence of two words displayed in the visual periphery at the offset of a fixation target. A step paradigm was used in which the sequence of words was displaced during the first saccade to it. Figure 1 presents the second saccade amplitude (top) and the second-fixation position (bottom) in the word n+1 (left) or the word n (right). It is evident that two different types of coordinate systems are used in the calculation of the saccade amplitude, depending on the selected target for the second saccade. When the following word is selected as the target, the eye movement is coded in retinotopic coordinates, and the saccade amplitude is determined with respect to the position of the second word on the retina. Consequently, the eyes land left of the center of the second word. When the saccade target is the first word (in this case, the first word is read with two fixations), the saccade is coded in orbital coordinates that are invariant with respect to the current position of the eye.

Previous work has shown that the amplitude of this refixation saccade is initially preplanned before the primary saccade, based on the letter string length (Beauvillain et al. 1998). In contrast to the model proposed by F&W, this result assigns considerable importance to the When system in the selection process. Indeed, interword and intraword saccades are triggered after two different classes of fixation duration (220–350 msec for the single fixation and 150–250 msec for the two-fixation cases). Consequently, the information is integrated at a higher level in the single-fixation cases. Thus, single-fixation duration is sensitive to the lexical property of the word, such as the frequency of use of the word, whereas the first of two-fixation cases is not (O'Regan & Lévy-Schoen 1987).

The data can be accommodated in a model of eye movement control that incorporates the planning of succeeding saccades. At the time a first saccade is planned based on the retinal error between the current position of gaze and the location of the first word in the field, a second saccade is preplanned that is coded in motor coordinates based on the word length. At that time, the intention to make a second fixation into the word is held in short-term memory. It is interesting that the change in eye position after the primary saccade causes a computation for a new representation of the second movement vector only when the second word is selected as the target for the subsequent saccade. This evidence indicates that the selection of a new target word for the recognition system causes the computation of the second movement and delivers the spatial coordinates of the intended target word. Thus, even though the execution of goal-directed eye movements may depend on specific control systems, the selection of appropriate goal objects and the action to be performed must depend in part on the perceptual systems mediating object recognition.

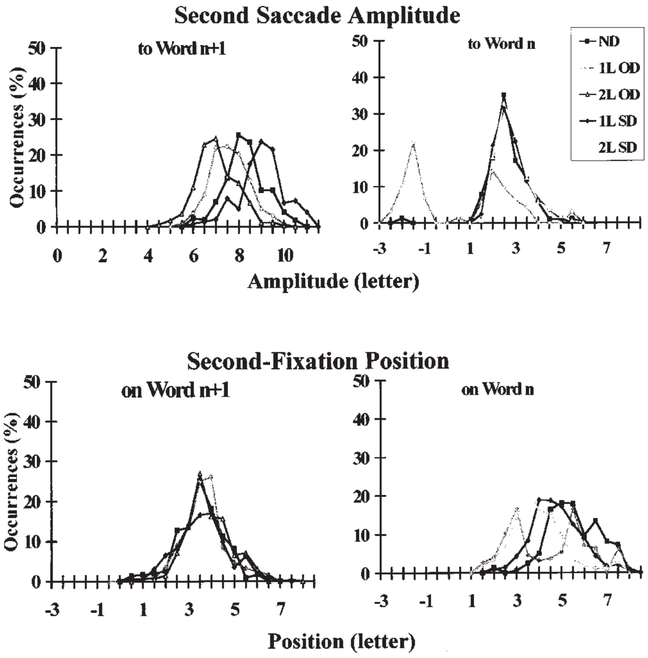

Figure 1 (Beauvillain). (Top) Distributions of second saccade amplitude to the word n+1 (left) or the word n (right) for displacements of the two word sequence in opposite direction (OD) (white diamond and triangle) or same direction (SD) (black diamond and triangle) to the primary saccade, and for the no displacement condition (ND) (black square). The amplitude of the displacement was one (diamond) or two letter-spaces (triangle). (Bottom) Respective distributions of second-fixation position in the word n+1 (left) or the word n (right).

Temporal delays, not underactivation of detection processes may be responsible for neglect

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Abstract: We have shown that FEF lesion-induced extinction could be compensated for by changing the relative temporal onsets of two targets presented on either side of the midline. Monkeys were trained to make saccades to either of two identical visual stimuli presented with various stimulus onset asynchronies (SOA). In intact animals the targets were chosen with equal probability when they appeared simultaneously. After unilateral FEF lesions an SOA of 67–116 msec had to be introduced, with the contralesional target appearing first, to obtain equal probability choice. With a smaller target separation, averaging saccades occurred with highest frequency at similar SOAs. Our findings suggest that neglect may be attributable to more time being required in the damaged hemisphere for converting sensory information into motor responses.

Findlay & Walker (F&W) propose that unilateral neglect and extinction result from damage to peripheral detection processes, leading to an imbalance in the signals sent to the salience map. They present data from humans with lesions of parietal cortex; but neglect can also ensue from frontal lesions. We present here an alternative explanation for extinction, in which the imbalance stems from a shift in temporal interactions between the hemispheres. We discuss data from monkeys with lesions of the frontal eye fields (FEFs).

We used the following paradigm, described in detail in Schiller and Chou (1998), first to observe the saccadic behavior of intact monkeys to targets presented in both hemifields, and then to investigate how that behavior was altered following FEF lesions. Monkeys were presented with two targets, located symmetrically across the vertical meridian, with an angular separation of 90°. The targets were presented with a range of stimulus onset asynchronies (SOAs) ranging from zero (simultaneous presentation) to one of the stimuli appearing 300 msec before the other. The monkeys were rewarded for making a saccade to either target.

When presented with simultaneously identical targets, intact monkeys generally made saccades to each of the targets with almost equal probability. When the two targets were presented with a temporal offset, monkeys made more saccades to whichever stimulus had appeared first. As the SOA was increased, they made an increasingly high proportion of saccades to the first target (pre-op curve in Fig. 1A). Immediately following lesions to the frontal eye fields, monkeys made saccades exclusively to the stimulus in the ipsilesional hemifield when the targets were presented simultaneously. However, if the stimulus appearing in the contralesional hemifield was presented a sufficient amount of time before the ipsilesional one, the monkeys could be induced to make saccades to it. When a range of SOAs was tested (as shown in Fig. 1) it was revealed that the monkeys still showed a relationship between SOA

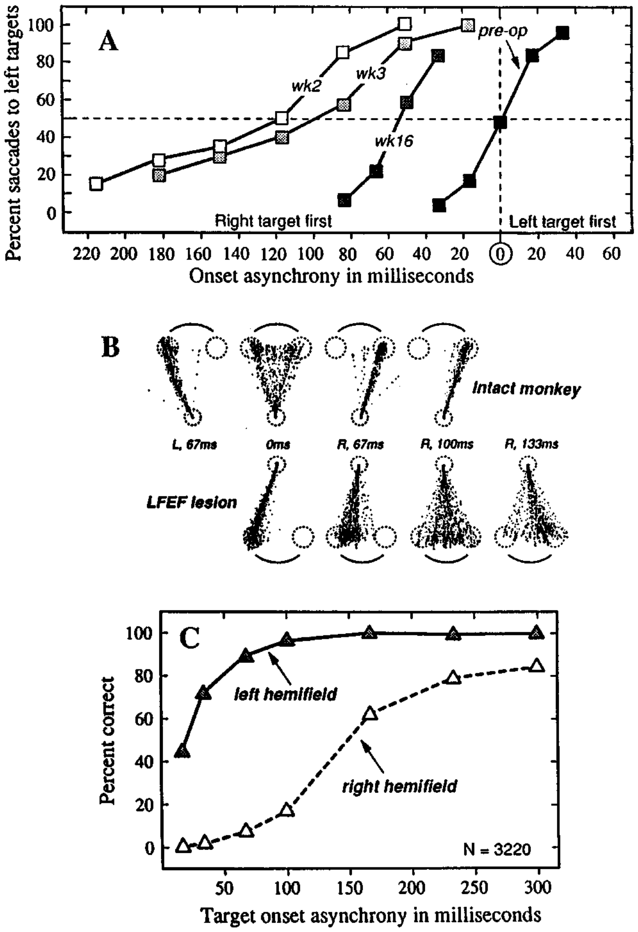

Figure 1 (Chou & Schiller). (A) Percent of saccades made to the left target as a function of the temporal offset between paired targets presented with various temporal asynchronies. Data collected preoperatively and 2, 3, and 16 weeks after a left FEF lesion are shown. (B) Records of saccadic eye movements made to targets presented with various temporal asynchronies and a 40% angular separation. The data are from an intact animal and from an animal with a left FEF lesion. (C) Percent correct performance on the temporal discrimination task following a lesion of the left FEF. Eight identical stimuli were presented, one of which (the target) appeared prior to the others by the times indicated on the abscissa. Data are plotted separately for the conditions in which the target appeared ipsilaterally or contralaterally to the lesion.

and the relative proportion of saccades contra and ipsiversive to the lesion similar to that of intact monkeys, but the entire function had shifted. Two weeks after the lesion, ipsi- and contraversive saccades were made with equal probability when the contralesional target appeared 116 msec prior to the ipsilesional target.

We hypothesized that damage to the FEFs led to a delay in the process of transforming a visual stimulus into the target of a saccade. Normally, the activity of some FEF neurons is tightly coupled to both the onset of the visual stimulus, and to the onset of the saccade (Hanes & Schall 1996; Shmolensky et al. 1998). The FEF projects in an organized and hierarchical manner to structures that participate in saccade generation, including the superior colliculus and saccade-related nuclei in the brainstem, which correspond to F&Ws putative salience map and move gate, respectively (reviewed in Schall 1998). Changes in the relative timing of signals arriving from the two hemispheres should have consequences for the computation of the final saccade vector.

To examine further how the imbalance in signals from the two FEFs might be reflected in the output, we considered how averaging saccades might be affected. Averaging saccades presumably occur as a result of the combination of two signals arriving simultaneously at the superior colliculus or the brainstem. We tested the effects of manipulating the SOA of two targets that had a smaller angular separation (40°). Intact animals made many averaging saccades when the targets appeared simultaneously but few when they were presented with various SOAs. Immediately after an FEF lesion, all saccades were directed toward the stimulus that had appeared in the ipsilesional hemifield when targets were presented simultaneously. To restore averaging saccades the contralesional target had to be presented 67–133 msec before the ipsilesional target (Fig. 1B).

Thus, rather than arising from underactivation of ipsilesional peripheral detection processes (sect. 4.7, para. 5), extinction can be conceived as a quantifiable *delay* between the left and right hemispheres that can be compensated by introducing a temporal offset in stimulus onset. This is consistent with reports that visually evoked potentials have a longer latency in human patients with neglect (e.g., Spinelli et al. 1994). It should be noted that the bias toward stimuli in the intact hemifield *can* be compensated by increasing the contrast of the stimulus in the contralesional hemifield, which would seem consistent with loss of detection sensitivity. However, decreasing the salience of stimuli also introduces delays in their processing. As luminance is decreased, the transmission time for stimuli already through the retina increases. Thus, the underlying reason why lower luminance stimuli are less salient may not be lower perceptual contrast per se, but the temporal lag that results from increases transmission time.

We have additional evidence that it is the temporal information that is degraded following FEF lesions. We have directly tested the monkey's ability to discriminate between stimuli based on their onset time and to indicate which stimulus they saw as appearing first. We presented eight identical targets, one of which appeared at a randomly determined amount of time before the other seven. The monkeys' task was to detect the earliest appearing target. Following frontal lesions, the monkeys were severely impaired in detecting the target when it was presented in the contralesional hemifield (Figure 1C).

Thus, we propose that the neglect commonly observed after unilateral frontal lobe damage may be in part caused by an increase in the time required to select and process the visual stimuli and to translate that information into a motor output. The increased time required for such processing may account for commonly reported symptoms such as circling behavior, deviation of the eyes toward the side of the lesion, and the paucity of scanning saccades made contraversive to the lesion. Following every fixation, stimuli that fall into the ipsilesional hemifield are processed faster, thereby increasing the probability that a saccade will be made into the intact hemifield. We are now in the process of examining monkeys and patients with parietal and occipital damage to determine whether the neglect seen after such lesions can also be accounted for by an increase in processing time.

Linking covert and overt attention

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Abstract: Findlay & Walker's target article questions whether covert attention plays any role in normal visual scanning (overt attention). My commentary suggests that there is indeed a very close link between the processes that govern covert and overt attention.

The model proposed in Findlay & Walker's (F&W's) target article is very compelling, but I would like to take issue with one aspect of it. In section 4.6, F&W question whether covert attention plays any role in normal visual scanning (overt attention). One of the reasons they give for their reluctance to ascribe any role to covert orienting in the generation of saccades is that covert shifts appear to be at least as slow as overt shifts, so that they would have no advantage in the scanning of scenes. I would argue that the similarity in speed in covert and overt attentional shifts indicates a possible common substrate for overt and covert orienting. There have been a number of studies demonstrating a close, if not exact, connection between neural mechanisms underlying overt and covert attention. For example, Desimone et al. (1989) have found that local deactivation of small zones in the superior colliculus impairs an animal's ability to attend to a target. More recently, Kustov and Robinson (1996) have demonstrated the effects of attentional manipulation on the trajectories of saccades evoked by electrical stimulation of the superior colliculus.

F&W propose that saccadic latency is determined mainly by the "conflict resolution" competitive push-pull interaction between the fixation centre and the move centre. Neither the idea that when a saccade is triggered its metrics are determined by the point of maximum salience nor that the triggering of a saccade is caused by the switching of a winner-take-all competition is new (Clark 1998). F&W's model differs from my own in two important ways, however, these being the role of fixation in triggering a saccade, and the mechanism that determines the latency of a saccade. In my model the transition of a competitive "winner-take-all" interaction between competing spatial locations is what triggers a saccade, as opposed to the transition of the interaction between the fixation and move centres.

In my model, shifts in (covert) spatial attention are associated with the transitions of winner-take-all competition between locations in the move centre. Thus, the model explicitly provided a link between covert and overt attention. It accounted for the quantitative aspects of a wide variety of oculumotor phenomena, including some of those used in F&W's model (gap effect, double step). This was supported by computer simulations, something missing in the target article. At the very least, this shows that fixation effects might not be necessary to explain many features of saccadic latency phenomena (although I do believe that fixation has some role to play).

My own model is clearly a simplistic one, as it is evident that not all covert attention shifts result in eye movements. This shortcoming is easily remedied, however, by adding a fixational process, as in the target article. With this addition, there will be a component of saccadic latency that depends on the functioning of the fixation process, and this may well account for phenomena such as express saccades, which cannot easily be explained by my model. [See Fischer & Weber: "Express Saccades and Visual Attention" *BBS* 16(3) 1993.]

In summary, I wish to promote a traditional "premotor" view of spatial attention (cf. Rizzolatti 1983) in which each and every covert attentional shift gives rise to a "command" to make a saccade. Whether this command gets expressed as an actual eye movement depends on the state of the fixation system. The (very nice) model described in F&W's target article could be easily extended to involve covert attention in this way, and in the process would gain significant explanatory power.

The effect of auditory distractors on saccades toward visual targets

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Abstract: The Findlay-Walker model does not consider saccades generated by auditory targets or nontargets (distractors), or by bimodal stimulation. Empirical results suggest that the effects of auditory stimulation cannot easily be incorporated into the model, neither in the WHEN nor in the WHERE system. A two-stage model by Colonius and Arndt gives a quantitative account of the facilitative effects of auditory distractors on saccadic latencies toward visual targets.

The Findlay & Walker (F&W) model provides a very useful general framework that should allow us to implement more specific, quantitative models in many of its parts. The target article does not take into account, however, an increasing body of empirical evidence on saccadic eye movements with *bimodal* stimuli. Both saccadic response time (SRT) to auditory target stimuli and the effect of the presence of auditory distractors on saccadic responses toward visual targets have been studied (e.g., Hughes et al. 1994). Auditory onsets, like visual onsets, appear to have automatic access to the eye control system via the lower levels, and bimodal stimulation has shown center-of-gravity effects with auditory targets (Frens et al. 1995; Lueck et al. 1990a), express saccades (Corneil & Munoz 1996), and remote distractor effects (Hughes et al. 1998).

Visual-auditory interaction in the generation of saccades is consistent with neurophysiological evidence from recordings in the deeper layers of the mammalian superior colliculus, where multimodal cells show profound enhancement or depression when multimodal stimuli are presented in spatial and temporal coincidence or disparity, respectively. However, the pattern of behavioral results with visual-auditory stimulation cannot be captured simply by replacing one of the visual stimuli by an auditory stimulus in the F&W model, neither in the WHERE nor in the WHEN system.

Instructed to fixate visual targets as quickly as possible while ignoring auditory distractors, subjects can generate saccades without changing the metric of the saccade significantly (i.e., there is no center-of-gravity [or global] effect) and without any latency increase, unlike the remote distractor effect observed for visual stimuli. On the contrary, several studies have found a reduction of saccadic latencies toward visual targets in the presence of auditory distractors, with the magnitude of the reduction depending on the specific spatio-temporal configuration of the bimodal stimulation. This facilitation effect tends to decrease with the distance of the auditory distractor from the visual target both within and across hemispheres (Frens et al. 1995); it also occurs with auditory stimuli presented over a virtual auditory environment (Colonius & Arndt 1998) and exceeds levels predictable by probabilistic summation of parallel, unimodal pathways (Hughes et al. 1998). Moreover, within a certain temporal range saccadic latency tends to increase with the delay of the auditory onset relative to the visual onset.

The spatial effect of an auditory distractor cannot be explained as a nonspecific activation on the fixate system analogous to that of a visual remote distractor in the F&W model (cf. sect. 4.1.2). There is no specific dependence on the distance of the auditory distractor from the fixation point; no global effect occurs for the auditory distractor in reasonably close proximity to the visual target, but there is a general speed-up of saccadic movements toward the visual target that does depend on the distance of the auditory distractor from the visual target. On the other hand, the effect of an auditory distractor is not analogous to that of a visual distractor in the salience map either. According to the F&W model, "multiple inhibitory cross-links between the various different regions of the map" (cf. sect. 2.2.3) would preclude the observed speed-up. Because the auditory distractors are not valid cues for the position of the visual targets, the speed-up cannot be attributed to an influence of spatial selection from level 4 in the F&W model either.

A recently developed quantitative model for saccadic latencies toward visual targets under auditory distractors (Colonius & Arndt 1998) accounts for the processes in the WHEN system as follows. In the first stage, sensory information from the visual and auditory periphery is processed in a parallel independent race toward a hypothetical decision center. Only if the auditory accessory stimulus is the winner of this race will the duration of the second, central stage of processing be affected by the auditory distractor and the specific spatial configuration of the stimuli. Stimulus characteristics like intensity and eccentricity directly affect the first stage of processing only (by influencing the outcome of the race) yielding a solution to the "normalization problem" (cf. sect. 3.3.3). A first empirical test of the two-stage model confirmed that the observed reduction of saccadic latencies toward visual targets in the presence of auditory distractors cannot be attributed entirely to a nonspecific warning effect of the auditory stimulus, that is, to temporal preparation by the auditory signal leading to disengagement at level 2 (cf. sect. 2.2.2).

Dopamine and impairment at the executive level

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Abstract: Patients with schizophrenia have an impairment in the inhibition of reflexive saccades, as a consequence of a functional impairment of the prefrontal cortex, which has not yet been encapsulated in terms of a formal model. A number of novel and testable hypotheses can be generated from the framework proposed by Findlay & Walker that will stimulate further research. Their framework therefore marks an important step in the development of a comprehensive functional model of saccadic eye movements. Further advances will be assisted by (1) a recognition of important distinctions in the executive control of volitional saccades and (2) addressing the capacity for cross-model integration of spatial information in the generation of the spatial properties of saccadic eye movements.

Saccadic inhibition in schizophrenia. Visually guided saccadic eye movements of patients with schizophrenia (SZ) have normal spatiotemporal properties. However, under specific conditions, these patients have a characteristic impairment in the inhibition of reflexive saccades. In terms of Findlay & Walker's (F&W's) proposed scheme, levels 1, 2, and 3 are therefore presumed to be intact. The antisaccade and memory-guided saccade paradigms have most clearly highlighted this impairment of inhibition (Crawford et al. 1989b; 1995a). The memory-guided task requires the formation of a mental representation of the target location that is presumed to be a function of spatial working memory, and is partially dependent on D1 cells of the prefrontal cortex (Williams & Goldman-Rakic 1995). A mental representation of a visual target in the prefrontal cortex can trigger a voluntary saccade via the descending projection to the superior colliculus. An impairment of the inhibitory projections, from prefrontal cortex, could result in an excessive rate of neuronal activity for "mentally represented" targets and cause a rapid rise to saccadic threshold of the movement-oriented neurons of the "salience map." Such a cascade of pathophysiological processes would account for the abnormal saccadic distractibility in schizophrenia and other frontally impaired patients (cf. Everling et al. 1996). Thus, processes intrinsic to the WHERE pathway, might result in an inhibition failure of the WHEN pathway. Alternatively, the failure of the higher cortical centres to maintain excitation of the fixation network may be a simple by-product of a capacity limitation, where the primary resources are allocated to generating and storing the mental representation of the target.

It has been widely suggested that the source of the abnormality in patients with schizophrenia is located at the level of the executive processes of the prefrontal cortex, a view that is supported by a strong correlation with performance on the Wisconsin Card Sorting Test, a putative prefrontal task (Crawford et al. 1995a). The frequent suppression errors in the antisaccade task of patients with schizophrenia, Huntington's or Alzheimer's disease suggests that a net reduction of inhibitory flow, from prefrontal, limbic, and basal ganglia neurons to the fixation system, could account for these errors. However, it is unclear whether the antisaccade abnormality is attributable chiefly to (1) excessive activation of salience neurons, (2) an impairment of the cognitive set, (3) impaired descending activation within the WHEN pathways, or (4) some permutation of these processes.

The eye movement pathology in schizophrenia has one fascinating component that is characteristic of even the most severe patients, namely, a rapid and spontaneous "corrective" saccade that accompanies 90–100% of all antisaccade "errors" (Crawford et al. 1989b; 1995a). This is observed even in the absence of direct visual feedback. Patients are aware of their errors post-hoc, but are unable to overcome the compulsive attraction of the visual target. This demonstrates a dissociation between the pathways of visual or efference-copy feedback and the operation of the "fixate" network.

Dopamine and saccades. Although abnormalities of saccadic eye movements have been widely reported in schizophrenia their pharmacological basis is unclear. Recent evidence suggests that the underlying pharmacology respects the functional and anatomical distinctions between the different types of saccadic eye movements. A distinct pattern is found in the pathophysiology of Parkinsonian eye movements, which has yielded some clues on the role of dopamine. Parkinson's patients (PD) are able to generate spatially accurate, reflexive (i.e., visually-guided) saccades and antisaccades. However, memory-guided and predictive saccades are hypometric, although the latency of these two latter types of saccades is relatively unimpaired. This pattern of selective impairments in PD suggests that, in man, the spatial properties of volitional eye movements, such as memory-guided and predictive saccades, are dopamine-sensitive (Crawford et al. 1989a; 1989b). Recent research also shows that an attenuation of dopaminergic function that is caused by either neuroleptic blockade of D2 receptors (Crawford et al. 1995b) or neurodegenerative cell loss, as in PD (Crawford et al. 1989b; Lueck et al. 1990b), has negligible effect on saccadic distractibility in the antisaccade or the memory-guided tasks. These data are consistent with the mounting evidence from clinical (Pierrot-Deseilligny 1994) and pharmacological studies (Crawford et al. 1995b) that the modulation of the different types of volitional saccades and their component spatiotemporal parameters is distributed across a number of overlapping neural systems.

Saccadic impairment in basal ganglia disease. In a series of experiments Lueck and colleagues (Lueck et al. 1992a; 1992b) varied the temporal overlap of a central fixation target and a peripheral target in a series of memory-guided and delayed response (i.e., no memory component) tasks. In contrast to saccadic latency, which appeared to be highly sensitive to the persistence of a central fixation target, saccadic amplitude was remarkably insensitive to this manipulation. This is consistent with the proposition of a WHERE stream that is highly tuned to peripheral visual events, and a WHEN stream that registers events at fixation and is also open to modulation by the neurocognitive context of the task.

Clinical research has also drawn attention to an important distinction between the processing of the amplitude of a primary saccade and that of the final eye position (FEP, i.e., after all corrective saccades have been completed). Although both the primary saccade and the FEP must be derived, at some level, from the output of the WHERE process, quite different views on the pathology of saccadic behaviour can emerge from these two parameters. An example comes from a study of memory-guided saccades in patients with PD, where it was found that the mean amplitude of the primary saccade in PD patients, compared to normals, was severely hypometric, although the FEP was unimpaired (Crawford et al. 1989b; 1995a). FEP could be generated from a latter, and more elaborated version of the primary saccade output or the two parameters may be independently derived.

Cross-modal integration. F&W may not have given sufficient consideration to the instances of nonvisual processing in the WHERE stream. The topographic and spatial alignment of the auditory and visual maps in the superior colliculus suggests a significant functional interaction across the auditory and visual modalities. How are the "salience peaks" determined for nonvisual stimuli? How does nonvisual stimulation interact with the visual modality? Lueck et al. (1990a) conducted a study in which they examined saccades that were elicited to an auditory target, whilst a simultaneous visual distractor was presented at one of several possible target positions. A number of findings were reported that are consistent with a process of cross-modal integration: (1) A "centre of gravity" effect was observed for ipsifield presentations of auditory-visual targets; (2) the primary saccade amplitude was a linear function of distractor position; and (3) there was no spatial averaging across visual hemifields. Clearly, spatial integration is computed both within and across spatial modalities.

F&W have presented a timely synthesis within a framework that has economically linked the perspectives of visual, cognitive, and motor operations in the control of saccadic eye movements. The model focuses on competitive connections at the subcortical level. However, there are also important neurochemically regulated operations at higher levels in the hierarchy that may interact with these information signals at the lower levels.

Is attention required in a model of saccade generation?

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Abstract: Removing attention from the saccade generation system should also remove the paradoxical loops that can occur with attention terminology. At least one such loop is still apparent in the current model, however. The benefits of an attention-free approach are assessed through comparison with a recent theory of attention (Logan 1996).

Findlay & Walker (F&W) are to be congratulated for attempting to describe saccade generation without recourse to attention, and this separation will be the focus of our discussion. How can an important means of relocating attention be described without a model of attention? F&W's main innovation is the use of competitive inhibition to limit the system. Though the authors acknowledge that their theory is compatible with attentional models such as the spotlight and zoom lens, their necessity is questioned. There is no requirement to resort to a limited capacity beam to explain the constraints. Instead, the visual scene creates its own constraints on what we process. Salient areas on the map compete for the right to attract the next saccade through the use of inhibition. Instead of attention being constrained to a particular area because of capacity limitations, leaving a vacant area of unattended space, this unattended part of the visual field is stimulated with various stimuli whose competition for fixation has been overwhelmed by the inhibitive signals from the salient heavyweights.

Despite this opportunity to avoid some of the endless loops that attention research can sometimes enter, F&W's reliance on bottom-up processes does not fully achieve this. For example, one of the factors that has direct input to the saliency map is the *intrinsic salience* of the items that are represented. A feature of greater contrast with its surroundings may produce a higher spike on the map than other objects. F&W suggest that not only may some stimuli have greater intrinsic salience than others, this salience can be modified by learning, such that some stimuli may accrue greater conspicuity. This takes us into one such paradoxical loop: How can we learn to give more salience to objects that we have not yet processed? Familiarity simply with one stimulus over other stimuli should not increase saliency because until attention is directed to it we cannot know what it is. Loftus and Mackworth (1978) argued the reverse side of the coin, that novel items in a visual scene accrue more salience. In their original study it was found that subjects quickly fixated the semantically incongruent elements in a picture, such as an octopus in a farmyard scene. However, it has to be asked how subjects knew that the octopus was there and was semantically incongruent, without first processing the object?

Henderson and Hollingworth (1998) suggest that one explanation for this evidence may be a correlation between visual and semantic incongruity. An octopus in a farmyard scene may not attract attention because it has greater saliency due to semantic novelty, but because it is a collection of close curves within a farmyard scene of predominately straight lines. Their research suggests that semantic incongruity in the peripheral field has little effect on the time taken to fixate the stimulus when visual novelty is controlled.

Though F&W's model allows items within a 5° radius to influence the fixate centre, this does not include semantic processing. Therefore we must ask how learning can increase the salience of preattended stimuli before they are identified. To avoid this loop one could argue that such learning must be context-dependent. For example, when reading we devote attention to the right of the currently fixated word, with little to the left. This does not occur because the words to the right of fixation are more familiar to us than the words on the left but because our familiarity with the context dictates that this would be the more relevant and meaningful source of new information. Instead of the saliency of familiar stimuli increasing, we may learn to extend the spotlight in an asymmetric shape in favour of the words on the right. Cognitive influences do not feed into the lowest levels of the system and modify the map, but instead modify the criteria with which we view that map.

A similar theory in many respects has recently been published by Logan (1996). Both F&W and Logan employ a saliency map with distributed coding, and provide mechanisms to calculate which stimulus should be processed next. Both theories focus on the lower levels of input, leaving the higher cognitive influences to be specified by others. The greatest difference between these two theories is that, despite their similarities, one uses the terminology of attention, whereas the other positively avoids it.

The first divergence of the two theories according to their use or avoidance of attention comes with Logan's application of a threshold to the salience map. This top-down process represents the application of attention to the salience map. The threshold cuts off the saliency peaks from the map with increasing proportion the lower the threshold is set. The areas underneath the flattened peaks are called the *feature catches* of perceptual objects, which are then available for processing. Logan suggests that different thresholds could theoretically be applied to different areas of the saliency map. Thus one could learn to place lower thresholds in certain areas of the map according to task demands. Instead of an asymmetric spotlight in reading, Logan might argue for reduced thresholds to the right of fixation. This top-down application of attention avoids the paradoxical loop that occurs with learned effects on intrinsic salience.

The conflict between the fixate and move centres can also be discussed in terms of feature catches. F&W refer to the decline of activity that occurs in the fixate centre as *disengagement.* This title may have been derived from the fact that forced disengagement at a fixated point decreases saccade latency to a peripheral target (the gap effect). Disengagement need not be just a powering down of the fixation once it has served its purpose, however. It could also be viewed as *exhaustion* of the information content of the stimulus that occurs during the fixation. If the stimulus were the sole point of interest in an otherwise empty visual field, then the individual could interrogate it until every drop of information had been wrung from it. There are usually other stimuli in the periphery competing for attention, however. As we extract information from the current fixation point, the benefits to be gained by remaining fixated at that point are reduced. Correspondingly adjacent stimuli become more alluring because the cost required to extract information from these stimuli is small compared to the benefits of mining untapped information. The diminishing returns that are left in the stimulus under current fixation are then forgone in favour of more promising targets of interest. This exhaustion of a fixated stimulus could be viewed as a decrease in the salience of that object on the map. In a system that still acknowledges the limits of attentional capacity the reduction of the fixated feature catch may allow one to lower the thresholds on surrounding perceptual objects. Thus as the feature catch of the fixated object decreases through processing, so those of adjacent objects are increased. Alternatively, the decline of the fixated feature catch may be the result of an increase in the local threshold for that object. This mechanism could then be used to explain Inhibition of Return. A cue may direct attention to a spatial location and, as it contains very little inherent information, it may result in a local threshold increase, which correspondingly encourages saccades or attention shifts to other areas of the visual field with lower thresholds and larger feature catches. Though the cue quickly disappears, the threshold increase may persist such that any subsequent abrupt onsets in that area do not achieve the size of feature catch that would normally occur with the default threshold level. Regardless of which precise mechanism occurs, this could partially account for the conflict between the fixate and move centres.

The current model has at least one paradoxical loop that is typical of theories of attention, yet it seems (paradoxically) that it can be overcome by allowing attention back into their model. The setting of Logan's (1996) threshold on the salience map represents the potential allocation of attention. This threshold and the subsequent feature catches can supplement this model of saccade generation but it requires the acceptance of attention as a concept back into their theory.

Where and When does the What system play a role in eye movement control?

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Abstract: This commentary focuses on Findlay & Walker's model and more specifically, on its underestimation of the role of cognitive processes in eye movement control during complex activities such as text scanning. In particular, the issue of the complexity of the subject's task/behavior is discussed to stress the importance of the link between selection for perceptual processing on the one hand, and the selection of a target for a saccade, on the other. Future models will have to account for the fact that the goal of any saccade is to bring the eyes to a relevant object and that the selection of this saccade target is closely related to object recognition.

The starting point of Findlay & Walker's (F&W's) model is the notion of separate pathways for the When and Where decisions in saccade programming. Their model accounts for saccadic eye movements in different situations in which saccades are generally elicited by simple targets. In these cases, the control over eye movements is largely bottom-up and reveals the automatic, reflexive components of saccadic eye movements (level 3). The use of simple targets induced an obvious relationship between target selections to achieve both the perceptual and the motor task. Indeed, saccade target results from the task and/or the physical properties of stimuli. F&W's position concerning a potential effect of higher level information relies on the critical role of processing speed. The salience peak can be determined by this kind of information only when saccade latencies are sufficiently long. In their recent model of eye movement control in reading, Reichle et al. (1998) postulate a relationship between lexical access of the currently fixated word and the programming of the next saccade (which may be a refixation into the same word *n,* a saccade to the word $n+1$ or a skip of the word $n+1$). The relative familiarity of the fixated word seems a good candidate to signal to the eye movement system that lexical access is imminent and that a saccade to the subsequent word should be planned.

Several arguments support the existence of a common mechanism of saccade target selection for recognition and action (e.g., Deubel & Schneider 1996; Doré & Beauvillain 1998). The same object is selected for perceptual and spatial analysis (usually called the "What" system within the ventral stream, which underlies object recognition) and motor control (usually called "Where" system within the dorsal stream, responsible for computing spatial information about objects). Doré and Beauvillain (1998) showed that in reading-like situations involving saccades to a string of letters, information from a parafoveal stimulus can be available with sufficient rapidity (even when saccade latency is normal) to modify the perception for action (e.g., word length effect on landing position, O'Regan 1979; Rayner 1979), as well as for recognition (detection performance of a brief change in a letter).

In reading situations, each word can be viewed as a spatial window (cf. sect. 4.4 of the target article) with the salience peak in the motor map as its centre of gravity. The global effect is seen here as a default option to calculate the landing position (cf. word length effect). In contrast with the model proposed by F&W, empirical data in reading suggest that information for visual object recognition – related to initial letter integration – can be made available quickly enough to influence the destination of the next saccade (e.g., Morris et al. 1990). Moreover, the frequency effect on refixation probability in reading is a well-established fact, infrequent words being more likely to be refixated than frequent ones (e.g., McConkie et al. 1989). The decision to remain on the current word or to leave it is taken during a 200–300 msec fixation and is at least in part related to the information being processed foveally (cf. target article, sect. 4.3). Saccadic eye movements bring the fovea rapidly to the "interesting objects" present in the text line.

Research in our laboratory has shown clearly that decisions about where to move the eyes do not depend exclusively on word boundary information. For a reader of a give language, unusual letter clusters provide a salient signal that "attracts" the next saccade (Beauvillain & Doré 1998; Beauvillain et al. 1996). Therefore, a selection process that delivers coordinates for the next movement should be influenced by information acquired from the word to which the eyes are directed prior to the eye movement. Coëffé and O'Regan (1987) have shown that saccade accuracy and latency are positively correlated, which is consistent with the ATF (amplitude transition function) of Becker and Jürgens (1979). With more complex stimuli (e.g., a word), delaying saccade latency caused the eyes to land further into the word, as a function of the informativeness (number of potential candidates) conveyed by the orthographic structure of the initial letters (Doré & Beauvillain 1997); this suggests a shift of the peak in the salience map.

We have also shown (unpublished manuscript) that the informativeness of these letters is critical: We could replicate this effect with words but not with a meaningless letter string beginning with an illegal orthographic cluster of letters. In the latter case, saccades bring the eye near the illegal beginning letters, whatever the saccade latency. These data clearly suggest that saccade programming is affected by abstract information related to word recognition. Obviously, the salience peak is primarily determined by the centre of gravity and is modified by intrinsic salience (orthographic structure). Yet the question is: How can it shift before saccade triggering and cause the eyes to land further into the word (than usually observed), when saccade latency delay does not exceed 150 msec? F&W's model fails to provide an explanation for this kind of result.

In summary, the main problem with F&W's new model is that many experiments (reviewed in the target article) suggest that information about a potential visual target for the saccade is relatively limited. Further experiments using more abstract stimuli (like words, pictures) should reveal that this kind of information is available and plays a role in the programming of saccadic eye movement. Indeed, reading has a particular status in psychological research. Stimuli are complex but relatively well defined (physically, as well as linguistically), and the high level of automaticity of adults' access to mental representations of words allows us to examine eye movements during a complex activity. Accounting for the close relationship between saccade target selection and object recognition is a challenge for the models to come. They will have to demonstrate that the goal of saccades is to bring the eyes to a relevant target and that the selection of this target is closely related to its recognition.

The underrated role of the "move system" in determining saccade latency

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Abstract: The Findlay & Walker target article emphasizes the role of the target-nonspecific "fixate" system while downplaying the role of the target-specific "move" system in determining saccade latency. We agree that disengagement of the fixate system is responsible for the target-nonspecific latency reduction associated with the gap effect. However, high target predictability and extensive training at a target location can also result in latency reductions, the culmination of this being express saccades. The target-specificity associated with the latter forms of latency reduction implicate a mechanism involving the move system. Recently discovered neurophysiological correlates underlying these behavioural phenomena reside in the superior colliculus.

Findlay & Walker's (F&W's) target article proposes a plausible five-level model of saccade generation that can account for a variety of oculomotor phenomena, including the gap effect and express saccades. The authors argue that the spatial selection of the upcoming saccade occurs in the WHERE pathway and make the "strong prediction" (sect. 4.4.1, para. 1) that the effects of such target selection on latencies will be small because the triggering stage is located in the entirely nonspatial WHEN pathway. Although F&W stress that this is a functional rather than a physiological model, for the phenomena of the gap effect and express saccades they speculate that these may result from the push-pull mechanism between the "fixate" (When pathway of level 2) and "move" (Where pathway of level 2) systems at the level of the superior colliculus (SC). In this scheme, the fixate system contains the triggering stage and thus determines saccade latency. Here we suggest that the contribution of the move system has been underrated in its role in the determination of saccade latency.

F&W base their claim that the WHERE pathway has little effect on saccade latency on the premise that "a number of studies have failed to find any effect of the number of potential target locations on saccade latencies (Heywood & Churcher 1980; Megaw & Armstrong 1973; Saslow 1967b)" (sect. 4.4.1, para. 2). In contrast, we have found that the majority of the literature supports quite the opposite notion that the number or predictability of potential target locations affects saccade latency (Abrams & Jonides 1988; Bartz 1962; Basso & Wurtz 1998; Carpenter & Williams 1995; Dorris & Munoz 1998; Hackman 1940; Klein & Pontefract 1994; Michard et al. 1974; Paré & Munoz 1996; Reuter-Lorenz & Fendrich 1992). These studies show that prior knowledge of where a target will be presented has a consistent effect on saccade latency in a manner that cannot be accounted for by the proposed spatially nonspecific fixate system. This attribute of the saccadic system has been implemented in a number of latency models in which saccades are elicited when a threshold level of activation in the spatially specific move system is surpassed (Carpenter & Williams 1995; Fischer et al. 1995; Hanes & Schall 1996; Kopecz 1995; Kopecz & Schoner 1995; see Pacut 1977 for review of threshold models).

The influence of the fixate system on saccade latencies is exemplified in the phenomenon known as the gap effect (sect. 4.1.1). When an initial fixation point is removed prior to the presentation of an eccentric target, saccade latencies are reduced compared to the condition in which the fixation point is not removed prior to target presentation. The gap effect occurs for saccades directed to any target location indicating that it is mediated by a spatially nonspecific mechanism unrelated to the move system (Kingstone & Klein 1993b; Walker et al. 1995). This view is bolstered by the physiological findings that both fixation-related neurons in the SC (Dorris & Munoz 1995) and frontal eye fields (Dias & Bruce 1994) show modulations in their activity in relation to fixation point disappearance in the gap paradigm.

The influence of the spatially specific move system on saccade latencies is exemplified in the reduction observed with the increased target predictability mentioned above and the phenomenon of express saccades (target article sect. 4.1.3). Although the target article heavily implicates a spatially extended fixate system in the generation of express saccades, two lines of evidence point to the importance of the move system in this phenomenon. First, as alluded to in the target article, express saccades are triggered only by suddenly appearing targets in the periphery. Express saccades are not generated to constantly present peripheral targets (Boch & Fischer 1986; Edelman & Keller 1996; Rohrer & Sparks 1993), nor are they directed away from targets as in the antisaccade paradigm (Everling et al. 1998; Fischer & Weber 1992). This view is supported by physiological evidence that suggests that the normally separate target- and saccade-aligned bursts of SC saccade-related neurons are fused into one larger burst equally aligned on both target appearance and the saccade during express saccades (Dorris et al. 1997; Edelman & Keller 1996).

Second, unlike the gap effect in which latencies are reduced to saccades directed to all targets in the visual field, the generation of express saccades is spatially specific. The percentage of express saccades directed toward a target location is dependent on both target predictability (Paré & Munoz 1996; Sommer 1997; however, see Rohrer & Sparks 1993) and the level of training to that target location (Fischer et al. 1984; Paré & Munoz 1996; Rohrer & Sparks 1993). A simple disengagement in the fixate system cannot explain this spatial specificity. Furthermore, F&W suggest that express saccades can be triggered by target presentation when the fixate system is disengaged during the gap paradigm. Again this cannot account for the spatial selectivity of express saccades because all areas of the move system should be disinhibited equally through the nonspecific disengagement of the fixate system. Although SC fixation neurons decrease their activity during the gap paradigm, thereby disinhibiting the move system as suggested, their activity does not show a greater decrease prior to the generation of express saccades compared to regular latency saccades (Dorris et al. 1997). However, a proportion of SC saccade-related neurons display early, low-frequency activity prior to the generation eye movements (Munoz & Wurtz 1995). This early activity has been shown to be related to the selection of targets from a number of possible stimuli (Basso & Wurtz 1998; Glimcher & Sparks 1992) and the probability of generating a saccade into the response field of a neuron (Dorris & Munoz 1998). Unlike SC fixation neurons, this buildup activity of saccade-related neurons is inversely related to saccade latency (Dorris et al. 1997; Dorris & Munoz 1998; Everling et al. 1999) and is significantly higher prior to express than regular latency saccades (Dorris et al. 1997).

Taken together, the evidence suggests that removal of the fixation point during the gap paradigm can reduce latencies of saccades directed to targets in all regions of the visual field through disengagement of the fixate system. In addition, there are the equally important, and often underrated, effects of spatially specific events such as target number and predictability, which can also influence saccade latency. Only when both disengagement of the fixate system and advanced preparation of oculomotor goals in the move system occur together can the initial target-aligned response of SC saccade-related neurons surpass saccadic threshold resulting in saccades of express latency.

Spatial programming and the representation of salience

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Abstract: The posterior parietal cortex and frontal eye field contain maps of visual salience on which the decision to choose a saccade may be based. However, an averaging express saccade is not represented by a victorious unimodal representation in the superior colliculus. Normalization as described by Findlay & Walker is not necessary for the generation of saccades.

Findlay & Walker (F&W) postulate that the oculomotor system chooses which saccade to make based on a visual "saliency map," a representation of visual space that contains only its most conspicuous or relevant features. From this representation one unequivocal peak representing an explicit "movement decision" for the saccade is selected at or upstream of the level of the superior colliculus. Although current neurophysiological data indeed support the existence of several "saliency maps," some of which may be tightly connected to saccade execution, the existence of a movement decision implemented explicitly in the superior colliculus is directly contradicted by recent findings.

We recently described a form of salience representation that may be directly relevant to saccadic eye movements. Neurons in the lateral intraparietal area (LIP), a subdivision of posterior parietal cortex, have long been known to respond exuberantly to abruptly appearing objects. We have found recently that these same neurons respond minimally, if at all, to the kind of visual stimulation a monkey is likely to encounter in a natural environment: continuously visible, inconspicuous objects that are not immediately relevant to behavior (Gottlieb et al. 1998). These stimuli enter the neurons' receptive fields by virtue of the monkey's saccades, instead of by their abrupt appearance or intrinsic motion. LIP neurons respond to such objects when the latter become behaviorally relevant, for example, if designated as the target in a search task. A similarly selective representation probably exists in the frontal eye field (Burman & Segraves 1994). When a monkey searches a stable environment, the decision to make a saccade probably occurs at the level of the presaccadic movement cells in the frontal eye field, based partially on parietal and frontal saliency representations. By the time this signal reaches the superior colliculus, the decision is probably already made. The selectivity of the parietal visual signals can explain many symptoms characteristic of parietal neglect, including the under-reactivity to flashed stimuli discussed by F&W.

F&W postulate that a number of mechanisms, such as competitive inhibition and response averaging, serve to create the salience maps of the visual environment. However, these processes have only been demonstrated in the processing of flashed stimuli (reviewed in Desimone & Duncan 1995; see also Reynolds et al. 1999). Because flashed stimuli constitute a special case both psychologically (Egeth & Yantis 1997) and physiologically (Gottlieb et al. 1998), such mechanistic processing of the on-response may not occur when stable stimuli enter the receptive field. During normal viewing, a large portion of the afferent visual input is suppressed based on expectations or assumptions about its stability and is then selectively reactivated based on behavioral context.

Not all saccades are processed in the frontal eye field. For example, express saccades require the superior colliculus and the geniculostriate pathway but not the frontal eye field (Schiller et al. 1987; 1990). One finding beginning to emerge clearly is that, in contrast with F&W's assumptions, a saccade need not be accompanied by an explicit, unequivocal selection of a unique peak of activity upstream from the brainstem saccade generator; instead, it can result from the processing of a more distributed collicular signal. F&W propose that, from a salience representation with multiple peaks "processing in the buildup of cells [of the superior colliculus] leads to the selection of an unequivocal activity peak"; burst neurons in the superior colliculus supposedly "only operate once a peak has emerged" (sect. 3.3.3). During express saccades, however, the visual response of burst cells actually provides the "unequivocal activity peak" (Edelman & Keller 1996). Although buildup neurons are active during the gap period prior to an express saccade, their activity cannot be target specific, because it can occur before the onset of a target appearing at a random location (Dorris et al. 1997). Furthermore, Edelman and Keller (1998) have recently demonstrated that saccades can be made in the presence of the activity of burst neurons at two locations on the collicular map. The collicular discharge accompanying express saccades to two targets (which include averaging saccades) codes better for the two targets than for the saccade vector, even at the time of the saccade. This dependence is particularly strong for neurons having sharply tuned movement fields, which tend to be classified as burst neurons (Anderson et al. 1998).

As F&W's model is not explicitly physiological, the authors might argue that an "unequivocal activity peak" exists downstream of the SC, possibly in neurons of the nucleus reticularis tegmenti pontis (NRTP) or the vector long-lead burst neurons described by Hepp et al. (1989). F&W believe that such a "normalized" signal would ensure that saccade dynamics are independent of the circumstances triggering them. But data clearly show that the normalization argument is overstated. For example, in both human and monkey, saccades to visual targets are faster than saccades of equivalent vectors made in the dark (Becker & Fuchs 1969; Gnadt et al. 1991; Smit & Van Gisbergen 1987; White et al. 1994). Discharge of most neurons in the superior colliculus is greater for saccades to visual targets than for those made in the dark (Edelman & Goldberg 1997), providing a mechanism for this velocity discrepancy. Microstimulation and reversible inactivation studies also show that saccade velocity depends on overall SC discharge (Lee et al. 1988; Stanford et al. 1996). It is clearly not the case, therefore, that the superior colliculus must display a "*fixed* and *stereotyped* burst of activity" (sect. 3.3, para. 2) for a saccade of a particular vector to occur.

How a particular movement is encoded, which (if any) supranuclear neurons encode it faithfully in all circumstances, and how these neurons come to operate, will have to be determined by future experimental studies in conjunction with physiological modeling of the saccade system.

Unwanted reflex-like saccades in visual extinction patients

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Abstract: We studied patients with left visual extinction following right hemisphere damage in a simple manual reaction time task using brief visual stimuli. With unilateral lateralized stimuli the patients showed a high proportion of unwanted, reflex-like saccades to either side of stimulation. In contrast, with bilateral stimuli there was an overall decrease in the proportion of unwanted saccades, and the vast majority of them were directed toward the ipsilesional side. The implications of these results for the Findlay & Walker model are discussed.

"Visual extinction" consists in the inability to detect stimuli presented to the visual half-field opposite to the side of brain injury (the contralesional hemifield) while simultaneously presenting another similar stimulus to the same side (the ipsilesional field). Single contralesional or ipsilesional stimuli are detected normally (Bisiach & Vallar 1988). A widely accepted hypothesis holds that extinction is related to an asymmetry in the allocation of spatial attention, which is biased toward the ipsilesional space. We have discussed elsewhere whether such an increased ipsilesional allocation of attention (the so-called hyperattention) concerns mainly controlled or automatic aspects of attention (Smania et al. 1998). To study the contribution of automatic attention to extinction we monitored the occurrence of unwanted, reflex-like saccades in patients with contralesional extinction during the lateralized presentation of brief visual stimuli in a manual reaction time task.

We asked four patients to fixate on a central point and press a key as fast as possible following the appearance of a patch of light presented tachistoscopically 7° to either the left or the right of the fixation point, or bilaterally. Immediately following response, the subjects were asked to say or signal the number and location of the stimuli. This allowed an estimate of extinction rate. Despite the instructions to keep fixation steady, patients made a saccade, as assessed by electro-oculographic (EOG) recording, in the direction of the stimulus on 24% of the trials, a proportion far longer than that found in normal controls or in patients with left cortical lesions (2% on average).

The pattern of results observed was quite similar for each patient: Following unilateral stimuli, the mean percentage of leftward (26%) and rightward (30%) saccades directed to the side of stimulation did not differ, whereas following bilateral stimuli the vast majority of reflex saccades were to the right (15%), that is, toward the ipsilesional side. Because the percentage of leftward and rightward saccades was approximately the same during unilateral presentations, the high preponderance of right saccades in the bilateral condition cannot be accounted for by oculomotor impairments; instead, it is likely related to an asymmetry in automatic focusing of attention.

As to latencies, average right saccades were about 110 msec faster than left saccades and did not differ in the unilateral and bilateral conditions (172 and 175 msec, respectively). At variance with what was found in normal subjects (Lévi-Schoen 1969; Walker et al. 1995) and in accordance with what was observed in other unilaterally brain damaged patients (Barbur et al. 1988; Walker & Findlay 1996; Walker et al. 1991), there was no inhibitory effect of the contralesional stimulus on ipsilesional saccade latencies to bilateral targets. It is interesting, however, that the overall number of unwanted saccades was drastically reduced in bilateral as opposed to unilateral presentations; this shows that bilateral stimuli had a stabilising effect, despite the lack of inhibitory effect with bilateral targets.

To determine whether extinction was correlated with reflex oculomotor behaviour we analysed separately reflexive saccades produced in trials in which the two stimuli were correctly reported and in trials in which the left (contralesional) stimulus was extinguished. It turned out that saccades to the right were present in both nonextinction and extinction trials, although there was a trend toward a higher percentage in the latter condition (14% vs. 24%). In contrast, there was no bilateral inhibition on the latency of right saccades in either nonextinction or extinction trials (mean latency: 174 msec and 171 msec, respectively). Thus, there was an interesting dissociation between the effect of bilateral stimuli on the proportion of ipsilesional unwanted saccades and their effect on latency of such saccades.

All in all, these results have two general implications: First, in the strong ipsilesional bias in an automatic reflex-like behaviour reinforces the view that ipsilesional hyperattention in extinction concerns automatic, as well as controlled attention (Smania et al. 1998). Second, the differential effect of brain lesions on the temporal and spatial features of the production of reflex-like saccades adds further support to Findlay & Walker's (F&W's) idea that there exist separate streams for the When and Where systems. In the F&W model, the critical steps in determining whether and where a saccade should be made are the resolution of the fixate/move conflict at level 2 and the automatic, hard-wired processes at level 3 that directly influence this conflict resolution. The absence of downstream biases from levels 5 and 4 as a result of cortical brain damage in our patients makes it unlikely that lower level processes can be overridden and, as a consequence, that reflexive saccades to abrupt visual onsets can be suppressed. This is in keeping with the higher overall proportion of reflex-like saccades observed in our patients. Just as F&W propose regarding hemineglect patients, the saccadic performance observed in our extinction patients can be accounted for by an underactivation of the system responsible for the automatic peripheral detection processes of the contralesional stimuli at level 3. The consequences of this imbalance involve both the when (*fixate*) and the where (*move*) streams. After the onset of contralesional stimuli, the *fixate* system is less activated than after ipsilesional stimuli; this explains the observed absence of automatic inhibitory effects in the bilateral as compared to the unilateral condition. By the same token, the underactivation of the contralesional salience map in the *move* system explains the lengthening of contralesional saccades during unilateral presentations, probably as a consequence of a slow buildup of the single peak in the contralesional salience map.

As to the relative proportion of left and right saccades, hemineglect patients show a general failure to initiate a saccade to a contralesional visual stimulus (Girotti et al. 1983; Walker & Findlay 1996; Walker et al. 1991), whereas in our visual extinction patients a less severe deficit is observed in that the bias toward the contralesional side of stimulation is present in the bilateral condition only, as shown in the monkey by Lynch and McLaren (1989). Our results show that the system involved in saccading to contralesional stimuli is impaired only in a situation of stimulus "rivalry," strongly suggesting a correlation with the perceptual impairment found in visual extinction, one supported by the observation that unwanted right saccades were more numerous in extinction than nonextinction trials. (Note that this correlation holds only for the proportion of ipsilesional saccades, not for their latency; no difference was found between extinction and nonextinction trials.) As mentioned above, this pattern of results argues in favour of the main feature of the F&W model, that is, the separation of the temporal and spatial programming of saccades. Finally, it suggests a tight correlation between attentional disorders and spatial rather than temporal properties of the saccadic system.

ACKNOWLEDGMENTS

We thank Nicola Smania for providing access to the patients and Sabrina Cecconi for help in testing them.

Voluntary and involuntary components in saccade and attention control

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Abstract: This commentary considers experimental material – some new, some from earlier studies – challenging the model presented by Findlay & Walker. It concentrates on the role of voluntary and involuntary visual attention versus fixation in saccade control and on the generation of antisaccades, reflexive prosaccades, and corrective saccades. The data of a large number of subjects are presented to show the systematic relationship between voluntary saccade generation, error production, and error correction in an antisaccade task.

General. Findlay & Walker (F&W) present a block diagram and a verbal description of how the elements might work together to generate saccades. Unlike an earlier neural model of saccade control by the superior colliculus (Grossberg et al. 1998), the F&W model does not allow for any quantitative computation to be compared with experimental data. This commentary considers experimental material that seems to be at variance with the model or needs further explanation.

Fixation – attention. The most robust effect in saccadic latencies is the gap effect. In the gap condition latencies are not only shorter, but in about 45% of the cases a separate, statistically significant peak of express saccades occurs in the distribution (Gezeck et al. 1997). The F&W model claims that a disengagement of fixation favours the generation of express saccades. This idea was first proposed by Mayfrank et al. in 1986, who at that time had already presented the basic concept of the Three-Loop-Model (Mayfrank et al. 1986), which would later be elaborated (Fischer et al. 1995). The finding of Mayfrank et al. was that attention permanently allocated to a peripheral location, which could also be the location of the next saccade target, reduced the number of express saccades. In fact, there was no significant difference, whether the attention target was placed at the fovea or at the target location. The conclusion was that it is not fixation of a foveal stimulus as such that suppresses the saccade system but rather attention being voluntarily directed to a visual stimulus. If the attended stimulus happens to be in the fovea, the subject fixates actively and attention has to be disengaged to allow short latency saccades. The effect of a foveal gap may be stronger than that of a peripheral gap, because foveal stimuli are more effective anyway. This early view of Mayfrank et al. has the advantage that fixation is a special instance of directed visual attention.

F&W do not seem to be aware of Mayfrank et al.'s work, nor do they refer to the later studies on the effect of the attention focus on express saccade generation (Weber & Fischer 1995). By systematically varying the relative location of the saccade and the attention target it was shown that the inhibitory effect of allocated attention was spatially selective. These results seem to be at variance with the notion of F&W when they state (sect. 4.6) that, "in our view, disengagement occurs in the channel, which is not spatially specific and so is not connected with the spatial aspect of attentional allocation." F&W in fact "entirely reject the idea that . . . whatever is disengaged is the same as what is moved," that is, they consider Posner's concept "flawed" (sect. 4.6).

F&W have pointed out the importance of visual onsets in both automatic saccade generation and attention allocation. Using short precues of various cue lead times it was indeed shown that more express saccades were obtained to the cued than to the uncued location (Cavegn 1996). However, as the cue lead time was increased above 300 msec the facilitation effect changed sign. With short cue lead times the effect of visual onsets was indeed so strong that consistently presenting a valid cue on the side opposite the target location (valid anticues for prosaccades) failed to produce any benefit on saccade latency. Instead, costs were obtained, even though the subjects could always know from the cue to which side the saccade should be made (Fischer & Weber 1998). The voluntary control of attention allocation "lost" against the automatic capture at short cue lead times.

Antisaccades–reflexive saccades–corrective saccades. Antisaccades are mentioned briefly in the target article. It is stated that the gap effect is smaller for anti- than for prosaccades, because only the warning effect by fixation offset is available for antisaccades. However, when the error rates between gap and overlap conditions are compared a very strong effect is obtained with many more errors in the gap condition. Similarly, the latencies of the error saccades show a clear gap effect. The warning effect, however, should be the same from trial to trial throughout the duration of the session regardless of whether an error has occurred. One could even argue that the warning effect caused by fixation offset should have reduced the error rate instead of increasing it. A more conclusive reading of the small gap effect in the latencies of the antisaccades could be that the benefit of short latency saccades is taken by the prosaccades, leaving long latencies only for those trials where the subject successfully suppressed the prosaccade and behaved as if the trial were an overlap trial (Fischer & Weber 1992).

The use of a valid spatial precue, which correctly indicates the location to which the next antisaccade must be made in a gap condition, had a completely counterintuitive effect: Instead of being reduced, the error rate was increased and the latencies of the antisaccades were longer (Fischer & Weber 1996). According to most models, including the F&W model, the opposite should have happened, because the required antisaccades are expected to profit from the automatic attention capture (Weber et al. 1998).

Functionally, it has been clearly stated by F&W, that a correct antisaccade needs two steps: the suppression of the reflexive saccade and the generation of the antisaccade. The production of errors and their corrections need extra consideration but should not need an extra component in a model. F&W do not say much about the error corrections. They mention that the reaction times of the antisaccades correlate to some extent with the reaction times of the errors. The upper panel of Figure 1 shows the corresponding scatterplots collected from 703 subjects. The second saccade has aspects of an antisaccade, because it has to take the eye to a position defined by instruction, not by a visual onset. It may therefore need a comparable time measured by the correction time. Accordingly, the middle panel of Figure 1 depicts the scatterplot of the correction times versus the reaction time of the antisaccades. The data points would fall along the thin line if the correction times were the same as the reaction times. Instead, the correction times are about 100 msec faster on average, the regression line having a slope of close to 1. The sum of the reaction times of the errors and the correction time gives an idea of how long the subjects need from the time of stimulus onset to reach the desired side after an error. The lower panel of Figure 1 shows this scatterplot. Again, a clear linear correlation can be seen, but this time the slope of the regression line is greater than one. Data of this kind may be useful for testing the predictive power and the generality of models of saccade generation.

Another issue in saccade generation is the question of corrective saccades in a prosaccade task. Obviously, we do not want an extra model or extra mechanisms to account for the rules in correcting over- or undershoots or anticipatory saccades. Smaller errors are corrected after longer intersaccadic intervals. Errors larger than 4–5° are corrected after about 100 msec, the express time. This classical feature may be accounted for by the F&W model as discussed earlier in relation to the dead zone for express saccades measuring 2° in size or less (Weber et al. 1992).

If, on the other hand, an anticipatory saccade happens to go in the direction opposite to the target, corrective saccades may occur after very short intervals. The distribution of the times of these saccades measured from target onset form 2 peaks, one at 100 msec and the other around 150 msec (Fischer et al. 1993). Therefore, one has to assume that two saccades were programmed in parallel: one involuntary and one voluntary saccade. Similar sequences of

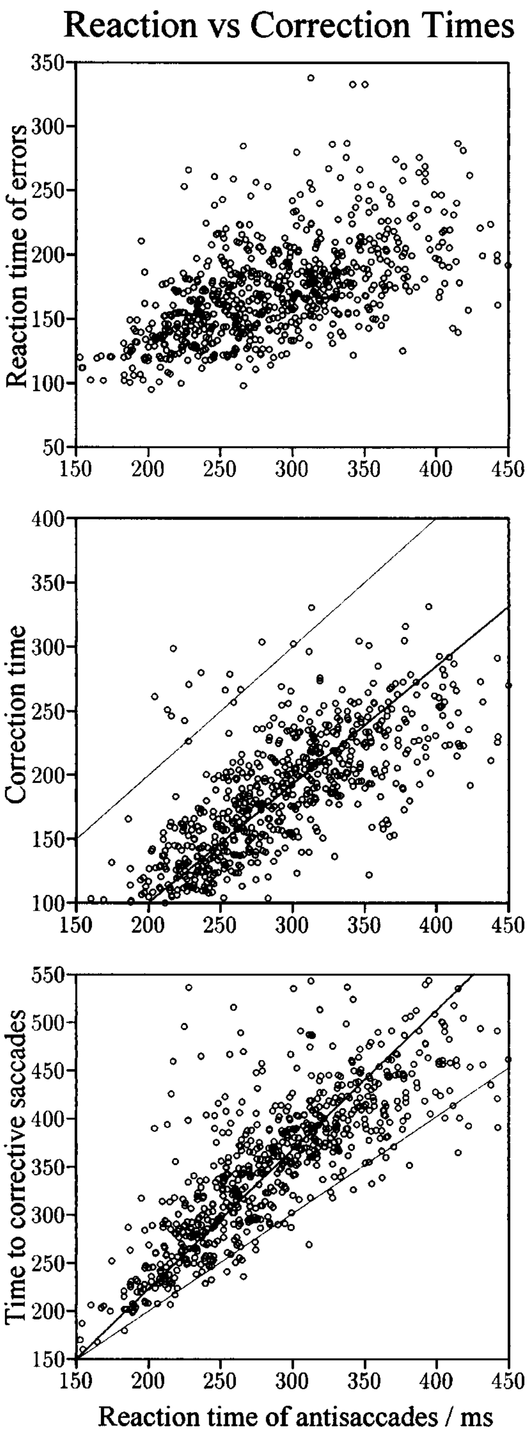

Figure 1 (Fischer). Scatterplots of the data obtained from 703 subjects of different ages, including those of dyslexic children. Each dot represents the mean value calculated for a given subject. The panels depict the reaction times of the correct antisaccades (horizontally) versus (upper) the reaction times of the errors (= prosaccades), (middle) the correction times (= intersaccadic intervals), and (lower) the sum of the two (= time of the corrective saccade measured from stimulus onset minus the duration of the prosaccade). The thick lines correspond to the linear regression lines. The thin line in the middle panel represents identity, in the lower panel it has a slope of one.

an involuntary and a voluntary saccade occur in an antisaccade task as described above. Here the corrections may also follow after extremely short intersaccadic intervals. But often the corrective saccades take much longer. The time depends on whether or not the subjects recognize the error and the corrective movement. For unrecognized errors (about 50% of the errors) the mean correction time is 95 msec, for recognized errors it is 145 msec. However, if the subjects are asked to generate a similar sequence of 2 saccades on purpose, the intersaccadic interval increases to a mean of 222 msec. Even though the subjects know in advance that they are not supposed to spend any time at the stimulus, they are unable to return their eyes as quickly, as in the case of an involuntary glance (Mokler & Fischer 1997). The important point in this observation is that the retinal events and the saccades are the same in both situations, but the intersaccadic interval is almost two times as long. An explanation of this finding may consider the remapping of the visual space taking place in different ways before consciously planned voluntary, as compared to involuntary, saccades.

In any case, a concept of saccade generation as complex as the one presented by F&W certainly comes closer to the neurobiological reality than other models presented previously. Yet it leaves a number of further important questions open. Among them are (1) the question of the development of saccade control during childhood and adolescence until the age of 20 (Fischer et al. 1997); (2) the question of express saccade makers, who behave very much like monkeys with their collicular fixation zone deactivated (Biscaldi et al. 1996; Cavegn & Biscaldi 1996); and (3) the question of the effects of daily practice being particularly strong in dyslexic children with developmental deficits in the voluntary component of saccade control (Biscaldi et al. 1998).

Can parallel processing and competitive inhibition explain the generation of saccades?

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Abstract: The framework of Findlay & Walker's target article provides a first attempt to model the saccadic system at all levels. Their scheme is based on two main principles. These are "parallel processing of saccade timing and metrics" and "competitive inhibition through winner-take-all strategies." In our opinion, however, both concepts are in their strictest sense at odds with the current knowledge of the saccadic system, and need to be refined to make the scheme more relevant.

The saccadic system serves to bring the eyes to objects of interest. This relatively simple control system has inspired many research groups to do experiments and to model their results. The scope of these studies is enormous, including highly complex scanning strategies, but also basic motor control. The framework that Findlay & Walker (F&W) sketch in their target article is a first attempt to merge all levels of knowledge about the saccadic system into a single scheme.

Such a framework gives researchers a way to communicate about their data, and provides a way of looking at the field as a whole. Therefore, F&W's initiative may be the first of many steps that may finally lead to an integrative view of the saccadic system. On the other hand, experts who look at this scheme will probably find components that do not match their data or ideas. We see no point in going into details of the scheme. However, we feel that the two key elements of the framework ("parallel processing of saccade timing and metrics" and "competitive inhibition through winner-take-all strategies") need refinement.

Parallel processing. The model consists of a WHEN and a WHERE system that are strictly separated at higher levels (3–5), but interact at lower levels (1–2). However, apart from the brainstem circuitry with burst (WHERE) and pause (WHEN) neurons there is no physiological evidence of a separation between WHEN and WHERE systems in the saccadic system.

At the midbrain level the rostral superior colliculus may function as a WHEN system, but this is still a matter of debate (Gandhi & Keller 1998; Munoz et al. 1996). Activity in higher centers, such as the frontal eye fields and various regions in parietal cortex, however, is topographically organized and strictly time locked to the saccade, and invariably leads to a saccade (e.g., Segraves 1992). This suggests that this activity encodes both the metrics and timing of the saccade.

From a functional point of view the strict separation between WHEN and WHERE would also pose problems for the saccadic system. For example, once a "search decision" is made, how does this decision lead to the generation of saccades? The only option the model offers is that activity in the "search decision" box reaches the WHEN system in level 2 and 1 through the inhibitory horizontal interactions. But then again, the search decision provides both the spatial and temporal codes for triggering the saccade, and the higher level WHEN components have no function.

Conversely, how do high-level WHEN centers receive information that there is a saccade ready to be executed in the WHERE system? The WHEN system would need information not only about the current state of visual processing (sect. 2.2.8), but about the current state of saccade programming, as well. This could only be effectuated by additional interactions between the WHERE and WHEN system at higher levels. In our opinion the processes that concern information about *what* is currently fixated (related to "cognitive processing"; sect. 2.2.8) and about the saccadic goal (e.g., "search selection"; sect. 2.2.7) should be connected.

Competitive inhibition. All researchers in the field probably agree that the metrics of a saccade are largely determined by population activity in topographic structures, such as the superior colliculus or the frontal eye fields. However, strict winner-take-all strategies, such as proposed by F&W, cannot account for some of the data.

For example, in a two-step paradigm, such as that presented in section 4.2.1, the scheme cannot produce two successive steps to the two targets. The first target apparently wins the competition. A winner-takes-all strategy makes sure that a saccade is made to this particular target. How can a saccade to the second target be generated afterward? There is no visual information left to specify its location, and its neural representation has been erased by the generation of the saccade to the first target. The model would need an (unlikely) additional map that has no competitive inhibition and that contains a code for "targets perceived but not yet responded to."

In conclusion, we feel that the framework presented in F&W's paper needs refinement to provide a model for the whole saccadic system. Its two key elements, "parallel processing of metrics and timing" and "competitive inhibition in neural maps" cannot fully account for the way the saccadic system functions. It should be considered that there is more interaction between the coding of spatial and temporal aspects of saccade preparation. However, the more interaction, the less clear the distinction that can be made between WHERE and WHEN systems. Furthermore, it seems likely that the rules for competitive inhibition are more complex than simple "winner-takes-all" mechanisms.

ACKNOWLEDGMENTS

M. A. Frens is funded by the Erasmus University, Rotterdam, I. T. C. Hooge, Human Frontier Science Program grant RG 34/96B, and H. H. C. M. Goossens, by Nederlandse Organisatie voor Wetenschappelijk Onderzoek grant 805-33.313.

The role of executive control in saccade generation

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Abstract: The Findlay & Walker model of saccade generation does not appear to account fully for saccadic performance deficits observed in schizophrenia patients. It would be enhanced by inclusion of a frontally mediated, central executive function system. A review of schizophrenia patients' antisaccade task deficits provides an example of the role of higher cortical functioning in saccade generation.

The Findlay & Walker (F&W) model of saccade generation is an intriguing one. However, it might be enhanced by giving the frontal lobes, especially the concept of their executive control function, a more prominent role. According to the F&W model, there are two separate pathways, namely, the spatial ("Where") and temporal ("When") processing pathways. I would posit that there is a supraordinate level of executive control that orchestrates the "When" and "Where" systems. The study of saccadic impairments displayed by a disproportionate number of schizophrenia patients can help refine F&W's model of saccade generation. Schizophrenia patients, who are hypothesized to have frontal lobe dysfunction (cf. Weinberger et al. 1994), frequently display executive functioning deficits.

The saccadic task deficits displayed by many schizophrenics are thought to be related to the underlying pathophysiology of their disorder. Typically, schizophrenics show normal performance on simple saccadic refixation ("prosaccade") tasks (Abel et al. 1992). Despite schizophrenics' largely normal performance on prosaccade tasks, they display considerable difficulty on antisaccade tasks, where it is necessary to inhibit the prepotent response and generate a saccade in the opposite direction. In a comparative study of saccadic performance in schizophrenia patients, neurological patients, and controls (Gooding et al. 1997), schizophrenic patients and frontal lesion patients displayed a clear dissociation in performance on the prosaccade and antisaccade tasks. Both the schizophrenics and the frontal lesion patients had difficulty suppressing their reflexive saccades, whereas the temporal lobe patients suppressed reflexive saccades as well as the normal controls. It is perhaps noteworthy that patients' erroneous reflexive saccades were typically not hypometric, rendering it unlikely that the source of the dysfunction was in the spatial processing pathway.

Temporal processing is clearly important in terms of antisaccade task performance. As F&W assert, if the automatic level 3 operations are completed before the cancellation signal is produced, then a reflexive saccade results. This is consistent with recent work (Gooding 1999), which indicates that correct antisaccade task performance requires slightly longer response latencies (typically on the order of 73–100 msec) than incorrect (reflexive) saccades. The importance of temporal processing during saccade generation is also evident in the observation that subjects typically generate fewer antisaccade errors during trials in which there is a temporal overlap between the appearance of the fixated stimulus and that of the target stimulus. The continued appearance of a fixated stimulus reduces the likelihood of a reflexive saccade to the target by increasing the firing rate of the omnipause cells.

Despite the importance of temporal processing, it appears that the frontal lobes, particularly the dorsolateral prefontal cortex (DLPFC), have an overriding role in correct antisaccade task performance. This assertion is made based on two observations: First, in general, schizophrenics do not differ significantly from controls in terms of their response latencies; and secondly, although their antisaccade latencies may vary according to task conditions, their response impairment does not. Clementz et al. (1994) demonstrated that the schizophrenia patients did not differ significantly from controls in terms of reaction times on the antisaccade task.

More recently, McDowell and Clementz (1997) demonstrated that schizophrenics' antisaccade reaction times varied according to fixation manipulations, with shorter response latencies in the gap condition and prolonged latencies during the overlap conditions. However, it should be noted that schizophrenics' antisaccade performance did not normalize under any of the varying conditions. Therefore, the effect of temporal parameters on antisaccade performance is not likely to be as crucial as the integrity of the DLPFC.

The F&W model is consistent with some working memory models (c.f. Kimberg & Farah 1993), in that it incorporates a hypothesized response competition process, as well as the role of salience in response activation. However, working memory can map onto various regions within the frontal cortex (Kimberg et al. 1998). Working memory models that do not include an executive control function are less able to account for the role of hierarchical processing that occurs during antisaccade task performance.

At present, the F&W model takes into account the superior colliculus (at level 2) and the frontal eye fields (FEF) at level 5; the DLPFC is not discussed. The DLPFC plays an important role in the inhibition of reflexive saccades and the production of voluntary saccades (Fukushima et al. 1994; Kennard et al. 1994). In their comparative study of patients with neurological lesions located in various frontal (FEF, supplementary motor area, DLPFC) regions with parietal lesion patients and controls, Pierrot-Deseilligny et al. (1991) observed that only the DLPFC lesions produced significantly more errors on the antisaccade task than controls. If one assumes that the DLPFC is supraordinate to the FEF, then another level of control is needed.

A hypothesized supervisory attentional system (Norman & Shallice 1986; Stuss et al. 1998) might well serve as a sixth level in F&W's model of saccade generation. In this way, there is an overarching supervisory system that exerts high-level control in cases where more automatic processing is not only inadequate but where the automatic prepotent response must be actively inhibited. According to this alternative viewpoint, the subject with DLPFC dysfunction is unlikely to be able to make use of peripheral visual cues provided by the overlap condition because the overriding, supervisory inhibitory processes are impaired. This account would be more consistent with schizophrenia patients' observed antisaccade task deficits.

In summary, the antisaccade task illustrates the role of higher cortical functioning in the generation of voluntary saccades. The F&W model appears the least robust in its ability to account for schizophrenia patients' antisaccade task deficits. Similarity between the saccadic impairments observed in schizophrenic patients and frontal lesion patients (Fukushima et al. 1994; Gooding et al. 1997; Guitton et al. 1985), along with reports (cf. McDowell & Clementz 1997) that schizophrenics' antisaccade task deficits persisted despite varying task parameters, buttress support for the role of an executive control, presumably in the DLPFC, in saccade generation.

Learning from cerebellar lesions about the temporal and spatial aspects of saccadic control

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Abstract: In the model proposed by Findlay & Walker, the programming of saccadic eye movements is achieved by two parallel processes, one dedicated to the coding of saccade metrics (Where) and the other controlling saccade initiation (When). One outcome of the "winner-take-all" characteristics of the salience map, the main node of the model, is an independence between the metrics and the latency of saccades. We report on some observations, made in the head-unrestrained cat under pathological conditions, of a correlation between accuracy and latency of saccadic gaze shifts. To account for such a correlation, the link between metrics specification (Where) and saccade triggering (When) should be amended in the model.

The main point of the model proposed by Findlay & Walker (F&W) is that the spatial and temporal programming of saccadic eye movements is related to two parallel neural processes (WHERE vs. WHEN), interact at two different levels (sect. 2.2). At level 1, a reciprocal inhibition between "WHERE" and "WHEN" ensures the "optimum speed and efficiency" of a saccade. At level 2, a second cross-talk corresponds to the interaction between a movement drive ("Move"), topographically represented in a salience map, and a fixation (no-movement) drive ("Fixate"). The functional role of the salience map (i.e., a "winner-take-all" selection of a single peak of activity that will trigger the saccade when exceeding the "Fixate" threshold) is compatible with an absence of relation, in general, between saccade latency and metrics.

In this commentary, we report some observations that suggest that, under pathological conditions, the decision to trigger to saccade may not be independent from the specification of its metrics. We then discuss whether and how this interaction can be accounted for by F&W's model.

These observations were made in the awake head-unrestrained cat, during unilateral reversible inactivation of the caudal part of the cerebellar fastigial nucleus (Goffart & Pélisson 1997; see also Pélisson et al. 1998). The caudal part of the fastigial nucleus (cFN) is the region by which the medio-dorsal cerebellum controls saccadic eye movements through efferent projections toward the pontine reticular formation (Carpenter & Batton 1982; Noda et al. 1990), the deep superior colliculus (May et al. 1990; Sugimoto et al. 1982), and the thalamic nuclei (Katoh & Deura 1993; Kyuhou & Kawaguchi 1987; Steriade 1995). After local injection of muscimol (a GABA agonist inducing a temporary inactivation) in the cFN, saccadic gaze shifts directed toward the inactivated side (ipsilesional) are hypermetric, whereas gaze shifts directed away from the inactivated side (contralesional) are hypometric. These changes in metrics are associated with changes in latency, which also depend on the direction of the movement with respect to the injected side. The latency of hypermetric ipsilesional gaze shifts are shorter than the preinjection responses, whereas hypometric contralesional movements have a longer latency (Goffart & Pélisson 1997). Note that a recent lesion study of the mediodorsal cerebellum in the head-fixed monkey (Takagi et al. 1998) revealed a similar association of hypometria and increased latency for one movement direction. It is interesting that we further observed in our study that, for the contralesional gaze shifts, the temporal and spatial deficits are correlated. For a given eccentricity of the target relative to gaze, the hypometria of contralesional movements depends on their latency: Responses with a long latency are more hypometric than shorter latency responses, as revealed by a significant negative correlation between gaze shift gain and latency. This result is counterintuitive because a longer latency should allow the animal to gain more information about the location of the target.

These observations directly raise the question of the independence of the processes specifying the metrics of the gaze shift (WHERE) from those contributing to its triggering (WHEN). One could propose that the inactivation of cFN simultaneously perturbs neural activity in several target structures, some "belonging to" the WHERE pathway and some to the WHEN pathway. This hypothesis is compatible with the known anatomical connections of the cFN but does not predict the observed correlation between the gain and the latency of contralesional gaze shifts. Thus, we favor another hypothesis that, though not exclusive, suggests that the cFN exerts some influence on a single site when the WHEN and the WHERE pathways interact. In F&W's model, this postulated site of action could be the salience map because it represents the node that controls both the initiation and the metrics of saccades. However, in the actual structure of the model, it seems that a perturbation of the salience map can affect only one movement variable: modifying the growing speed of the peak of activity would influence saccade latency, whereas modifying the position of the peak of activity would influence saccade metrics. In the same perspective, we would like to argue about the way F&W explain the increased latency and hypometria of contralesional saccades observed in hemineglect patients (sect. 4.7, para. 5). Whereas the increased latency can easily be accounted for by the underactivation of the salience map proposed by the authors, it is difficult to conceive how such an underactivation can, by itself (without change of the location of the peak of activity), lead to hypometric saccades.

Altogether, these observations underline the limits of the model, in its actual form, to predict the consequence of experimental or spontaneous lesions on the cooperative control of the metrics and initiation of saccadic movements. Specifically, we suggest that the interaction proposed in the model, occurring at level 2 between the WHERE and the WHEN pathways, should be amended to account for these empirical data. Finally, we would like to stress that neurological symptoms of different origins (parietal lesion in hemineglect patients, unilateral inactivation or lesion of the cerebellum) can reveal some fundamental processes that should be incorporated in general models of saccade generation.

Higher level influences on saccade generation in normals and patients with visual hemineglect

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Abstract: In this commentary we describe findings in normal human subjects and in patients with visual hemineglect that support the importance of higher-level influences on saccade generation during visual exploration. As the duration of fixations increases with increases in the cognitive demand of the task, the timing of exploratory saccades is controlled more by centers of cognitive and perceptual processing at levels 4 and 5 than by reflex-like automatic processes at level 3. In line with this, unilateral frontal eye field lesions impair systematic, intentional saccadic exploration of visual scenes, causing prolonged fixations and contralesional hemineglect, but leave visually triggered reflexive saccades largely intact.

If saccades are *externally triggered* by the appearance of a peripheral visual target or by extinction of the central fixation point, they are initiated by reflex-like processes on level 3 that Findlay & Walker (F&W) call automatic. In contrast, during complex perceptual activity, such as text reading or visual exploration, the timing of saccade generation (When pathway, see sect. 2.2.8) is *internally triggered,* being controlled by centers of cognitive and perceptual processing (levels 4 and 5) that can influence the fixate center at level 2 directly and rapidly. So it can be shown that the mean duration of fixations in such tasks increases with the cognitive demand of the task, when higher levels of processing are involved. Accordingly, in section 4.3, F&W mention earlier reports that have linked the duration of a fixation to the amount of information processing of the fixated material at the fovea (Gould 1973; Rayner 1995). Recently, one of us collaborated in an oculographic study (Velichkovsky et al. 1997) where normal subjects exhibited fixation durations of more than 500 msec during an implicit memory test (semantic encodings) of the pictures of nonfamiliar faces, whereas fixation durations were about 120 to 250 msec during an explicit recognition test (perceptual encodings) of the same materials. These authors recorded similar long fixations (>500 msec) in association with decision making or communicative functions.

In natural situations, too (e.g., during car driving in normal human subjects), important features of saccadic eye movements depend on higher-level influences, not only on the actual traffic-related demands, but also on personal attitudes toward driving behavior. For example, if the driver is willing to reduce his speed as required by a traffic sign, multiple saccadic eye movements occur between the traffic sign and the speedometer. The difference between the speed limit and current speed influences not only the frequency, but also the velocity of these saccades (Sprenger 1994). Even in visual search tasks with abstract displays higher-level processes are active. Recently, Pomplun (1998) has shown that modelling eye movements in comparative visual search cannot be based solely on the saliency map, but must take into account global search strategies, in combination with local properties of the search items. These are all situations in which the timing of exploratory saccades is controlled more by cognitive processing at levels 4 and 5, than by automatic mechanisms operating at level 3.

Our oculographic data, recorded during visual exploration in patients with visual hemineglect (Heide & Kömpf 1998; Moser & Kömpf 1990), have yielded further evidence of the importance of higher-level saccadic control. If left visual hemineglect was caused by unilateral lesions of the posterior parietal lobe, contralesional visually triggered saccades were indeed delayed and hypometric, in correlation with the severity of contralesional neglect. This accords with F&W's hypothesis that in the ipsilesional hemisphere of neglect patients the automatic detection processes (operating at level 3) are permanently underactivated. In contrast, if left hemineglect was caused by unilateral lesions of the right frontal eye field (FEF), contralesional visually triggered saccades had normal latencies and amplitudes, even though the classical neglect tests confirmed manifest contralesional visual neglect. So this frontal type of neglect cannot be explained by an underactivation of automatic detection processes, rather it concerns internally triggered or self-paced contralesional saccades that are associated with higher-level processes. Frontal neglect was obvious during exploration of stationary visual scenes where these patients neglected the left (contralesional) half of the display and had a significantly prolonged mean duration of fixations, thus exhibiting both a spatial and a temporal deficit. These deficits were most pronounced in a task that involved level 5 processes, namely, during systematic voluntary saccadic exploration of an abstract and uniform visual display in terms of four rows of colored squares that had to be fixated successively. In contrast, parietal neglect patients performed this task almost normally. Mainly level 4 processes are involved during saccadic exploration of a natural scene with semantic contents and attractors of visual attention in both hemifields. With such a display (the famous kitchen scene with the cookie theft) prolonged fixation durations and a partial neglect of the contralesional half were found to some extent in both groups of patients.

Moreover, both types of neglect were manifest in a double-step task (Heide et al. 1995), where two saccades had to be performed in darkness toward the remembered locations of two peripheral targets that had been flashed in rapid succession. If the two targets were located in opposite visual hemifields with respect to the vertical meridian, patients with right FEF lesions, as well as patients with right parietal lesions, neglected the target in the left hemifield, although visually triggered saccades to left-sided peripheral targets were within normal limits (Heide et al. 1995). In cases with focal lesions of the left FEF, other investigators (Rivaud et al. 1994) reported an analogous impairment of internally triggered intentional saccades into the contralesional hemifield, whereas reflexive visually triggered saccades were unimpaired.

We conclude that visual hemineglect in patients with FEF lesions involves predominantly exploratory-motor functions, being reflected in a deficient control of internally triggered (intentional) saccades by higher cognitive and perceptual processes of levels 4 and 5. In contrast, visual hemineglect in patients with posterior parietal lesions impairs mainly perceptual-sensory functions and visually-triggered (reflexive) saccades, because of deficient level 3 processes for the automatic detection of peripheral targets in the contralesional hemifield. Consequently, the results of clinical lesion studies lead to the assumption that the posterior parietal cortex and its efferent projections to the superior colliculus can be regarded as critical for *reflexive (automatic) exploration of space,* whereas the FEF controls *intentional exploration of space* (Pierrot-Deseilligny et al. 1995; Heide & Kömpf 1998). This is, of course, an oversimplification and does not exclude an additional role of level 4 processes in parietal neglect.

Contextual factors in the generation of express and regular saccades

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Abstract: Experiments using a modified gap paradigm, where regular trials are intermingled with catch trials (trials without saccade target), demonstrate that the relative frequency of express versus regular saccades distinctly depends on catch trial frequency. More specifically, it has been shown that the probability of an express saccade depends stochastically on the type of the preceding trial, that is, on the sequence of stimuli. We discuss whether such contextual effects can be accommodated within the framework of Findlay & Walker's model.

In a previous study on express saccades (Jüttner & Wolf 1992) we studied the effect of catch trials (i.e., trials where no target appeared after the gap and in which the subject must maintain fixation) on the saccadic latency distribution of human observers in the gap paradigm. For low catch trial rates we observed a distinct short-latency "express" population and a much smaller longer latency "regular" population – in accordance with earlier observations made by Fischer and coworkers (e.g., Fischer & Ramsperger 1984; Fischer & Weber 1993). However, with increasing frequency of catch trial events (from 0% up to 90%) the shape of the distribution changed markedly: The peak of the express saccades shrank, whereas that of the regular saccades increased accordingly. This effect occurred within the same subject in subsequent blocks, and despite the fact that because of the experimental schedule the observer should have had a training benefit in generating express saccades in blocks with higher catch trial rates.

A subsequent analysis of the latency data (Jüttner & Wolf 1993; 1994) revealed that this catch trial effect is not a purely global statistical phenomenon. Rather, it is related to the particular sequence of regular and catch trials within the experiment. More specifically, regular trials following catch trials are associated with a distinctly reduced probability of an express saccade occurring as compared to those following noncatch trials, where this probability is increased. This effect of context or "trial history" concerning the occurrence or nonoccurrence of express saccades could be quite well fitted by a first-order Markov model (Jüttner & Wolf 1994). Basically, the model consisted of two preparatory states (for express or regular saccades) between which the system changed, depending on the state and the stimulus of the preceding trial.

This demonstration of contextual factors in the generation of express saccades has recently been confirmed by a study with behaving monkeys (Paré & Munoz 1996). In a paradigm where gap and no-gap trials were randomly mixed, the highest percentage of express saccades was observed after an express saccade in a preceding gap trial, whereas the lowest percentage was obtained after a regular saccade in a preceding gap trial. Paré & Munoz interpreted their results in terms of a direct influence of the level of motor intention in a given trial exerted on the saccadic reaction time in the subsequent trial. Because the occurrence of express saccades proved to be selective for trained target locations they concluded that advanced motor preparation of saccadic programs might be primarily responsible for the occurrence of express saccades. This interpretation has received further neurophysiological support from cell recordings in the superior colliculus, where preparatory activity has been observed that is correlated both with saccadic reaction time and express saccade occurrence (Dorris et al. 1997).

Together these findings suggest that, in terms of Findlay & Walker's (F&W's) model, the generation of express saccades depends critically on activity in the WHERE system. However, the WHERE system may not be characterized exclusively in spatial terms as the model in its current version does suggest. As indicated by the contextual effects outlined above there also seems to be a temporal component (or "memory") in the organization of the spatial map specifically taking into account the sequence of preceding motor activity. Although its consideration somewhat undermines the basic architecture of F&W's approach concerning their strict WHEN-WHERE distinction of spatial and temporal aspects in the generation of saccades, such an extension of the model would seem worthwhile.

Oculomotor capture by abrupt onsets reveals concurrent programming of voluntary and involuntary saccades

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Abstract: In several recent experiments we have found that the eyes are often captured by the appearance of a sudden onset in a display, even though subjects intend to move their eyes elsewhere. Very brief fixations are made on the abrupt onset before the eyes complete their intended movement to the previously defined target. These results indicate concurrent programming of a voluntary saccade to the defined saccade target and an involuntary saccade to the sudden onset. This is inconsistent with the idea that a single salience map determines the location of a saccade in a winner-take-all fashion. Other results indicate that subjects attend to more than one location in a display during saccade preparation, contrary to the claim that covert attentional scanning plays no role in saccade generation.

A key assumption of the Findlay & Walker (F&W) model of saccade generation is that there is a single salience map that determines the location of a saccadic movement in a winner-take-all fashion (sect. 2.2.3, para. 2). A second, critical, assumption is that there is no role for internal attentional scanning in the model (sect. 4.6, para. 3). In several recent papers (Kramer et al. in press; Theeuwes et al. 1998; in press) we report findings that appear to contradict both of these assumptions. In this commentary we describe our evidence, say why it presents problems for the F&W model, and suggest ways in which it might be modified to account for our results.

Capture of the eyes by new objects. In our first study (Theeuwes et al. 1998) observers viewed displays containing 6 gray circles (3.7° in diameter) spaced equally around an imaginary circle whose radius was 12.6°. Centered within each circle was a small (0.4° × 0.2°) figure-eight premask. After 1 sec, all circles except one changed to red and the premasks inside the circles were converted to small letters. Subjects were told to move their eyes to the remaining gray circle (a color singleton) and determine whether the letter inside it was a "c" or a reverse "c." They pressed one of two buttons to indicate their responses; latency and accuracy were recorded. Because the letter was so small, accurate identification could be achieved only when the letter was fixated. On half the trials, an additional red circle (an onset or new object) was added to the display at the same time that the color singleton and the letters were revealed. This onset stimulus also contained a small letter, but never the target; thus, it was irrelevant to the subject's task. Despite this, on nearly half the trials subjects made a saccade toward the new object before moving their eyes to the color singleton; in other words, the eyes were captured by the appearance of a sudden onset in the display even though subjects intended to move their eyes elsewhere. This occurred even when the new object was presented 150° of arc away from the color singleton. Fixations on the new object were very brief (median = 100 msec), even though a complete change in the direction of the eye movement was required to redirect the eyes toward the color singleton. Subjects reported being completely unaware of making saccades to the new object, even though they did it on half of the trials. Other experiments showed that saccades to the new object were eliminated if the location of the color singleton was precued for 400–600 msec prior to the color change that defined the target location (Theeuwes et al. 1998), or if the onset stimulus appeared 150 msec after the color change (Theeuwes et al., in press).

These results suggest parallel programming of two saccades: one voluntary, goal-directed eye movement toward the color-singleton target and one stimulus-driven eye movement reflexively and unconsciously elicited by the appearance of the task-irrelevant new object. Depending on which eye movement program was ready first, the eyes started moving in the direction of the onset or in the direction of the color singleton. These findings are inconsistent with the claim that the location of a saccadic movement is determined in a winner-take-all fashion in a single salience map. Two distinct saccades were produced in rapid succession, rather than a single saccade to some "average" location. To account for our results, we propose that there may be multiple salience maps, one for goal-directed (voluntary) saccades and another for reflexive (involuntary) saccades. Another possibility, however, is that multiple peaks in a single salience map result in the concurrent preparation of more than one saccade.

Attentional scanning can occur during saccade preparation. In another experiment Theeuwes et al. (in press) used the response compatibility paradigm (Eriksen & Hoffman 1972) to determine whether spatial attention shifted to the new object even when the eyes were not drawn to it. Using the same procedure described above, on some trials a large letter C or a large reversed C was presented inside the abrupt onset circle, which always appeared 150° of arc from the color singleton; half of the distractor letters in the other locations were also large. The large letters could be identified with peripheral vision (i.e., they did not have to be foveated) if a covert shift of attention was made to them. The letter inside the onset was either identical to the small letter inside the target color singleton (and thus compatible with the response) or different (and thus incompatible with the response). As before, subjects were instructed to saccade to the color singleton and to report the identity of the target letter contained there; the onset was irrelevant to their task. Nonetheless, on about 36% of the trials the eyes went in the direction of the onset, paused for a brief time, then reversed direction and went to the color singleton. Most important, an identical response compatibility effect was found on manual reaction time to the target letter inside the color singleton, regardless of whether the eyes went to the irrelevant onset. Thus, covert attention must have gone to the location of the onset even when the eyes went directly to the color singleton. F&W say that their model "would be invalidated if it could be demonstrated that a fast covert attentional scan over a number of locations was possible in the preparation period before a saccadic movement" (sect. 4.6). Contrary to their model, our results indicate that subjects do indeed engage in a fast covert attention scan over at least two locations in the preparation period before a saccadic movement.

Is there more to visual attention than meets the eye?

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Abstract: Models of saccade generation and visual selective attention must explain how and why particular targets are selected. Findlay & Walker do an excellent job of explaining the how of visual selection, but not the why. For a salience map to be more than a description of the relative importance of potential targets, there must be some account of the learning and inheritance that fashion its peaks and troughs. Point of gaze is not necessarily region of attention, and it may be premature to downgrade the role of covert attention in models of visual selection.

Learning and attention. Findlay & Walker (F&W) have presented an impression mechanism for saccade generation, but I am unsure of its status as a model of visual attention. At the outset of their target article, they note their interest in performance rather than learning, and their lack of concern for plasticity and the important adaptational processes operative in connection with saccades (sect. 1). Fair enough, but I am not sure that an acceptable theory of how visual attention may be directed can afford this luxury. The processes and effects of both learning and innate predispositions impinge so much on how and where the gaze is directed that they simply cannot be left in abeyance in any viable explanatory system. Early theorists struggled with the external and internal determinants of attention, and attempted to cope with the problems of multiple potential targets by reference to "the conditional probability of past events" (Broadbent 1958), "thresholds of dictionary units" (Treisman 1960), "pertinence" (Norman 1968), "enduring dispositions" and "momentary intentions" (Kahneman 1973), and they struggled with good reason. Without some thorough account of the forces that shape and mould the attentional system, there is a temptation to think of the gaze as self-directed and it is this notion of self-directedness that a deterministic psychology must eschew – see Maze (1983) for a detailed discussion of this issue.

The salience map. F&W sidestep the problems of self-direction and conflicting potential targets for attention by invoking the salience map, which is a three-dimensional contoured surface representing vertical and horizontal visual directions with salience on the z-coordinate. Salience is said to be influenced by a number of factors, including spatial selection, inhibition of return, search selection, and intrinsic salience, the latter referring to high-contrast areas of contours in the visual field, which are intrinsically salient (sect. 2.2.7). The point of highest salience then becomes the target for a saccade. However, if the salience map is not to become a mere post-hoc description of saccadic activity, there must be some clear and precise mechanistic account of how the peaks in the map develop and attract eye fixation. Accordingly, it is not enough to state that high-contrast contours and areas in the visual field have intrinsic salience. The influences that shape the salience map must be much more subtle. For example, organisms that direct saccades to high-contrast contours and not to low-contrast predators may not survive. F&W seem to suggest that competitive learning and a winner-take-all process assists in determining the salience peak to which the saccade is directed, but this suggestion also has problems. Competitive learning will assist in the discovery of useful and differentiating features by which objects in the visual field may be discriminated, categorised, and classified. However, unless objects also display their intrinsic and relative importance, pertinence, threat and survival values, and so forth directly in their visual features, it is not obvious how visual competitive learning alone could produce a realistically useful salience map. It was for these very reasons that earlier theorists of attention wrestled with the explanation of why some inputs receive attention and others do not, and if the salience map is to be a predictive and explanatory basis for saccadic generation, F&W must also provide some, albeit rudimentary, mechanistic influences of learning, experience, and innate predispositions in their model.

Covert attention and point of gaze. F&W note that a theory of saccadic programming is necessarily a theory of attentional deployment, but take the further step of denying any significant role of covert attention. Insofar as their remarks refer to covert scanning of the visual field, I agree with them (Latimer 1999), but their seeming rejection of the importance of covert attention to regions other than fixation point overstates the strength of the relationship between point of gaze and region of attention. Evidence (even phenomenal experience) suggests that the link between fixation point and the region of attention is much more tenuous. Indeed, it is only under artificial and restricted conditions that the point of gaze can be considered as a reliable index of attention, for example, when stimuli are presented under high background illumination and low contrast (Latimer 1988) or within a small computer-generated window whose centre is made contingent on fixation point (Watanabe & Yoshida 1973). Such conditions simulate tunnel vision, and without such restriction, attention is free to diverge from point of gaze. In these terms, it may also be argued that attention is primary, whereas saccadic movement is secondary, as in the Henderson model (sect. 4.6.) where attention (not gaze direction) centres on the stimulus location with the largest weight. Only after attention has been captured by this peak in the salience map is a saccade directed to the peak.

A second reason for believing in a disjunction between attention and point of gaze is the difference between the distribution of visual acuity around the fovea and (for want of a better description) the distribution of attentional resources around point of gaze. Visual acuity is greatest in the fovea and falls off fairly uniformly in the extrafoveal regions. On the other hand, studies of attentional bias (Avrahami 1998; Latimer & Stevens 1993) suggest that stimulus elements above and to the right of point of gaze are attentionally privileged. It may be that, unlike the distribution of visual acuity around the fovea, attentional resources are distributed as a skewed Gaussian whose peak is located above and to the right of gaze direction. It cannot, of course, be denied that the mechanisms underlying saccade generation and those mediating visual attention are linked, but it would be premature to regard these as one and the same thing and thus to disregard the importance of covert attention.

Concurrent processing of saccades

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Abstract: We summarize several experiments indicating that the saccadic system is capable of simultaneously programming two movements toward different goals. This concurrent processing of saccades can lead to the execution of two saccades separated by an extremely short intersaccadic interval. This supports the idea of target competition proposed in Findlay & Walker's article, but suggests a greater degree of parallel processing. We provide evidence that concurrent processing of two saccades is not limited to higher-level planning subsystems; rather, it also involves both regions close enough to the motor output that it can systematically affect saccade trajectory.

We find much to agree with in Findlay & Walker's (F&W's) proposed model of the saccadic system, particularly with regard to the idea of saccade target selection in a distributed, coarse-coded network with competition among active sites. However, in our work on saccades in visual search, we have made several findings that suggest that the saccadic system's ability to simultaneously program multiple movements may be more extensive than suggested by their model.

We examined saccade target selection using a pop-out visual search task in which subjects make a saccade to an odd-colored target. When the color of the target changes from trial to trial, performance is worse than when it remains the same. This is the result of a phenomenon called the "priming of pop-out," which affects saccades in humans (McPeek et al. 1999) and rhesus monkeys (McPeek & Keller 1998), as well as the deployment of focal attention in the absence of eye movements (Maljkovic & Nakayama 1994).

We have exploited this priming effect to provoke a strong competition between target and distractor stimuli in our search task. We find that when subjects make an incorrect saccade to a distractor, such error saccades may be followed by a second saccade to t he correct target after only a very short intersaccadic interval (~10–100 msec; see Fig. 1 for an example). Initially found in human subjects (McPeek et al. 1996), this finding has been replicated in the rhesus monkey (McPeek & Keller 1998). The brief intersaccadic intervals, often shorter than the latency of express saccades (Fischer & Weber 1993), suggest that the system has processed the two saccades in parallel. According to this view, subjects begin programming a saccade to a distractor, but soon after, become aware of the correct location of the target. As a result, the subject begins programming a second saccade to the correct target, which is processed in parallel with the initial incorrect saccade. The two saccades are effectively "pipelined" by the system, such that their preparation overlaps in time. The saccade that was programmed first is executed first, and is quickly followed by the second saccade as soon as its programming is complete.

This view is supported by results from the double-step paradigm. Becker and Jürgens (1979) observed that when two sequential, but temporally closely spaced, target steps are presented on opposite sides of fixation, an initial saccade directed toward the first target position is often followed after a very brief fixation by a second saccade to the second target position. The presumption is that programming of the initial saccade is triggered by the first target step, and programming of the second saccade is triggered by the second target step. The short intersaccadic interval results from the fact that the programming of the two saccades overlaps in time. If this is true, the second saccade should always occur one normal saccadic reaction time after the presentation of the second target step, regardless of when the initial saccade occurs. Becker and Jürgens (1979) confirmed this prediction for horizontal target steps. In our own double-step experiments with target steps in two dimensions, we have also found that the second saccade consis-

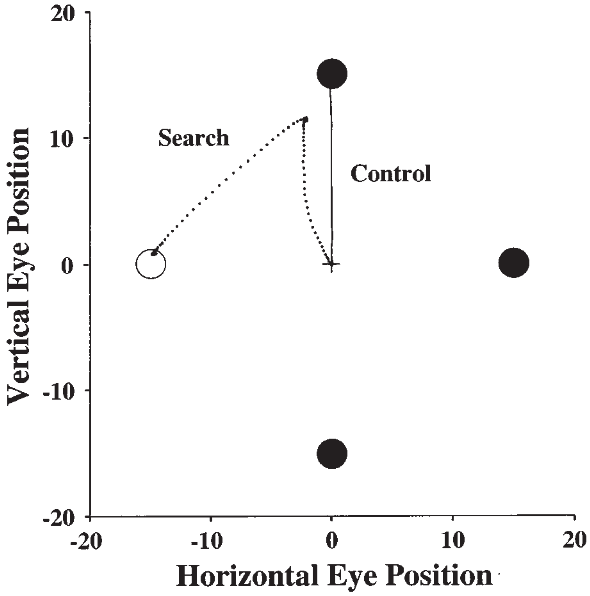

Figure 1 (McPeek et al.). Dotted trace shows an example of a two-saccade response in visual search. Initial fixation is in the center and is marked by a plus-sign. The first saccade is directed up, toward a distractor. After a 45-msec fixation, a second saccade is made to the target. Note that the first saccade falls slightly short of the distractor and is curved toward the goal of the second saccade. For comparison, the solid trace shows a typical saccade to a single target at the same position as the distractor stimulus. (Rhesus monkey, magnetic search coil sampled at 1,000 Hz.)

tently occurs approximately 200–250 msec after the presentation of the second target step, regardless of the timing of the initial saccade, and across a wide range of intersaccadic intervals (McPeek 1997). This clearly supports the idea that these two-saccade responses reflect the parallel or "pipelined" processing of two movements, each triggered by the presentation of a target step.

Concurrent processing is not limited to the higher-level planning stages of the saccadic system. In both our search experiments and in our double-step experiments, we observed that when two saccades to different goals are executed in rapid succession, the first movement of the pair may be hypometric, falling short of the stimulus toward which it is directed. When the fixation interval between the first and second saccades is very brief, this reduction in amplitude of the initial saccade is most prominent (McPeek & Keller 1998; McPeek et al. 1996). This points to an effect of the impending readiness of the second saccade on the execution of the initial saccade.

We have found further evidence for an effect of concurrent processing of a second saccade on the execution of an initial saccade. In the rhesus monkey, we have observed that for two-saccade responses in search, the initial incorrect saccade tends to show a relatively large amount of curvature, compared to saccades to single targets, or even to correct saccades in search (McPeek & Keller 1998). Furthermore, we have shown that these incorrect initial saccades are systematically curved toward the goal of the second saccade (see Fig. 1). This effect of the subsequent saccade goal on the execution of the initial saccade does more than support the idea that the two saccades are processed concurrently; it also provides additional evidence that this parallel processing is not limited to higher-level saccade planning centers. Apparently, the processing of the second saccade involves brain regions close enough to the motor output that it can result in systematic changes in the trajectory of the initial saccade.

To summarize, we argue that two saccades to different targets can be processed concurrently and executed in rapid succession. Furthermore, this parallel processing engages even the lower levels of the saccadic system, as evidenced by the systematic effects of the processing of the second saccade on the amplitude and the curvature of the initially executed saccade. Several recent studies of search indicate that subjects often program an initial saccade before visual analysis at the current site is complete (Hooge & Erkelens 1996; 1998; Zelinsky 1996). The ability of the system to program two saccades concurrently makes this seemingly suboptimal search strategy more understandable: Because concurrent processing reduces the penalty for an initial incorrect goal selection, it encourages an early saccade based on the probable target location rather than a slower, more conservative search strategy.

ACKNOWLEDGMENT

Supported by NIH grant 1F32-EY06881-01 to R.M. McPeek, grant EY08060 to E.L. Keller, and Air Force Office of Scientific Research grant F49620-92-J-0016 to K. Nakayama.

Winner-takes-all and action selection

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Abstract: Winner-takes-all (WTA) typically describes a mechanism for selecting the highest peak of activity in a sensory map that encodes independent representations of potential targets. To Findlay & Walker, WTA is an inherent property of a motor map that is incapable of representing multiple targets independently. Although the output of a WTA system should be characteristic of only one target, actions can be influenced by multiple targets.

Findlay & Walker's (F&W's) use of the term *winner-takes-all* (WTA) to describe the process of selecting saccade metrics is confusing, given its traditional usage in models of selection. The concept of WTA is typically invoked when two or more components of the sensory array compete for the guidance of behavior. Examples include models of visual selective attention that use WTA mechanisms to distinguish relevant from irrelevant stimuli in cluttered scenes (Koch & Ullman 1985; Tsotsos et al. 1995), and models of visual perception that use WTA mechanisms to select which aspect of a complex input will determine the percept (Salzman & Newsome 1994). Ironically, action selection is often considered the quintessential case in which WTA is *not* the mechanism of selection (Boussaoud et al. 1996; Lisberger & Ferrera 1997; Salzman & Newsome 1994). F&W's WTA model differs in at least three ways from previous WTA models:

1. One requirement of a WTA system is that the various potential targets have independent representations. In this way the representation of the winner can be isolated from those of the losers. However, population coding in the saccade system (Lee et al. 1988), and other action systems (e.g., Georgopoulos et al. 1986), does not allow independent representations of multiple targets. In the words of F&W: "The disadvantage of distributed coding is the lack of ability to code two simultaneous targets" (sect. 2.2.4).

2. The output of a WTA system should be characteristic of only a single target. For example, Lisberger and Ferrera (1997) rejected the possibility that a WTA mechanism selects the direction of smooth pursuit eye movements because movements were made in a direction intermediate to the directions of two potential target stimuli. F&W suggest a WTA selection of saccade metrics despite the fact that saccades, under certain conditions, are directed to locations intermediate to two stimuli. It should be noted, however, that intermediate actions or perceptions do not eliminate the possibility of WTA. In their experiments on direction-of-motion discrimination, Salzman and Newsome (1994) reported a high proportion of perceptions of one or the other direction when the two directions varied considerably (suggesting WTA), but when the directions were more similar, perceptions of intermediate di-

rection were common. Although the latter finding would seem to be inconsistent with WTA, they argued that a WTA mechanism could produce intermediate perceptions because of broad tuning of motion direction. One might argue that similar logic could be applied to saccade selection, because intermediate actions occur only when the two stimuli are in close proximity.

3. WTA is usually considered a separate process or mechanism that assesses activity in a salience map. In their model of selective attention, Koch and Ullman (1985) use a distinct WTA mechanism to select one of several peaks of activity in maps of elementary visual features. Salzman and Newsome (1994) consider WTA a decision process that evaluates activity in a columnarly organized map of perceptual attributes. F&W, on the other hand, consider WTA an inherent characteristic of the map itself, a state to which the map evolves: "We propose that conflict resolution is *only* resolved in this implicit way with no overriding supervisory decisions or more elaborate processing" (sect. 2.2.6).

In summary, WTA mechanisms are typically used to determine the highest peak among several competing loci of activity in a salience map. Given that F&W's map of saccade metrics has inherent conflict resolution capabilities, it is unclear why the concept of WTA was invoked in this context. Of course WTA mechanisms might be used to resolve competition in their level 4 salience maps that feed their level 2 map of saccade metrics. For example, models of selective attention commonly use WTA mechanisms to solve the problem of searching for a target distinguished by its identifying features. In the F&W model, the *search decision* process could be a WTA mechanism that evaluates activity in the *search selection* salience map. It is interesting that in this case search behavior may not necessarily be determined by the WTA mechanism, because vision-for-action and vision-for-identification are processed in parallel (Meegan & Tipper 1999); in the language of the model, *movement decisions* are independent of *search decisions.* Thus, if the identification pathway is slow to find a winner of search selection, intermediate actions may be selected. Consistent with this suggestion, intermediate actions (Ottes et al. 1985; Tipper et al. 1997) have been reported in search tasks.

Close interactions between "When" and "Where" in saccade target selection: Multiple saliency and distractor effects

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Abstract: A model of when and where saccades are made necessarily incorporates a model of the "When" and "Where" of target selection. We suggest that the framework proposed by Findlay & Walker does not specify sufficiently how (and by what means) selection processes contribute to the spatial and temporal determinants of saccade generation. Examples from across-trial priming in visual search and from the inhibition of temporally segmented distractors show linkage between the processes involved in computing when and where selection operates, so that there is cooperation rather than competition between so-called Where and When pathways. Aspects of spatial selection may also determine the remote distractor effect on saccades. The detailed relations between the processes involved in selection and saccade generation may be best understood in relation to detailed computational accounts of the processes.

Findlay & Walker (F&W) outline a model to explain the timing and accuracy of saccadic eye movements, with a major distinction being drawn between a "When" system (concerned with initiating the saccade in time) and a "Where" system (concerned with directing the saccade to the target location in space). As the authors note, several aspects of the framework are to be found in other accounts of visual processing, and in particular, aspects of the Where system are common to various models of visual selection (especially as such models typically assume some form of competitive interaction between elements to determine which wins the competition for selection; see Humphreys & Heinke 1998; Mozer & Sitton 1998; Wolfe 1994, for examples). The novel step is to link these aspects of spatial selection to computations concerning the timing of visual signals. To date, theories of visual information processing have paid little heed to the question of how visual events are selected over time (though see Watson & Humphreys 1997). We agree with F&W's thinking that detailed accounts of visually guided behaviour will need to explain selection over time (and synchronization of motor actions to temporal selection), as well as selection over space.

That said, however, there remain many questions concerning how these coupled "When" and "Where" systems might operate in practice. We list two examples. First, consider the operation of the Where system. Here F&W propose one mechanism (a saliency map) and three processes (spatial selection, intrinsic salience, and search selection) that, in tandem, lead to the computation of the spatial code of the target for a saccade. Spatial selection refers to a form of regulation of the saliency map. This can include apparently bottom-up effects such as "inhibition of return" and perhaps forms of top-down activation and inhibition of the map (e.g., as in endogenously controlled attention), as well. Search selection involves the computation of different feature values, the location of which may be used for a saccade. Intrinsic salience involves computations that may be learned over time, specific to the stimulus presented. Each of these processes feeds down to affect activation in the saliency map, which is used to determine the spatial position of a saccade. However, we suggest that it is far from clear whether the different processes specified in this framework are functionally independent of one another, or whether they are represented at different brain sites. For example, F&W discuss effects of learning solely in terms of the process of intrinsic saliency tied to specific stimuli. In studies of search, this might involve carry-over effects from the feature values of specific targets across trials (Maljkovic & Nakayama 1994). Nevertheless, other research shows that there are even stronger carry-over effects from feature dimensions in search than from specific feature values (e.g., Müller & Found 1996; Müller et al. 1995), so the facilitation of search from having successive trials with two colour-defined targets (say) is almost as powerful as the effect of having exactly the same colour target. Müller et al. (1995) proposed that each dimension computes its own saliency map, integrated across different feature values, which is then used in the computation of a supra-dimensional saliency map. Carry-over (learning) effects in search may be based on temporarily increased weighting of signals from the saliency map from one dimension when activation is integrated in a supra-dimensional map. Now the relations between this account and the framework put forward by F&W are not transparent. Are learning effects apparent in the search selection process as well as in the intrinsic saliency process? Is there any evidence for a process of intrinsic saliency that is independent of search selection processes?

Second, consider the operation of the When system. Here F&W discuss two processes: temporal preparation and cognitive control of saccade timing parameters. In the way the framework is defined, these processes would appear to operate independently of the Where system. On the other hand, evidence concerning our ability to select visual information over time (e.g., to optimise initiation of a saccade to a new target) suggests that this can involve inhibition applied to the locations of old objects (Watson & Humphreys 1997). The When signal for action may be contingent on operations within the Where pathway, and "temporal preparation" may itself be derived from forms of spatial selection. Similarly, the mechanisms underlying cognitive control of the temporal parameters of eye movements may not be independent of those involved in cognitive control of selection (e.g., endogenous orienting; Coull & Nobre 1998).

These points essentially concern details of the operations of these systems, and the degree to which they are functionally independent of one another. Our own experience is that it is difficult to address this level of specificity without taking the further step of attempting to model whole-system behaviour. Once processes become fully articulated within the architecture of a working model, it becomes easier to analyse their operation and interaction. We suggest that detailed modelling of this form is needed as the next stage in the work.

Once this step is taken, it is often the case that the need to hypothesize some processes becomes redundant, because an effect may arise not through an individuated process but through the more general operation of the system. Again to give an example: F&W propose that saccades to a target are disrupted by remote distractors because the distractors stimulate a "fixate centre." They argue this because the effect of the distractors becomes more potent as they are presented closer to fixation, which F&W attribute to stronger activation of the fixate centre. On the other hand, it may be that distractors presented close to fixation are particularly strong competitors for visual selection with nonfixated targets, partly because of acuity, and partly because fixations to close stimuli may normally provide the most economical scan path for saccades (Lévy-Schoen 1969). In a system to which visual selection is determined by competition between targets and distractors it may be possible to capture effects caused by proximity to fixation, not in terms of an additional factor (stimulation of the fixate centre), but as a natural consequence of the dynamics of competition. Such an account would also explain the finding that saccades become relatively less disrupted with targets falling closer to fixation (e.g., Walker et al. 1997), whereas the currently presented model seems to predict the opposite. These and other effects may emerge once a detailed computational model of performance is developed.

ACKNOWLEDGMENTS
This work was supported by grants from the European Union and the Medical Research Council (U.K.) to the first three authors and by a grant from the Humboldt Foundation and by the Leibniz Professorship at the University of Leipzig awarded to the third author.

Lateral interactions in the superior colliculus, not an extended fixation zone, can account for the remote distractor effect

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Abstract: Recordings of neuronal activity in the monkey superior colliculus (SC) suggest that the two apparently independent effects of a visual distractor on both temporal (latency) and spatial (metrics) saccade parameters may be the result of lateral interactions between subpopulations of saccade-related neurons located at different sites on the motor map of the superior colliculus. One subpopulation is activated during the planing and initiation of a saccade; the other is activated by the appearance of a distractor. The inhibitory or facilitative nature of this interaction depends on the distance between the distractor and the target and is consistent with the complex pattern of intrinsic and commissural collicular connections.

Presenting a visual cue (a "distractor") simultaneously with a target affects either the timing (increased reaction time) or the metrics ("averaged saccades") of visually guided saccades, depending on the position of the distractor relative to the actual target (Walker et al. 1997). Findlay & Walker (F&W) regarded this finding as evidence for the existence of two independent processes separately controlling the metrics ("Where") and the timing ("When") of saccades. Furthermore, because this increase in saccade reaction time (SRT) persisted even when the distractor was presented at a rather eccentric position (up to 10°), Walker et al. (1997) concluded that the collicular fixation zone is probably much larger than originally inferred from monkey experiments (Munoz & Wurtz 1993a; 1995b). F&W then conclude in section 2.2.5 and elsewhere that "visual onsets, even in the periphery, act to enhance fixation centre activity." They suggest that the main effect of a remote distractor is activation of the fixate system, which would slow the triggering process (sect. 4.1.2). The "fixate system is accessed by stimulation from an extended central region of the visual field." Their conclusion suggests that a delay in saccade initiation is caused by a delay in the drop-off of SC fixation cell activity known to precede any saccade (Munoz & Wurtz 1992). F&W therefore envisage an increase in fixation activity following visual onsets in the periphery that manifest themselves at level 2 in their scheme. The results of recent physiological studies have demonstrated that this mechanism must be modified. The visual receptive fields of collicular fixation neurons are small and encompass only foveal and parafoveal regions of the contralateral visual field (Krauzlis et al. 1997; Munoz & Wurtz 1993a). Only a small percentage of fixation neurons have visual receptive fields that extend out to 10° of visual angle in the contralateral hemifield (Everling et al. 1998).

A more plausible mechanism that could account for the increase in SRT following the presentation of a remote distractor is the lateral inhibitory network within the intermediate layers of the SC itself. Anatomical studies have shown that there are many GABAergic inhibitory interconnections that are both intra- and intercollicular (Behan & Kime 1996; Mize et al. 1991; Olivier et al. 1998). In addition, electrophysiological recordings in slices of ferret SC (Meredith & Ramoa 1998) and the SC of awake monkeys (Munoz & Istvan 1998) have also revealed strong intrinsic and commisural inhibitory interactions following electrical stimulation at remote locations on the SC motor map. Therefore, in the scheme of F&W, it is likely that the presentation of a remote distractor would serve to activate a second population of saccade-related neurons in the salience map, rather than lead to direct activation of neurons comprising the fixate system. Then, via lateral inhibitory interactions within the salience map at level 2, the generation of the motor command to initiate a saccade would be delayed.

Another interesting result obtained with the presentation of a simultaneous distractor is that presentation of a distractor in close proximity to the target can produce the global effect in which the saccade actually goes to an intermediate position between the target and the distractor (sect. 4.2.2). In this situation, the visually evoked activity induced by the distractor is close to the location, within the salience map, of the visually evoked activity induced by the target, resulting in two overlapping regions of activity. There is evidence for excitatory lateral interactions between near sites within the SC (McIlwain 1982; Munoz & Istvan 1998) that could facilitate the generation of these averaging saccades. As a consequence, presentation of a near distractor could produce a shift of the center of gravity of active cells within the salience map and, consistent with the "population-averaging" hypothesis (Lee et al. 1988), change the amplitude and direction of the saccade. This could explain the "global effect" (averaged saccades) observed when the distractor is presented in the vicinity of the actual target.

To test these hypotheses directly, we recorded the activity of SC neurons in monkeys performing a gap paradigm in which the fixation point disappears 300 msec before a target appears in the center of the neuron's response field and a distractor is presented somewhere else in the visual field. To separate the neural response elicited by the distractor from the phasic saccade-related activity of SC neurons, distractors were presented at various locations in the visual field 100 msec prior to target appearance. Figure 1 shows the activity of a single saccade-related neuron with buildup activity when only a target (T) was presented (Fig. 1A – control)

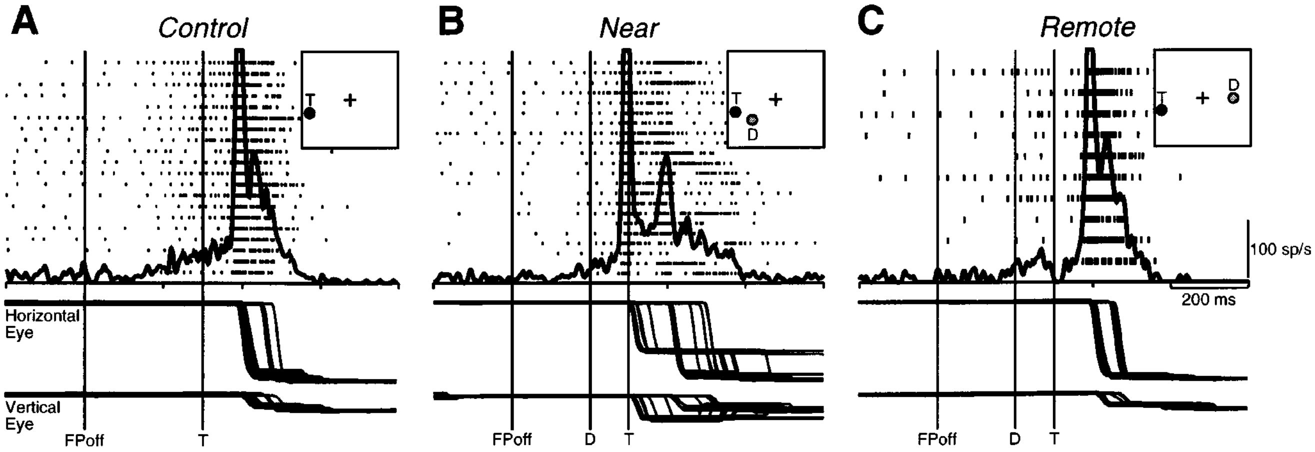

Figure 1 (Olivier et al.). The effect of distractors on the discharge rate of a SC neuron with buildup activity. (A) The neuronal discharge during visually guided saccades is shown when there was no distractor, (B) the distractor was presented near the center of the neuron's response field, and (C) when the distractor was presented at a remote location relative to the neuron's response field, as depicted by the schematic in each inset. Each line of rasters represents the neuronal activity from one trial and the average activity of the cell for all trials in a given condition is illustrated by the spike density function. The accompanying horizontal and vertical eye position traces are shown at the bottom of each panel.

and when a distractor (D) was presented at either a near (Fig. 1B) or remote (Fig. 1C) location. In all trials the monkey was rewarded only if it made a visually triggered saccade to the target, which was always presented in the center of the neuron's response field. In the control condition, the neuron displayed low-frequency motor preparation activity during the gap period and both visual and motor bursts associated with target appearance and saccade generation, respectively. The influence of the distractor depended on its position with respect to the target. When the distractor was presented near the target location (Fig. 1B), the neuron showed a transient visual burst that, because of the already elevated level of motor preparation near that location, sometimes triggered short-latency saccades to the distractor itself. When the distractor was presented far from the target location (Fig. 1C), there was a transient inhibitory pause in discharge and no saccades were triggered to the distractor. Therefore, we can speculate that, when the remote distractor is presented simultaneously with the target, as in the original experiment of Walker et al. (1997), inhibition delays the saccade-related neurons from reaching the level of discharge required to initiate a saccade and therefore delays its initiation.

We suggest that the two distinct effects of a remote distractor on both the temporal and spatial saccade parameters can be explained by a single mechanism: the interaction between two zones of active, saccade-related neurons within the salience map at level 2 in the F&W scheme. One population of saccade-related neurons is activated by the target and the other one is activated by the distractor. The nature of this interaction will depend on the relative location of these two active cell populations within the salience map and is consistent with the complex pattern of inhibitory and excitatory intrinsic and commissural connections within the SC (Meredith & Ramoa 1998; Munoz & Istvan 1998; Olivier et al. 1997; 1998).

Is covert attention really unnecessary?

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Abstract: We are largely in agreement with the Findlay & Walker model. However, they appear to dismiss the role of covert spatial attention in tasks in which people are free to move their eyes. We argue that an account of the facts about the perceptual span in reading requires a window of attention not centered around the fovea. Moreover, a computational model of reading that we (Reichle et al. 1998) developed gives a good account of eye movement control in reading and would be unable to do so without relying heavily on covert attention.

The model proposed by Findlay & Walker (F&W) is a parsimonious account of a considerable amount of visual search data. We are in agreement with the general outlines of the model, as well as many of the specifics. However, we feel that their discussion of covert attention is too brief and, as a result, may be misleading. In particular, we take issue with the sentence: "We question whether covert attention plays any role in normal visual scanning" [with the suggestion that covert attention is irrelevant in normal vision where the eyes are free to move] (sect. 4.6, para. 3). Perhaps we are over interpreting this statement, and if so, we welcome any clarification by the authors in their responses.

We agree with what we understand to be one of the motivations for this statement. That is, in normal vision the eyes move every quarter of a second or so to fixate some new information. Hence, the relevance of the standard paradigm for studying covert attention, in which a person is required to maintain fixation for an extended (and unnatural) length of time while covertly attending to a different location, is unclear. (It might be relevant in certain social situations in which we need to avert our gaze from the face of another person but still monitor the facial expressions.) However, the fact that overt orienting by eye movements is relatively rapid does not imply that covert attention is of no functional value. On the contrary, we feel covert attention serves two important functions in the usual ecology where the eyes are constantly moving: (1) It allows a new object of interest to be attended before it is actually fixated; and (2) it frees the perceiver from necessarily having to process the part of the visual field that is fixated. The latter is important, because although it is likely that the intended target of fixation is often fixated in most real-world tasks, it may not always be (as we shall discuss below).

Given space limitations, we will restrict our discussion to reading; however, we think that the essential argument can be extended to other situations, such as scene perception, as well. First, consider "moving window" studies in reading (see Rayner [1998] and Rayner & Pollatsek [1989] for reviews), which have shown that the area of text processed by a reader of English usually includes the fixated word and a word or two to the right of the fixated word, but not words to the left or below the fixated word. We find this hard to explain without some recourse to a concept like "attention," which is designating some part of the visual field for processing and excluding other parts. This window is not "hardwired," as it is asymmetric in the opposite direction for Israeli readers reading Hebrew, but asymmetric in the same direction when they read English (Pollatsek et al. 1981). Moreover, the size of the window changes "on line," as it shrinks when a fixated word is difficult (Henderson & Ferreira 1990; Inhoff et al. 1989; Rayner 1986).

We think that it is necessary, therefore, to include the concept of covert attention – in the sense of "selection for processing" – when discussing reading. That does not necessarily imply that covert attention can shift within a given fixation. F&W seem to think that such attention shifts are unlikely in normal vision because covert attention shifts in laboratory studies often take longer than fixation times in normal vision. However, these estimates are derived from situations where people are required to maintain fixation. Such a situation may induce something like fixedness of attention and therefore may not be applicable to natural tasks in which the eyes are free to move. Moreover, work by Wurtz et al. (1982) indicates that increased firing in the parietal lobes (which presumably registers an attention shift) normally precedes an eye movement.

We think it is therefore plausible that attention can move to a new location in text before it is fixated and the existence of preview effects in reading (see Rayner [1998] and Rayner & Pollatsek [1989] for reviews) are at least consistent with the notion of an attention shift. When a reader has a preview of a word prior to fixating it, fixation time on the word is shorter than when there was no preview (where the word is replaced by x's or random letters prior to fixation). Furthermore, the computational model of reading that we developed, the E-Z Reader model (Reichle et al. 1998; see also Rayner et al. 1998) gives a good account of how the eyes move through text, and it could not do so without the concepts of covert attention and attention shifting. The E-Z Reader model accounts for fixation times on a word, the number of fixations on a word, whether or not a word is skipped, and a number of other effects typically observed in the eye movement record; simulations run with the model closely match the observed data. In the model, the mechanism of attention shifting is not coupled with programming a saccade. Instead, a saccadic program is triggered by partial processing of a word, whereas an attentional shift occurs when the word is fully processed. However, because of the latency of the actual saccades, the attention shift often precedes the actual saccade. Such a decoupling is necessary to explain "spillover effects" in reading (e.g., the frequency of a word affects not only the amount of time that a word is fixated, but also the duration of the fixation after the reader leaves that word), and helps explain regressions back to the prior word (when the actual saccade to the next word is too far ahead of the attention shift). This model posits a strictly serial movement of attention from word to word, which may be an oversimplification, as it is likely that in some cases more than one word can be processed in parallel or that longer words may not be processed without an attentional shift. However, we feel that the E-Z Reader model, in which covert attention plays a central role, is a parsimonious explanation of eye movement control in reading and we think it is unlikely that a model that does not posit some sort of flexible covert attentional mechanism can provide a coherent account of reading. Moreover, although it is possible that reading is "special" and not generalizable to other visual tasks, we think that there is no reason for people to develop a special visual routine for reading other than the need to process the information in the essentially linear fashion imposed by the logic of text.

No "When" without "Where"

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Abstract: Deciding where to look is a very complicated process, but deciding when to look is probably much simpler. Once the brain is certain of where it wants to look, the saccade-generating pathway may simply start autonomously. Higher cognitive areas of the brain can only override this automatic start by preventing all saccades. Hence, the brain has no ability to say when to go; it can only say "go there" or "stay here."

The role of the saccadic system is to direct the fovea to a region of interest. Saccades must be very fast, because visual acuity is low during rapid eye movements. An extensive amount of neuronal processing is clearly required to determine what the target for the saccade should be, as summarized in the target article. Findlay & Walker (F&W) reasonably divide these processes into five serial stages, forming a "Where" pathway. They also propose a set of five serial stages forming a parallel "When" pathway. This leads to their main hypothesis, that saccades are generated by interactions between two parallel pathways: one determines where the saccade should land, and the other determines when the saccade should start. Whereas the evidence for the "Where" pathway is extensive, we think that the evidence for a parallel "When" pathway is rather weak. Even though, at least in highly evolved animals, signals must exist that allow them to decide *whether* to make or not make saccades, there is no evidence that the role of these signals is to determine *when* to make a movement. Instead, we think it is more probable that the process that determines "where" to go also determines "when" to go.

We believe that this claim is corroborated by several neurophysiological findings. For example, the activity in frontal eye field (FEF) movement neurons, discussed in the target article, increases after a target is flashed, but before the saccade. The time for the activity to cross a fixed threshold is highly correlated with the latency of the saccade (Hanes & Schall 1996). Although this looks like evidence for a "when"-type cell, it is important to remember that these FEF cells also have movement fields, that is, they also specify where to go. Thus, these cells intermingle the "when" and "where" signals. This intermingling is also seen in the buildup neurons of the superior colliculus (Munoz & Wurtz 1995).

The best argument for a pure "When" pathway may come from early studies of the fixation neurons in the rostral zone of the superior colliculus (Munoz & Guitton 1989; Munoz & Wurtz 1993). Fixation cells fire during fixation, and pause for saccades, as pointed out in the target article. However, recent studies of their function reveals that fixation neurons and buildup neurons have many features in common (Gandhi & Keller 1997; Munoz & Wurtz 1995), and thus may form a single population. Hence, fixation neurons may be more related to very small target eccentricities (Krauzlis et al. 1997), a "where" question, rather than strictly determining "when" saccades should be made. Under this hypothesis, the gap effect could be interpreted as a special case of the remote distractor effect, which has been shown to act at the level of the collicular buildup neurons (part of the "Where" system) with no effect on the fixation neurons (Basso & Wurtz 1997; 1998).

We know of no neurophysiological evidence for cortical neurons that encode *only* when to start a saccade and not where to go. However, the situation for subcortical neurons, like the gate cells that constitute the common final element of the "When" pathway, is different. In contrast to the idea put forth by F&W, we propose that the main role of the gate cells is to allow a sizeable buildup of motor activity in the "Where" pathway before saccade start, which guarantees the maximum acceleration of the eyes. This would allow saccades to be as fast as possible (which limits the epoch of poor visual acuity), and would explain why, for manual reactions, only the warning component (which could be the result of increased alertness) is present. Evidence for such a role can be found in a study by Sparks et al. (1987).

It is important to point out that the presence, in highly evolved animals, of signals that can force the gate to stay closed would not alter the role proposed here. Furthermore, this role explains why, when a subject is trying to make a saccade as quickly as possible, the reaction time is much longer than the sum of the visual and motor delays: Some time is needed to allow the system to charge up so as to produce a fast movement.

In conclusion, the main pathway necessary to make a saccade is the "Where" pathway, as outlined by F&W. Other processes, related to cognitive decisions to make a saccade or not, could act by influencing different stages within the "Where" pathway. However, once the "Where" pathway is certain of which target to look at, the saccade starts. The only effect other areas can really have on this automatic decision to go is to just say no.

Top-down influences on saccade generation in cognitive tasks

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Abstract: The theoretical framework laid out by Findlay & Walker has direct implications for central topics in research on saccades in reading and other cognitive activities and these in turn may also have implications to be considered in the context of Findlay & Walker's model. The present commentary focuses on the problem of selecting a target for a saccade. It is argued that there are indirect and direct top-down influences on this process and that direct influences are not adequately represented in Findlay & Walker's theory.

In Findlay & Walker's (F&W's) theory, saccade target selection is accomplished via parallel processing and competitive inhibition in a two-dimensional salience map. This could provide an elegant basis for a selection mechanism in reading, avoiding the complexities inherent in the dominant class of models in the domain, sequential attention models (Morrison 1984; see Reichle et al. 1998 for the most recent version). In sequential attention models of eye movement control in reading, visual attention, lexical processing, and saccade preparation are tightly coupled. At every point in time there are default saccade programs in operation and, on the basis of processing results, saccades are frequently canceled and reprogrammed following a complex set of rules. F&W's proposal may offer a more parsimonious alternative, as multiple targets are assumed to compete in the salience map and only after one has emerged as a winner is saccade programming initiated. However, I believe that F&W's present conception of top-down influences on saccade generation is not in harmony with experimental data and limits its use as an explanation of saccade generation.

In reading and perhaps in many other cognitive activities that require systematic visual scanning, every saccade is directed to a specific target object rather then to a region from which new information is sought (see Radach & McConkie [1998] for a recent discussion). In the case of reading, this selection takes the form of deciding which of the words within the current "perceptual span," including the one currently fixated, should be the goal for the next saccade. The most important low-level sources of influence on this decision are the length and the eccentricity of words located around the current point of fixation (Kerr 1992; McConkie et al. 1994). Following F&W, it can be assumed that the potential target words are represented in a salience map and, depending on the particular visual configuration, their salience values form a preference list of potential targets.

Cognition may influence these salience values, and hence the selection of saccade targets, in different ways. Although somewhat speculative, there is evidence in support of two classes of influence. First, *indirect influences* can be identified, in analogy to the suggestion by F&W that implicit learning and memory play a significant role in the level 4 stages. For example, such long- and medium-term learning might include an estimation of how likely the successful parafoveal recognition of a word will be, given the current fixation position and the length and eccentricity of this next word. The decision of whether to fixate or skip a subsequent word could then be based on this type of "educated guessing" (Brysbaert & Vitu 1998). Second, readers may acquire a limited repertoire of spatial configurations (for example, a short word followed by a much longer word) that are likely to correspond to a frequent linguistic unit (e.g., a nominal phrase), which could then serve as a useful unified saccade target (Radach 1996). In this case, a short word may be skipped, not because of a decision to cancel a saccade (as assumed in the context of sequential attention models), but simply because it forms the beginning of a two-word target.

The evidence in support of *direct cognitive influences* is far less speculative, with many secure experimental demonstrations indicating immediate feedback of cognitive processing to the saccade generation system during the current fixation. As an example, Rayner et al. (1996) investigated the effects of word frequency (as a measure of lexical processing difficulty) on the visual processing of target words during sentence reading. They showed that this cognitive variable has a significant influence on both fixation duration measures *and* the decision to fixate or skip the target word. A number of similar studies including manipulations of word frequency and contextual predictability have recently been discussed in a meta-analysis by Brysbaert and Vitu (1998). Although it is certainly the case that the bulk of the variance can be explained in terms of low-level visuomotor factors, there remains a significant residual contribution from immediate cognitive processing (see also McConkie et al. 1994).

To account for such immediate effects of cognitive processing on fixation duration, F&W suggest that their level 2 fixate centre can be influenced directly and rapidly from cognitive processing centres. Note, however, that the routes reserved in their theory for top-down influences on saccade target selection do not provide for such feedback. For example, word frequency effects are unlikely to be related to *intrinsic salience,* because low-frequency words are not necessarily visually salient and the occurrence of atypical saccades to salient letter clusters appears to be limited to a small number of irregular word beginnings (Hyona 1995). On the other hand, the orthographic frequency of word initial letters can slightly shift the spatial landing site distribution of saccades into parafoveal words, but this is likely to be a result of sublexical processing rather than the detection of an "intrinsic" property of the stimulus (Vonk et al. 1999). Another potential route for top-down processing, *spatial selection,* is described in terms of a modification of the salience map in certain regions, either in a potentiating or an inhibitory manner. F&W assume that this spatial window is quite large because of constraints of distributed coding. However, in reading we are dealing with target objects that can be smaller than 1° in the case of a 3-letter word. For F&W's theory to work in this context, these objects must be represented on the salience map and their salience needs to be modifiable. Most important, the nature of the relevant information is no longer visual, and yet must have a significant on-line influence on saccade target selection. As with the temporal processing stream, this requires a direct route from cognitive processing centres to the level 2 move centres.

As a consequence of the distributed nature of letter-level processing in reading (e.g., Kennedy 1998; Inhoff et al., in press) we propose that sublexical linguistic processing (and, by analogy, other types of cognitive processing in similar tasks) may operate on more then one unit (e.g., word) at a time and that information from this processing is fed back to target representations in the move centre. This proposition has similarities with the suggestion of Henderson and Hollingworth (1998), in the domain of picture perception, that ongoing cognitive processing might modify saliency. However, I agree with Findlay & Walker that not much is gained by assuming that "attention" is disengaged, moved, and reallocated as a function of saliency and that it is these processes that, in turn, trigger saccade programming. Parallel processing and competitive inhibition within a two-dimensional salience map may well be necessary and sufficient to explain the selection of saccade targets in complex visual tasks like reading.

Ocular disengagement inhibited by target onset in periphery?

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Abstract: The postulate that events in peripheral vision enhance activity in the "fixate center" is called into question. An alternative explanation is used to account for the "remote distractor effect." It is pointed out that a critical element of the model is missing.

Findlay & Walker's (F&W's) effort to put together a "model" for understanding the production of saccades, based on a wide range of psychophysical and physiological data, is commendable. I would like to focus my comments on a single point. Their postulate that events in peripheral vision act to "enhance fixation center activity" is inconsistent with the fundamental tenet of their model, which is based on competitive inhibition. The postulate was made to explain why latencies of saccades are longer when there is a simultaneous second stimulus than when there is only a single stimulus. Enhancement of activity in the "fixate center" by a peripheral event that would typically evoke a saccade is counterintuitive. A more plausible explanation would be that a simultaneous second stimulus competes with the target stimulus, perhaps requiring a Level 4 or 5 process to resolve the competition/conflict. The inflated latency may reflect this resolution process rather than an enhanced activity in the "fixate center." This account also explains why an increase in latency depends on the location of the second (distractor) stimulus, away from the fixation point, and not on the distance between the distractor and target: salience is not determined by the distance between them but by the distance of each from the fixation point.

F&W's postulate, mentioned above, also makes it difficult to characterize the exact conditions under which ocular disengagement will occur. F&W note that, through reciprocal inhibition, any increased activity in the move center will promote ocular disengagement. However, they also note that events in the periphery (presumably also the peripheral target) could enhance activity in the fixated center, thus inhibiting disengagement. Given these assertions, it is not clear what the model would predict for the trivial case in which a single target appears in the periphery. Specifying the exact conditions that will initiate disengagement should be a critical feature of any model of saccade generation, especially when it puts great emphasis on the concept of ocular disengagement.

Salience, saccades, and the role of cortex

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Abstract: Findlay & Walker's target article proposes a model of saccade generation related to the underlying neuroscience. A problem with such models is the number of brain areas showing oculomotor function. Traditionally, therefore, models have been partial, usually concentrating either on cortex (Liu et al. 1997; Pierrot Deseilligny et al. 1995) or on the superior colliculus and brainstem circuits (Moschovakis 1994; Van Gisbergen et al. 1993). Findlay & Walker's model attempts to integrate both levels within a functional framework. To some extent it falls between two stools. For example, some functions that the authors ascribe to subcortical regions may actually occur at the cortical level.

In their target article, Findlay & Walker (F&W) provide a thorough, highly informative exposition of their field. The article should prove extremely useful to other researchers studying saccades, not only for its concise summary of known data, but because it brings together a number of important statements about saccade generation that have not been previously incorporated into a single model. The model itself seems able to explain several puzzling phenomena, including the gap and global effects. It undoubtedly sets a standard for future computational approaches. There are two main points I would like to add.

First, one area where the model does seem somewhat thin is in how it relates computational function to cortical neuroanatomy. F&W do discuss low-level oculomotor circuits, referring the reader to standard reviews on the subject. However, they give much less attention to cortical areas such as the posterior parietal lobe, frontal and supplementary eye fields, and dorsolateral prefrontal cortex, all of which have oculomotor function (Anderson et al. 1987; Buttner & Fuhry 1995). Instead, they refer to Levels 4 and 5 of their model in terms of automated or voluntary "cognitive processing." These are ill-defined terms and they raise a number of questions. For example: What computational mechanisms are involved in voluntary as opposed to automated "cognitive processing"? Does the automated/voluntary distinction in saccade processing reflect distinct underlying neuroanatomical networks or areas (presumably it does not correspond to cortex/subcortex divisions)? Numerous studies exist, both in monkeys and humans, addressing these issues (e.g., Doricchi et al. 1997; Fischer & Weber 1996; Treisman et al. 1992), which are largely ignored by F&W. The detail of how low-level circuits execute saccades is of course an important component of any complete computational model, but this model, unlike many of its predecessors, appears to be designed to incorporate higher level functions, as well. So, given that the relevant data are increasingly available, it would have been nice to see some of them set more firmly within the model's context.

A consequence of this concentration on subcortical mechanisms at the expense of cortical ones is that the article tends to give the impression that most of the work done in controlling saccades is done at the collicular level, or below. For example, F&W appear to be suggesting that the rate-limiting process of conflict resolution is mainly carried out in the colliculus (by the interactions between their Level 2 fixate and move centres). However, it is arguable that many other important factors at the cortical level (including random noise in the system) will help resolve most realistic conflicts well before the saccade generation signal reaches the colliculus. In other words, it tends to be high-level information that "tips the balance." If no new sensory information is coming in to resolve a conflict, there is nevertheless a reservoir of stored information that can weight one of the conflicting stimuli over the other. The process of conflict resolution is therefore likely to be widely distributed beyond the colliculus.

In addition, F&W rely on the Wurtz opponent processing model for superior colliculus (Munoz & Wurtz 1992). However, a recent article by the same group (Krauzlis et al. 1997) suggests that this model should be refined. It proposes a continuum processing approach – in essence using the observation that a fixation is a saccade of zero-amplitude. This is consonant with other data, for example, the small corrective saccades typically seen during fixation. It also meshes, computationally speaking, with the observations of Schlag Rey et al. (1992) to which F&W do refer. These authors did not observe opponent processing in the frontal eye fields; rather, stimulating frontal eye field cells coding a particular saccade vector inhibited collicular cells coding all other vectors. This holds for the zero-amplitude vector case.

Second, F&W propose a winner-take-all process operating in their salience representation. Their discussion of this representation's distributed coding is convincing, as is their suggestion that "the metrics are based on the *location of the activity peak* rather than on integrated neural activity" (sect. 3.3.3, para. 2, authors' emphasis). It has recently been shown that such a mechanism, implemented by lateral inhibition, can act as a basis for saccadic targeting by helping to resolve conflicting inputs (Taylor & Stein 1999). Indeed, as F&W point out, the great advantage of such a mechanism is that it does not require external influences; the conflict resolution occurs locally by competitive inhibition.

This raises two additional issues. First, stating the obvious: Although the competitive inhibition mechanism itself may be local, it is not the only determinant of salience. The inputs to the salience representation play a major part in providing units in the representation with their "activity levels" (the "depth" of the two-dimensional contoured surface described by F&W in sect. 2.2.6, para. 2). The second issue follows from this. From their diagram and text, it seems that F&W's salience representation is maintained in the move/fixate centres of Level 2. The move centre they appear to localize to the superior colliculus (they acknowledge (section 3.2.2, para. 4) that "the fixate system may be more widely distributed than the collicular fixation system."). However, any system functioning as a salience representation must have the following properties: (1) It must be able to operate over a wide and continuously varying range of input modalities; (2) it must be able to send information to a wide range of output modalities, because salient targets (whether auditory, visual, somaesthetic or more abstract) can trigger eye, head or limb movements, or verbal output, depending on circumstances; and (3) it must be able to be influenced by stored (cognitive, mnemonic) information (i.e., to be adjusted on a voluntary as well as an automatic basis). Given these properties it is possible that the salience representation is purely cortical (e.g., in the posterior parietal cortex [Stein 1992]), or that both cortical (e.g., parietal) and subcortical (e.g., collicular) centres serve as salience representations. However, it seems unlikely that *only* the colliculus has such functions.

Frontal eye field: A cortical salience map

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Abstract: The concept of a salience map has become important for the development of theories of visual attention and saccade generation. Recent studies have shown that the frontal eye fields have all of the characteristics of a salience map.

A key aspect of the model of saccade generation proposed by Findlay & Walker (F&W) is a map of visual salience that has the following characteristics. It uses spatially distributed coding through large receptive fields. It is modified by spatial selection, by a selection for features during a visual search, and by intrinsically salient stimuli. F&W also suggest that learning and adaptive processes should affect activation of the salience map.

F&W correctly point out that the superior colliculus is a likely candidate for a salience map. In fact, in section 3.3.3 they go to great lengths to describe the salience map in terms of superior colliculus activity. However, some key experiments that test the hypothesis of the existence of a salience map have not yet been carried out in the superior colliculus. On the other hand, recent findings support the emerging view that an important role of the frontal eye field is to provide a salience map of the visual field in which stimulus locations are tagged for behavioral relevance derived from intrinsic salience, as well as prior knowledge or expectancy (Schall & Bichot 1998; Schall & Thompson 1999).

The frontal eye field, located in the prefrontal cortex, is reciprocally connected to visual areas of both the dorsal and ventral streams (Schall et al. 1995b), and projects directly to the intermediate layers of the superior colliculus where the buildup neurons are found (Segraves & Goldberg 1987), as well as to the brainstem saccade generator (Segraves 1992). The frontal eye field contains

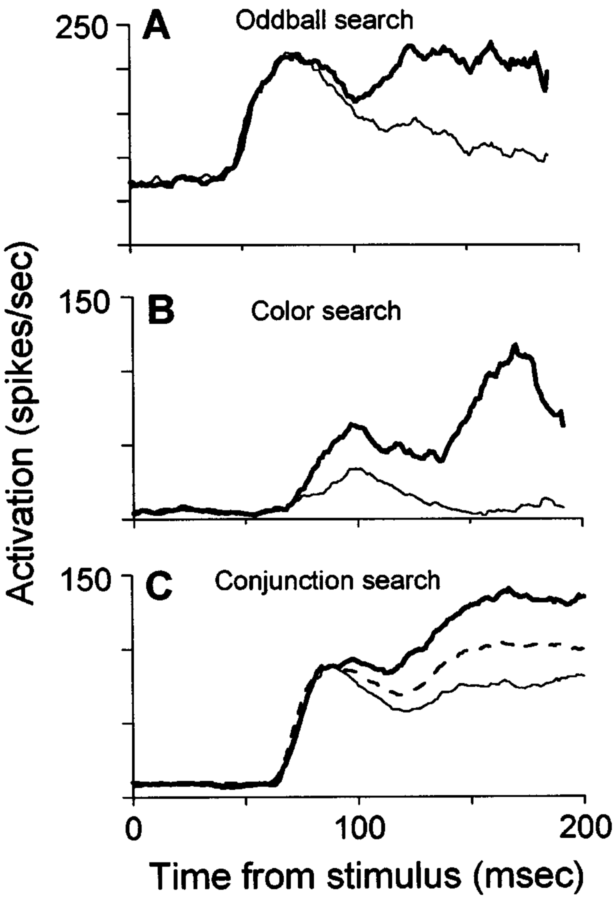

Figure 1 (Thompson & Bichot). Neural correlates of visual salience in frontal eye field. Monkeys were shown visual search arrays and were required to make a single saccade to the target of the array. Average firing rate as a function of time is shown for frontal eye field visually responsive neurons recorded in: (A) a monkey that was trained on both complements of a visual search array in which the target differed from the distractors in color (e.g., red target among green distractors or green target among red distractors); (B) a monkey that was trained on just one complement of the search array; and (C) a monkey that was trained to search for a conjunction of shape and color. Only activity occurring before saccades is shown. Thick lines: activity evoked by the target in the receptive field. Thin lines: activity evoked by distractors in the receptive field. Dashed line: activity evoked by distractors that shared a feature with the target (e.g., same color or same shape) during the conjunction search condition.

visual- and movement-related neurons with large receptive fields, as well as fixation-related neurons (Goldberg & Segraves 1989; Hanes et al. 1998). Early experiments showed that frontal eye field neurons exhibit a selective response following instructions to make a saccade to a specific spatial location (Goldberg & Segraves 1989). More recently, we have studied the activity of frontal eye field visual neurons during a visual search for an intrinsically salient stimulus (e.g., a red item among green items, Fig. 1A). The initial activity of visually responsive neurons in the frontal eye field did not discriminate whether the target or only distractors of the search array appeared in their receptive field. Over time, before a saccade was made to fixate the target, the activity of these neurons evolved to signal the location of the target as reflected by an attenuation of the activity evoked by distractors (Schall et al. 1995a; Thompson et al. 1996). Selection of the oddball stimulus occurred whether or not a saccade was made (Thompson et al. 1997), thus reflecting the automatic selection of intrinsically salient stimuli.

F&W suggest that learning may modify the salience of stimuli. We have tested this hypothesis for frontal eye field neurons (Bichot et al. 1996). When monkeys learn to make saccades to stimuli of a specific color (e.g., a red target among green distractors exclusively) instead of making a saccade to the oddball of the search array (e.g., either red among green or green among red), the initial response of frontal eye field visual neurons acquires a selectivity for the learned color (Fig. 1B). When presented with an array in which the target and distractor colors were switched, instead of looking at the salient oddball stimulus, these monkeys looked at a distractor that was the same color as the target in the learned complementary array.

We have also studied the selection process during a visual search in which locating the target requires knowledge of its properties (Fig. 1C). Neural activity in the frontal eye field during a search for a target defined by a conjunction of color and shape (Bichot & Schall 1998) revealed that target selection is guided by the similarity among stimuli (Duncan & Humphreys 1989), most likely through parallel processing of the individual features that define the conjunction stimuli (e.g., Cave & Wolfe 1990). Neurons not only discriminated the target from distractors, but also exhibited more activation for distractors that shared a target feature than for distractors that did not share any. These neurophysiological data further support the notion of the frontal eye field as a salience map and are consistent with patterns of gaze of both monkeys (Bichot & Schall 1999) and humans (Findlay 1997) during conjunction search.

In conclusion, a map of visual salience, as proposed by Findlay & Walker, is physiologically plausible as suggested by studies of superior colliculus, and we have found ample evidence that one exists in the frontal eye field.

Generating oculomotor and neuronal behavior in a neural field model of the superior colliculus

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Abstract: The functional schema in the Findlay & Walker target article presents an understanding of oculomotor behavior primarily at an algorithmic level of analysis. Although such an analysis is an important first step, present knowledge of the neuroscientific substrate for oculomotor behavior is sufficiently advanced to support, if not warrant, computationally explicit models explaining how oculomotor behavior is implemented by this substrate. The literature contains a growing number of examples of this strategy, which we illustrate using our work.

It cannot be overemphasized how educational functional schemata, like that presented in the information flow diagram of the Findlay & Walker (F&W) target article, can be. Their purpose is to communicate our accumulated knowledge in a comprehensive way, even at the expense of the specificity necessary for scientific verification. However, to verify the assumptions incorporated within such a general framework, a more explicit model is required. Moreover, because the typical nonlinearity of complex systems limits intuitive understanding and analytical tractability, quantitative analysis with the help of model-based simulations is desirable. Following the lead of Kopecz and Schoener (1995; Kopecz 1995) we have developed a simple model of the superior colliculus that can closely simulate oculomotor behavior (e.g., saccadic reaction times, SRTs) in four paradigms (gap, antisaccade, distractor, stimulus probability) using pseudo-neural units whose dynamic activity closely matches that of the fixation, buildup, and burst neurons (Munoz & Wurtz 1993a; 1995a) in the superior colliculus during these four paradigms (Simpson et al. 1998; Trappenberg et al. 1997). As in the target article, the central idea realized by our model is that various exogenous and endogenous inputs are integrated on a motor map resembling the salience map at level 2 of the target article. Our work can therefore be seen as complementary to the proposal by F&W.

Central to our model is an interaction structure within the motor map that is both cooperative and competitive. By cooperative we mean that active cells will have an excitatory influence on their near neighbors, whereas competition occurs at large spatial separations through inhibitory interactions. Converging onto this integrative map are spatially specific (topographic) and spatially nonspecific signals, each of which may be exogenous or endogenous in nature. The relative timing of these signals, together with the self-contained dynamic of the map, determines the generation of saccadic eye movements. A strict division into a temporal and spatial processing stream, as suggested by the target article, therefore seems misleading. We suggest that a "spatially specific" versus "spatially nonspecific" characterization of the streams, for which ample evidence is provided in the target article, would be more appropriate.

Models with a cooperative and competitive interaction structure were first explored many years ago by Amari (1977). Kopecz and Schoener (1995) have demonstrated that such models can account for various saccadic phenomena, including the variations of SRTs within the gap/overlap paradigm (Kopecz 1995). It is of utmost importance, however, to explore the predictive nature of such models by their application in a quantitative manner to other experimental paradigms. Two contributions of the target article are its presentation of a representative set of paradigms and phenomena suitable for this purpose and its suggested links to functional systems in their framework. Missing, however, is a more explicit model and the kind of quantitative analysis that is standard in many other disciplines.

Here we provide an example from our modeling efforts (Simpson et al. 1998) in which oculomotor behavior in a distractor paradigm (Corneil & Munoz 1996) is linked to neuronal behavior (of fixation, buildup, and burst neurons) in the superior colliculus (Olivier et al., this issue). In this example targets are accompanied by distractors presented within the gap period at various spatial locations relative to the target (see also Theeuwes et al. 1998; Walker et al. 1997). The human behavior data (Corneil & Munoz 1996) show a clear reduction of SRTs – relative to the gap condition without distractors – for distractors near the target, and increased SRTs for far distractors. This behavior is reproduced by our simulation (Fig. 1a). The activity of a model "buildup neuron" at the location of the motor map corresponding to the target position is shown in Figure 1b-d. In these experiments a fixation signal is removed at $t = -300$ msec before a target signal is presented at $t = 0$ msec. Typical for cells of this type is a buildup of activity during the gap period after the fixation stimulus is removed. This is followed by a much stronger activity in response to the exogenous signal representing target onset (Fig. 1b). Usually, the sensory response by itself is insufficient to elicit the saccade. The subsequent removal of endogenous fixation signals (Taylor et al. 1998), which, in the distractor paradigm are time-locked to the target signal, results in the final buildup leading to saccade initiation. The presentation of a distractor at $t = -100$ msec at the same location as the target, or at nearby locations, adds an earlier peak to the exogenous signal of the upcoming target, but does not elicit the saccade because a suprathreshold level of activity is still prevented by the endogenous fixation signal. It does, however, facilitate the final buildup of activity after target onset and removal of the endogenous fixation signal (Fig. 1c). The effect of inhibitory interaction can clearly be seen for a far distractor (Fig. 1d). This distractor evokes a sensory response in cells corresponding to its position on the motormap (not shown), which, via inhibitory interaction, reduces the buildup activity of the cell (shown here) in whose receptive field the target will be presented during the gap period. This reduction retards the final buildup of activity leading to the saccade initiation, thereby lengthening SRTs. This behavior of our model neurons closely resembles the average waveforms of buildup neurons recorded in the intermediate layer of monkeys' SC (see Fig. 1 of Olivier et al., this issue).

Computational models of behavioral phenomena are explicitly designed to satisfy "top-down" constraints, that is, to predict or generate the behavior in question. Partly because a multitude of such models can be formulated to generate a particular behavioral pattern and partly because cognitive neuroscience seeks to understand how behavior is implemented in the brain, we have argued (Klein 1998) that, whenever possible, such models should also be designed to satisfy the "bottom-up" constraint of generating the behavior of the neurons thought to be responsible for the target behavior. Two strengths of our approach are that it is rooted in a variety of behavioral phenomena and that our model generates both oculomotor and neuronal behavior. Several advanced and instructive models of the SC (see for example, Arai et al. 1995; Dominey & Arbib 1992; Grossberg et al. 1997) have also reached this stage.

ACKNOWLEDGMENT

The research reported here was supported by a Natural Science and Engineering Research Council (Canada), collaborative grant to R. Klein, D. Munoz, P. McMullen, and T. Trappenberg.

Adding depth to the picture

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Abstract: Recent studies showing that pontine burst cells carry a monocular code for rapid eye movements raise questions about the organisation of signals at more central levels. Evidence that the superior colliculus may also be involved in the coding of movements in depth is reviewed. Recent work showing that the global effect is a property of refixations in 3-D space is another indication that the oculomotor systems for direction and depth are centrally coupled.

Findlay & Walker's (F&W's) target article illustrates nicely that considerable progress has been made in unifying the different viewpoints and approaches of neurophysiologists, theoreticians, and behavioural scientists to yield a coherent account of the oculomotor system that highlights where these disciplines can benefit from one another. Gradually, the emphasis in neurophysiological studies has shifted from seeking relations with elementary behavioural attributes, such as the metrical and dynamical aspects of eye movements, toward the more challenging questions about the When and Where aspects of oculomotor control that have emerged from cognitive studies.

As they state in the beginning of their paper, F&W have limited the scope of their target article by leaving out depth. As a result, it ignores some issues that deserve close attention. It has become clear in the past decade that the systems responsible for changing the point of fixation in direction and in depth are not independent. Several groups have shown that a movement in depth is much faster when executed in conjunction with a saccade than when made in isolation. To explain this phenomenon, Zee et al. (1992) proposed that omnipause neurons may be involved in gating burst neurons specialised in depth movement along with their already

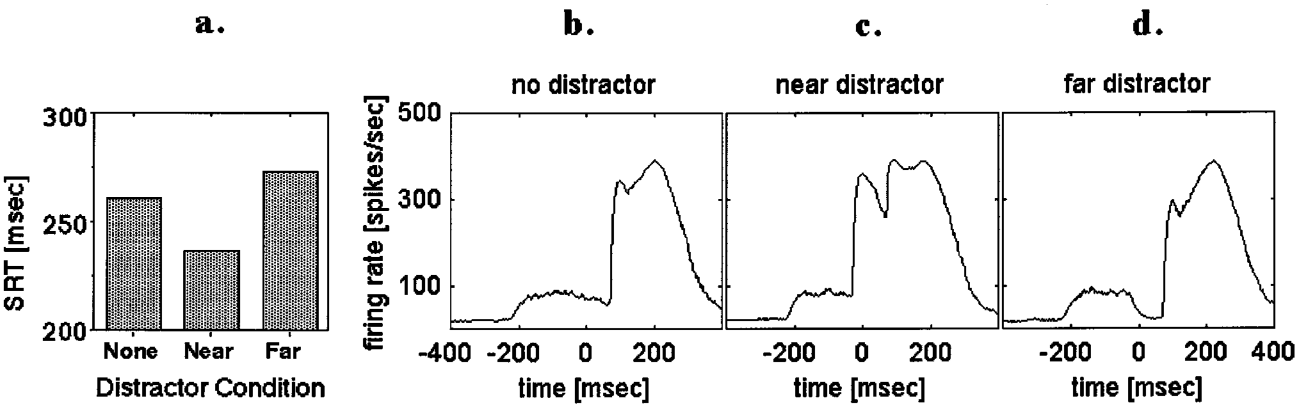

Figure 1 (Trappenberg & Klein). Results of a neural field simulation of oculomotor behavior (a) and neuronal activity (b-d) in a distractor paradigm (see text for details). Simulates saccadic reaction time is shown in panel (a); the remaining panels show simulated discharge rate for a "buildup neuron" at the target location in the no distractor (b), near distractor (c), and far distractor (d) conditions.

well-established role in gating rapid conjugate movements. The idea that the pause cell system may not be dedicated solely to saccadic gating, but rather seems involved in the initiation of 3-D refixations, has received support from the work of Mays and Gamlin (1996) who found that electrical stimulation of pause cells causes a clear suppression of vergence movements.

Recently, Zhou and King (1998; see also their accompanying commentary, this issue) have shown that classical concepts on how saccades are controlled at the premotor level require revision. Before this, it was believed that the horizontal burst cells in the pons issue a binocular velocity command signal specifying a conjugate saccade that moves both eyes equally in the same direction. Zhou and King trained their monkeys to track a target that moved back and forth in depth. This was done when either one or the other eye was aligned with the path of the target so that only the nonaligned eye moved. It appears that most pontine burst cells code the movement of either the left or the right eye, irrespective of what the other eye is doing. Their finding suggests that the population of pontine burst cells can code rapid refixations in 3-D space, based on unequal saccades in the two eyes. In other words, the two groups of binocular burst cells postulated in the Zee et al. model, both gated by pause cells (see above), may in fact be embodied by a single group of monocular neurons.

The finding that pontine burst cells are monocular and the implication that they may be involved in 3-D refixations raises questions for the organisation at upstream levels. Because it is thought that brainstem burst cells get a major input from the superior colliculus, the question arises how these connections are organised. The target article depicts the colliculus as a structure containing a 2-D neural map of visual space, which is responsible for generating conjugate saccadic eye movements. Several lines of evidence suggest, however, that the colliculus has access to depth information. For example, a study by Bacon et al. (1998) in the cat has shown that cells in the superficial layers are disparity sensitive. Another indication is the recent demonstration that the superior colliculus in the monkey receives depth-related, as well as directional information, from the parietal cortex (Gnadt & Beyer 1998).

Recently, we have performed experiments in the monkey to test the idea that the colliculus may be involved in coding the rapid depth component of refixations in 3-D space (Chaturvedi & Van Gisbergen 1999; Van Gisbergen & Chaturvedi 1998). A caudal site was stimulated at various times after the monkey was confronted with a visual target requiring both a directional and a depth change in fixation. We found that the electrical stimulus in isolation caused only a saccade with no overt depth component. If the electrical stimulus was given at a time when the monkey was just preparing, or had just initiated, a refixation to the visual target, we saw a clear averaging effect in the saccade, reflecting a compromise between the electrically- and the visually-induced rapid eye movement. Remarkably, we also saw a clear perturbation of the vergence response, which suggested that the eyes were making a compromise response in 3-D, blending the effects seen when electrical and visual stimulation were given in isolation. These results, showing obvious effects of collicular stimulation on vergence, are compatible with a 3-D coding of the desired refixation in the colliculus where the mode for direction is organised topographically on the well-known collicular motor map. To explain the depth effects, we propose that depth may be coded logically in the recruited population of collicular burst cells, with neighbouring neurons being tuned to different depths. Clearly, further evaluation of the model must await the results of a neurophysiological investigation of the 3-D tuning properties of collicular movement fields.

The possibility that the coding of rapid eye movements may be organised in 3-D also has interesting implications for target selection. As becomes clear from the present target article, several interesting findings have emerged from frontal-plane studies where the subject had the task to follow a jumping target of one colour and to ignore a nontarget stimulus marked by a different colour. These studies have revealed that the oculomotor system can make the required target-nontarget discrimination when latency is sufficiently long. When subjects are urged to make short-latency responses, errors inevitably occur. When the target-nontarget stimulus paid has a modest spatial separation, in either direction or in eccentricity, the response is not simply either correct or incorrect, but often takes the form of a compromise (or averaging) response, a manifestation of the so-called global effect.

We wondered what would happen if subjects had to perform this task in 3-D space (Chaturvedi & Van Gisbergen 1998). If distinct oculomotor systems are responsible for movements in direction and depth, as has often been assumed, the problem arises of how the brain can ensure that the direction and depth systems will choose the same target. In our experiments, the target and the nontarget stimulus pair were always presented jointly on the right or on the left but at different elevations and at different depths, and subjects were urged to make short-latency responses. Because of the way the study was designed, we could readily identify responses where the direction system chose one stimulus and the depth system chose the other. But, in fact, such discordant responses were extremely rare. The typical response was an averaging response in 3-D space where the binocular point of fixation moved to a locus somewhere between target and nontarget. The amount of error in such responses, measured along a scale from wholly correct to wholly incorrect, was strongly correlated in the saccadic and in the vergence response.

This work has shown that the global effect is not limited to the frontal plane but is a generalised property of 3-D refixations. The results strongly suggest that target selection occurs jointly for direction and depth at a stage where potential targets are represented in 3-D. As we have made clear above, the study by Zhou and King (1998) has provided a new perspective on saccade-vergence cooperation. If the fast component of 3-D refixations is executed by pontine burst cells, the averaging responses that we have seen in 3-D space may still be a property of the saccade system. What would be new in this concept is that the saccadic system is not strictly conjugate but capable of making unequal saccades in the two eyes.

About saccade generation in reading

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Abstract: In their model, Findlay & Walker propose that where and when the eyes move is determined by two relatively independent processing streams. Whereas both saccade direction and amplitude result from a low-level visual analysis of the peripheral visual stimulation, saccade latency results mainly from higher-level processes related to processing of the central information. In the present commentary, reading eye movement data are put forward as evidence against a strict autonomy of "Where" and "When" processing streams. First, saccade direction and amplitude might be modified by high-level processes related to word identification. Second, the direction of a saccade directly affects its latency.

In Findlay & Walker's (F&W's) model, saccade generation results from the competition between two processing streams that progress in parallel and that determine respectively where and when the eyes move. Whereas the "Where" stream depends on a low-level visual analysis of the peripheral stimulation, the "When" stream results mainly from high-level decisional and cognitive processes related to processing of the foveal information. Both processing streams occur in a totally independent manner until a response is available from either the "fixate" or "move" system. This suggests, first, that high-level processes related to both foveal and peripheral stimulation cannot affect the saccade metrics, and second, that the saccade target location in the visual field cannot modify the saccade latency. In the present commentary, evidence from reading eye movement data is put forward that contradict both of these statements and suggest the need for a more largely interactive model.

With each new eye fixation in reading, a variety of potential targets are made available to the system; these comprise the currently fixated word, the next word(s), and the previous word(s) located respectively in the right and left parafovea. The most common pattern is the eyes moving forward to land either on the next word, or on one of the words following it. However, in some instances (about 20% for adults and 40% for 5th-grade children), the eyes regress to a prior word, or refixate the fixated word with an intraword regressive or progressive saccade (Vitu & McConkie, in press; Vitu et al. 1998).

The likelihood of occurrence of a progressive interword saccade is related to the necessities of ongoing processing. It depends, first, on the need to return the eyes to one of the prior words, which is a function of high-level processes associated with both sentence processing (Frazier & Rayner 1982) and word identification (Vitu & McConkie, in press; Vitu et al. 1998). It also depends on whether the fixated word needs to be refixated, which clearly varies with the efficiency of processing associated with the word (Vitu 1991b; Vitu & O'Regan 1995). In contrast, the exact position in the text where the eyes land following a progressive interword saccade depends mainly on low-level visual factors that affect the visual configuration formed by the next words, although it might in some instances vary with the lexical and linguistic characteristics of the next parafoveal word (Brysbaert & Vitu 1998; Lavigne-Tomps et al., submitted).

Thus, saccade metrics in reading are not only determined by the visual properties of the peripheral stimuli as F&W assume; they also depend on higher-level processes related to the identification of both foveal and parafoveal words. It must therefore be envisaged that word identification processes can modify the salience map, by means of excitatory and inhibitory links, in the same way low-level visual spatial and search selection processes do. This would operate in a highly interactive and dynamic manner, and would depend on the respective time course of both word identification processes (in the When stream) and visual processes in the Where stream. As long as a word has not been identified, it would produce inhibitions over all other potential target words. The salience map would therefore vary continuously, depending on the state of ongoing processing associated with the prior and next parafoveal word(s), as well as the fixated word.

Given the fact that an average word can be identified with a single eye fixation when it is embedded in a text, regressions to the prior word and within-word refixations would retain the eyes to move forward only when a word was skipped and could not be identified before skipping, and/or when the word is difficult to process (Vitu 1991b; Vitu et al. 1998). In addition, because the time required to identify a word located in parafovea might extend the time necessary for the emergence of a visually high-salience peak, high-level influences on the size of forward saccades would be rather rare. Only when the parafoveal word is very easy to process or the time spent fixating word "*n*" is particularly long (which allows more parafoveal word preprocessing) would such an influence be observed (see O'Regan 1990).

The fact that the information related to both left and right parafoveal words, as well as the foveal word, might participate in the decision of where to send the eyes next suggests several major changes in the model. First, contrary to F&W's proposal, not only the When but also Where stream can be affected by information located in central vision. Second, there might be no need to read for a spatial selection process that specifies a spatial window within which the eyes are more likely to be sent. Indeed, this would imply a rather large window that includes both left and right parafoveal words, as well as the fixated word. A way around this is to assume that the spatial selection process operates only after the system knows whether or not the eyes should regress to the prior word(s) or refixate the fixated word. However, this suggests that saccade direction is computed before and independently of saccade amplitude, which is opposite to F&W's hypothesis of a perfect autonomy between temporal and directional decisions.

In the case of reading, saccade direction might actually be computed before saccade amplitude. As Vitu et al. (1998) recently noted, regressions in reading are preceded by shorter fixation times than forward saccades. This fact can hardly be explained by alternative hypotheses. First, it is very unlikely that regressions serve as corrective saccades that return the eyes to the primary saccade target location and that are characterized with shorter latencies than primary saccades (Becker 1989). Indeed, whereas both inter- and intraword regressive saccades show reduced latencies, only interword regressive saccades return the eyes to a single missed target location (e.g., the prior skipped word in most cases). Intraword saccades always bring the eyes to the part of the word that is opposite to where the eyes initially landed, and that might provide complementary visual information from the word (O'Regan & Lévy-Schoen 1987). On the other hand, unlike progressive saccades, regressions may not wait until the fixated word is identified to be initiated. However, this might again account only for the latency of interword regressive saccades. Indeed, both progressive and regressive intraword saccades occur before the fixated word is identified (Vitu 1991b), and yet intraword regressions have shorter latencies than intraword progressive saccades.

Another problem raised here concerns the question of whether parafoveal word information should be processed by the When or Where streams. The fact that high-level influences on saccades' landing position are more likely to emerge following long fixation durations suggests that the processing of parafoveal word information is carried over by the When system. Indeed, this allows a race to occur between word identification and low-level visual processes performed respectively by When and Where streams. However, this implies that parafoveal word information can influence fixation time, a fact that has not been clearly demonstrated up to now (see Henderson & Ferreira [1993] and Kennedy [1998] for opposite findings).

Exorcising the devil: Adding details to a descriptive account of oculomotor control

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Abstract: Findlay & Walker give voice to several common lines of thought regarding oculomotor control but do not provide sufficient detail for a critical evaluation of their theory. I argue that arbitrary spatial and temporal saccade metrics can be produced simply by manipulating the initial activation values in their model – values that the authors never specify. This lack of detail makes it difficult to anticipate the model's specific oculomotor behavior, or to compare this behavior to models opting for a more quantitative framework.

Findlay & Walker (F&W) do an excellent job of integrating current neurophysiological, computational, and behavioral treatments of oculomotor control under a single unifying framework – and in so doing provide a broad review that will serve researchers in all of these areas. However, as is often the case with large-scale unimplemented descriptions of brain-behavior systems, the "devil is in the details" – and this piece of conventional wisdom unfortunately applies to the target article. For example, F&W propose that effects of (1) onset-offset transients, (2) inhibition of return, (3) search selection, and (4) cognitive control on oculomotor behavior all result from a "bias" being introduced into a saliency map determining target selection. Note, however, that this notion of a bias is simply a restatement that these factors affect eye movements – offering no additional understanding of the representational or computational underpinnings of these influences. Moreover, a major innovative aspect of this proposal, that all of these influences converge in a common saliency map, is left unsupported by references to evidence arguing for such a commonality. As a result of this lack of detail, the proposed theory is as strong as the physiological, behavioral, and computational parts from which it is constructed, but not any stronger.

This commentary focuses first on one detail left unspecified by the current account, the assignment of activation values to points on the saliency map, then describes an alternative set of computations that might act on these values to generate saccades. Both the WHEN and WHERE systems of the F&W proposal are extremely sensitive to the initial setting of activation values. In the case of the WHEN system, the eye fixates because no "point" on the saliency map has achieved an activation level exceeding the saccade initiation threshold. Similar to an earlier model proposed by Sheinberg and Zelinsky (1993), only after a process of signal enhancement accompanying winner-take-all (WTA) competition does one of these values eventually surpass threshold – thereby gating the fixate system and triggering a saccade. This timing of the trigger signal is therefore influenced by the WTA dynamics required to boost the signal above threshold, but is ultimately determined by the initial activation values on the saliency map. The determination of "where" this saccade will be directed is an even more direct consequence of these initial activation settings. F&W do not articulate the details of their proposed WTA algorithm, but presumably, each unit propagates a nonlinear inhibitory signal to its lateral neighbors in proportion to its activation strength. The implication of such an algorithm is that the eventual saccade target is determined from the moment the saliency map is created. Barring any ill-specified biases affecting this map, the spatiotemporal control of eye movements according to this account is therefore completely determined by these initial activation values.

Given that much of the proposed model's behavior depends on the initial state of the system, some detailed description of this initial state would seem to be in order. One promising method of quantifying this initial activation state uses the responses from Gaussian derivative filters in the computation of saliency. Because these filters are based on a Gaussian function, they can be applied to arbitrarily complex real-world stimuli and a variety of tasks. Recent applications using this filter-based approach range from oculomotor search (Rao et al. 1996) to block copying (Ballard et al. 1997) to change detection (Zelinsky 1998). In all of these cases, filter responses are used to represent one or more objects in a scene, with computations then acting on these representations to accomplish some task. Taking visual search as an example, filter responses can be collected for an arbitrary point on a target object, then this target vector can be compared to response vectors computed for every point in the search image. The quality of the match between the target vector and any one response vector is a single saliency value, and plotting these matches for the entire search image yields a saliency map similar in kind to the one described by F&W – only in considerably more detail.

Building on this filter-derived saliency map, recent work in my lab adds spatio-temporal system dynamics to account for many of the oculomotor phenomena listed in the target article. These dynamics, however, take a form markedly different from those proposed by F&W. Rather than a WTA network that is highly susceptible to problematic oscillation, my model uses a modified gradient descent algorithm. According to this model, a target is defined by the centroid of points on the saliency map, weighted by their activation values. The key spatial parameter is an upwardly-moving threshold that gates the points to be included on the saliency map. When the saliency threshold is low, even points with minimal activation values will be included in the centroid computation; when the threshold is high, fewer active points will be excluded from the saliency map – resulting in the saccade dynamics converging toward the target (Zelinsky et al. 1997). Unlike F&W who propose that "the point of highest salience in the map becomes the target for the saccade" (sect. 2.2.6, para. 2), the target in this model can be determined either by multiple points (i.e., centroid averaging) or by a single point when the threshold becomes maximally restrictive.

Determining "when" a saccade is initiated is accomplished by a second parameter. Because a new target is suggested after each iterative change of the saliency threshold, some of these suggested target locations will be very close to the current fixation, whereas others will be more distant. My model imposes a minimum distance threshold on this variability. If the Euclidean distance between a suggested location and the current fixation point exceeds this threshold, an eye movement will be initiated; otherwise, gaze will remain in fixation and the saliency threshold will increase a notch. As points continue to drop off the saliency map, this distance threshold will eventually be surpassed and an eye movement will be initiated. Note that, unlike the F&W account, factors determining "where" and "when" a saccade is made are highly interrelated in my model. However, like the F&W model, both saccade metrics are ultimately determined by the distribution of initial activation values and the signal-in-noise characteristics of the stimulus image.

This commentary highlights the need for quantitative details when theorizing about a neurocomputational system. The available behavioral and neurophysiological data on oculomotor control, although impressive, is still insufficient to fully constrain neurocomputational modeling – and for this reason many schemes exist that might explain these data. The scheme proposed here by F&W is one such approach; my model is another, and there are undoubtedly many more. Although F&W might be excused for omitting details from a model as broad and integrative as the one they propose, failing to include these details will necessarily make it difficult to assess the descriptive power of their model or to judge its merits relative to alternative models of oculomotor control. Adding quantitative details to a computational model is more than just an exercise in implementation. Often, it is in the specification of these details where true understanding takes place – where one is forced to confront the hard questions of representation and process.

Monocular and binocular mechanisms in saccade generation

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Abstract: The target article retains the traditional account of saccades as conjugate eye movements. However, recent single-unit recordings of premotor cells in the saccade pathway (excitatory burster neurons [EBNs]) found that they do not encode conjugate eye velocity, but rather, monocular eye velocity. These data argue against the traditional concept of saccades as inherently conjugate. Instead, they suggest a monocular mechanism in the sensorimotor transformation stage of saccade generation. This commentary will discuss the implications of these data for the saccade generation model proposed in Findlay & Walker's target article.

Saccades have been generally thought to be conjugate, that is, the two eyes move in the same direction with the same amplitude. This view of saccade generation is consistent with Hering's Law of Equal Innervation, which assumes that both eyes are innervated by the same motor command, thereby yoking their movements (Hering 1868). Hering suggested that two types of eye movement control signals: one that is conjugate, and another that is vergence (i.e., which moves the eyes in opposite directions with the same amplitude). The modern interpretation of Hering's law is that EBNs generate the velocity command for conjugate saccades (for a review, see Fuchs et al. 1985). Furthermore, near response cells found in the midbrain encode what appears to be a vergence command (Mays 1984). To account for disjunctive gaze shifts between points at different distances, Hering suggested that they are generated by linear summation of conjugate and vergence commands. However, behavioral studies of disjunctive saccades found that linear summation of conjugate and vergence motor commands could not account for the time courses of gaze shifts in depth (Enright 1984; Erkelens et al. 1989; Kenyon et al. 1980; Maxwell & King 1991; Ono et al. 1978; Zee et al. 1992). To reconcile these behavioral data and Hering's law, Zee et al. (1992) suggested that there is a nonlinear interaction between a conjugate saccade generator and vergence.

Other evidence supports an alternative theory. Helmholtz (1910) suggested that the two eyes are independently controlled, and that binocular coordination is learned to prevent diplopia. Thus saccades could be inherently disjunctive. Neurophysiological evidence provides support for this idea. Vilis et al. (1983) reported that cerebellar-induced saccadic dysmetria is not equal in the two eyes. They suggested that two populations of neurons might exist in the paramedian pontine reticular formation (PPRF), one group generating commands for the left eye and the other, commands for the right eye. The cerebellum would be capable of exerting differential influences on the movements of either eye. Sparks et al. (1985) found that the eyes of animals raised under conditions of monocular visual deprivation were misaligned, and that some brainstem neurons had firing rates related to the position of the deprived eye, whereas others fired at frequencies related to the position of the nondeprived eye. These studies suggested that the motor command signals for saccade generation might be monocular rather than conjugate, but they were not definitive.

Hering's law is widely accepted, and many neurophysiological, behavioral, and anatomical studies have been interpreted in its favor (for a review, see Mays 1998). Given this history, it is not surprising that the target article assumed saccades were conjugate eye movements. Our recent study (Zhou & King 1998), however, provided direct evidence for monocular control of saccades. We recorded single-unit discharges of EBNs while monkeys tracked targets that moved in depth so that eye movements were strongly disjunctive. The firing behavior of the neurons was then correlated to the movements of each eye. If a neuron encodes a conjugate command, then its discharge should be related similarly to the motion of both eyes. If a neuron encodes a vergence command, then its discharge should be related to each eye's motion, but with an opposite sign. Alternatively, if Helmholtz were right, one should find a significant number of monocular neurons, that is, neurons with discharges related to the movement of one eye alone. Our findings were unexpected. The majority of EBNs are monocular. In other words, the saccadic burst generator is organized in a left/right eye coordinate frame.

Given these unexpected new results, the basic assumptions of oculomotor control should be reexamined. In particular, these new findings have important implications for the saccade generation model described in the target article. For disjunctive saccades, the model assumes that visual information from the two eyes is integrated to form a coherent, three-dimensional representation of the visual world. Then, the direction and the depth of the target are computed and transformed into corresponding conjugate and vergence motor commands. The sensorimotor transformation in the Where pathway should be modified to take into consideration the monocular characteristic of the saccade generator. We suggest that the saccade amplitude for each eye is programming independently. The basic function of slow vergence eye movements is to maintain binocular alignment during fixation rather than to make gaze shifts in space. However, the timing of saccades in each eye is coordinated by a common pool of pause neurons. This view is supported by the evidence that the saccade duration – pause duration relationship for conjugate and disjunctive saccades is identical (Zhou & King, unpublished observation). Furthermore, the organization of the superior colliculus motor map may also be monocular, because some collicular cells provide direct inputs to EBNs. We suggest that, similar to the organization in the PPRF, motor maps for the left and right eyes may overlap in the superior colliculus. Thus, for disjunctive saccades, there would be separate activation sites in the superior colliculus motor maps for each eye. This hypothesis remains to be proved or disproved by further analysis of burst and built-up neurons in the superior colliculus.

It is interesting to speculate about the extent to which sensorimotor transformation processes remain monocular in cortical oculomotor areas. Poggio and Talbot (1981) found that for about half the foveal neurons, the response selectivity for the direction of object motion in depth depended chiefly on one eye, even though these neurons received inputs from both eyes, which determined their positional depth sensitivity. These results were consistent with a behavioral study of the initiation of disjunctive smooth pursuit eye movements (King & Zhou 1995). The open loop acceleration of smooth pursuit in one eye is a function of the retinal slip experienced by that eye, independent of the retinal slip of the other eye. Many other cortical areas remain unexamined, such as the frontal eye and parietal eye fields.

There are certainly binocular mechanisms involved in oculomotor control. The movements of a covered eye are not fixed but variable, depending on prior knowledge about possible target trajectories in space (King & Zhou 1995). Although it is likely that the basic organization of primate oculomotor pathways is monocular, it is overlaid with binocular mechanisms that are revealed when sensory inflows are insufficient or ambiguous. It will be exciting and challenging to study the interactions of monocular and binocular mechanisms in the control of eye movements. Such studies should shed light on general questions about how sensory information from multiple sources (i.e., two retinas) is transformed into motor commands for the movements of multiple joints (i.e., two eyeballs).

Authors' Response

How are saccades generated?

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Abstract: Our target article discussed how emerging knowledge of the physiological processes involved in the control of saccadic eye movements provided the basis for a functional framework in which to understand the programming of such movements. The commentators raised many interesting issues in their varied responses that ranged from detailed discussion of the physiological substrate through issues of saccade control in reading. New evidence at the physiological level demonstrates that some elaborations are needed to the framework we proposed. Most clearly, the spatial selection process operates in a manner different from our suggestion of an increase in activity in the salience map. Some commentators make the interesting and welcome proposal that the functional processes we outline may in fact be implemented with an even more unified physiological substrate (continuity between collicular fixation and build-up cells) than we envisaged. Extensions to the framework are discussed involving the planning of sequential saccades, saccades made in crossmodal situations, the influences of learning and memory, and binocular saccades. We consider carefully the commentaries proposing explicit attentional and/or executive processes in the programming of saccades. We integrate the comments of researchers investigating saccade control in neurological and neuropsychiatric patients and finally discuss whether the framework can account for saccades made in the course of reading.

R1. Introduction

Our target article was prompted by our appreciation of a convergence between low level studies of the saccadic system from a physiological standpoint and studies investigating saccadic eye movements in a behavioural context. We felt it was appropriate to attempt a synthesis and we are gratified that our article attracted interest from workers in both areas. About one third of the commentaries are on the underlying physiology of the saccadic system, with the remainder addressing points concerned with saccadic behaviour in intact human observers. The target article was originally submitted in 1996 with some revisions and updating before the final submission early in 1997. The area is a fast-developing one and we are grateful to many of our commentators who have reported relevant material which has appeared in the literature since our submission.

We start by giving a brief recapitulation of the main points of our framework while taking the opportunity to discuss a few cases where we believe commentators have misinterpreted or overinterpreted our suggestions. Our model is predicated on separate WHEN and WHERE systems whose final stages (in particular level 2) control fixation and saccadic movement and are cross-connected with a push-pull competitive inhibitory linking. Fixation is maintained until the activity in the fixate system falls below a critical level, at which point a saccade is triggered. The destination of this saccade is then determined by the peak activation in the salience map of the move system. This salience map receives topographically mapped excitatory and inhibitory inputs from higher centres (levels 4 and 5), allowing for high-level selective processes. Transient visual inputs have privileged access (level 3) to these low level processes.

We discussed (sect. 2.2.3) the operation of processes intrinsic to the salience map and in particular the operation of mutually inhibitory cross connections between regions that operate in a winner-take-all manner. We perhaps did not stress sufficiently that we regard the salience map as in a state of continuous dynamic flux with continued input from higher levels as well as the within-level inhibitory process contributing to the changes. It was not our intention to propose that the saccade destination was determined by letting the winner-take-all process run to completion as implied in some commentaries (**Kramer et al., Radach, Zelinsky**). A further minor point arises in connection with our statement that any spatial selection window has to be constrained by the distributed representation at the level of the salience map. Radach suggests that this will not allow isolated representation of an object smaller than about one degree. Because of the centre-dominated nature of visual projections, the minimum window size will vary with eccentricity and, within a central region, window sizes smaller than one degree may occur.

An important theme, taken up by several commentators, concerns the relative influences of low and high level processes on the salience map. Several commentaries, particularly in the area of reading (**Doré-Mazars, Radach, Vitu**), take issue with our framework by referring to results showing that high level processing can influence the selection of saccade destinations. The control of saccades during text reading has long been the arena for debating this issue. We shall discuss this work in detail in a later section but (as acknowledged by **Beauvillain**) our framework did not exclude use of such perceptual information in guiding the eyes. Our suggestion that only relatively simple information could influence the salience map was made quite tentatively, and in our discussion in section 4.5.1, we explicitly stated that we lacked firm knowledge of the relevant processing speeds for various types of information. Since our article was written, more information has become available. We would accept that our model would have limited generality if high level influences could indeed be shown regularly to be the dominant influence determining saccade landing points for normal latency saccades. But as Doré-Mazars and others point out, it seems accepted that the saccade destination is in many situations primarily determined by low-level factors with high-level factors providing interesting and important modulatory influences.

Finally, some misunderstandings are attributable to our choice of terminology. Although in our description of level 4 processes, we outlined a role for long term modifications due to learning, this was not directly reflected in our diagram (Fig. 1) and some commentators (**Crundall & Underwood, Latimer**) have rightly pointed out that our "intrinsic salience" box is inadequate unless interpreted in the context of the text. We also recognise that our term "search decision" to describe level 5 processes may have been suboptimal. **Frens et al.** appear to have assumed at one point that this reflects a decision process operative whenever a saccade is made, whereas our intention was to let this reflect a strategic decision to search for a particular target over an epoch involving multiple individual movements.

R2. Predictions and level of detail

The brain is a complex organism and no simplification will do it full justice. Our use of the term framework indicated that we wished to present a viewpoint with wide potential for more detailed and quantitative instantiation, for example as discussed in the next section. We recognise the danger of a broad approach being insufficiently specified to have any predictive power. However, a framework, even at our level of generality, can make some predictions about the types of effect that may be found. This is shown by the number of commentators who argue that certain quite specific results are in conflict with the model (for example **Guillaume et al., Kramer et al., Colonius & Arndt**). In some cases, we wish to take issue with these arguments, in others, recognise that new information allows extension and elaboration of the framework. To reinforce the fact that our model does have some predictive power, we point to a result that we have to admit can only be accommodated in our model in a very ad hoc way. Guillaume et al. present new data on the effects of unilateral reversible inactivation of the cerebellar fastigial nucleus in the cat. This has a differential effect on saccades ipsilateral and contralateral to the lesion side with differential effects on both latencies and amplitudes of saccades. Moreover long latency contralesional saccades are reported as becoming progressively more hypometric. Although somewhat reminiscent of saccadic eye movement deficits that can occur with unilateral neglect (see sects. R11 and R12), we agree with Guillaume et al. that at the moment this result cannot easily be explained by our framework. To the best of our knowledge, neither can it be interpreted in terms of any other current model. We look forward to seeing further results from this preparation, for example whether the pattern of results is modified if the gap paradigm is used.

R3. Computational processes within the salience map

A group of commentators (**Clark, Meegan, Olivers et al., Tam, Taylor, Trappenberg & Klein, Zelinsky**) seems in broad sympathy with our approach but report or propose more detailed implementational schemes. As already discussed, we believe that our statements about winner-take-all processes were over-interpreted since we did not intend that the competitive inhibition would always iterate to a resting state before saccade triggering. Thus Meegan objects to our use of winner-take-all but accepts that inherent conflict resolution would occur in a map such as we describe. We are puzzled by the statement that the first requirement of a winner-take-all system is that targets have independent representation. We make clear in sections 3.2.3 and 4.2.2 that, in our framework, the salience map uses distributed coding in which neighbouring targets lose their individual representation so that competitive inhibition results only from the representations of distant targets. Zelinsky reports development of an alternative way in which selection of a saccade target could occur. This is based on a two-dimensional map but has considerable differences from our suggestion in using upwardly moving thresholds and a minimum distance algorithm. It will be important to demonstrate whether this rather baroque set of processes can be implemented in a realistic neural net. Trappenberg & Klein object to our division into a temporal and spatial processing stream and refer to their implementation in which spatially specific and spatially nonspecific processes overlap on the same map. This would be consistent with the finding discussed subsequently of a continuum between buildup and fixation cells. We believe this modification would be consistent with the spirit of our approach. Finally we note with interest the detailed model of Clark, which was in press when our response was prepared (Clark 1999).

R4. Competitive inhibition at level 3

We were at pains to point out that our level 3 operation was not intended to simply map onto collicular physiology, although we admitted that our thinking was heavily influenced by recent work in the colliculus. We postulated two competitive inhibition processes at work, first between the fixate centre and all other regions of the salience map and second a distributed process within different regions of the salience map. We argued that this second type of competition might occur at various levels (sects. 3.2.4 and 4.5) and provide a substrate for processes such as visual search. Several commentators have elaborated on this possibility although **Edelman et al.** argue that competitive inhibition in the superior colliculus has only been physiologically demonstrated with flashed stimuli.

Quaia & Optican and **Frens et al.** point out that there is no physiological evidence for cells at the cortical level that encode when without where. In the sense that cells in relevant cortical areas always have receptive fields, this is true, but equally many cortical cells exist with properties similar enough to fixation cells to warrant the term fixation related neurons (**Thompson & Bichot**). As discussed in the target article, there is considerable evidence from behavioural studies that the initiation of saccades is highly sensitive in an automatic way to the details of the ongoing processing of foveal material.

We proposed that the fixation zone was an extensive region which overlapped spatially with the map of the move regions. This was based on our evidence from the remote distractor effect. **Olivier et al.** have studied collicular events during the remote distractor paradigm. They present clear evidence that inhibitory effects do occur in buildup cells consequent on the presence of a remote distractor stimulus. Their preferred interpretation is that these effects result from direct cross interaction between regions of the collicular map rather than indirectly through the fixation region as suggested in our model. We see two problems with this interpretation. First, the interpretation cannot immediately explain the quantitative data shown in the experiments of Walker et al. (1997). The magnitude of the remote distractor effect was clearly dependent on the distance of the distractor from fixation rather than from the target and furthermore was identical for contralateral hemifield and ipsilateral hemifield distractors. Second, the inhibitory effect shown in the figure of Olivier et al. takes considerable time (about 100 msec) to appear. Neither finding is readily consistent with direct cross-inhibitory links. Olivier et al. appear to have slightly misinterpreted our position. We did not intend to imply that collicular fixation neurons had receptive fields extending to 10 deg of visual angle but rather that the entire distributed network of fixation neurons extends to this distance.

An important proposal, mentioned by several commentators, is that of Krauzlis et al. (1997), suggesting that fixation cells and build-up cells form a continuum. This is consistent with the earlier finding of Gandhi and Keller (1997) that both types of cell project to omnipause neurons. **Olivers et al.** refer to the possibility of the remote distractor effect arising from the natural dynamics of competition (see also the implementation suggested by **Trappenberg & Klein**). This raises the interesting possibility that the two positions in the previous paragraph could be reconciled if the collicular net had the properties that activation at one point promoted a spread of inhibitory activity and the rostral region was differentially sensitive.

Dorris & Munoz, while describing our proposal as a "plausible model," continue with arguments that the trigger for a saccade should be located as a result of a threshold being exceeded in the move centre rather than our suggestion of activity in the fixate centre falling to a certain level with a consequent pause in the brainstem omnipause neurons. The presence of reciprocal cross-connections make these two possibilities difficult to disentangle. We feel a general reluctance to shift the triggering to the move centre because an implication would be that burst cells would at least occasionally be triggered simultaneously at widely separated locations. However it may be that this does indeed occur (see recent data referenced by **Edelman et al.**). The evidence that express saccades are not generated in the anti-saccade paradigm can be interpreted as a manifestation of the remote distractor effect (Findlay 1993). However, the evidence from recent work about the spatial selectivity of express saccades is important and convincing. **Jüttner** also describes similar effects which he argues are incompatible with the WHERE system being exclusively devoted to spatial programming. These are based on a study (Jüttner & Wolf 1992) in which a target appeared at a known spatial location and also suggest that the spatial selection process operates not simply by adding an excitatory input. An alternative interpretation for these findings could be that the spatial selection process operates by local modification of the network dynamics, abolishing the inhibitory spread, rather than simply as an additional excitatory input. As well as accounting for the finding about express saccades, this might account for an anomaly mentioned by **Olivers et al.** and by **Tam.** In the Walker et al. (1997) studies of the remote distractor effect, the magnitude of the effect of a distractor at a fixed eccentricity was smaller for targets closer to fixation. Tam states that it is counterintuitive for a peripheral stimulus to enhance activity in the fixate centre. We agree but feel the continuity between the effects of events at fixation and those in the periphery require this counterintuitive postulate. We are not convinced by the suggestion that a result which seems so automatic and unavoidable (Walker et al. 1995) should be attributed to a high level process.

Fischer queries whether our model can explain the effects of a pre-cue at the location of a required anti-saccade. We accept that this is an interesting finding but do not agree that it presents a particular problem for our model. The anti-saccade situation is a complex one involving considerable higher level activity. In some way, a saccade must be made to a location in the salience map other than that of the peak produced through level 3 activity. This is the "spatial redefinition" process (target article, sect. 4.1.4). One way of viewing this could be to regard the process as involving a search for a location where activity is absent. This search process would be rendered more difficult by any residual activation from the pre-cue.

R5. Programming two saccades

A number of commentators reference interesting findings suggesting that two saccades can be produced in a rapid temporal sequence (**Beauvillain, Crawford et al., Fischer, Frens et al., Kramer et al., McPeek et al.**). McPeek et al. report that during visual search, fixations with very short duration often occur when the eye moves to a nontarget location, a phenomenon which we have also observed (Findlay et al. 1998). As pointed out by McPeek et al., this phenomenon was considered by Becker and Jürgens (1979), who attributed it to parallel processing of two saccades simultaneously. Such an interpretation is suggested by the very brief intersaccadic interval, too short for new information about the location of the second saccade endpoint to be extracted. The second movement (as shown in the McPeek et al. Fig. 1) is goal seeking thus suggesting the double movement is programming as a sequence. Similarly, as pointed out by Fischer, when the first saccade to a new target falls far from the goal, a second corrective saccade is made without further sampling of visual information (Becker 1972) although the majority of corrective saccades are dependent on visual sampling. A further demonstration of a situation where the second movement is preplanned comes from the elegant experiment of Beauvillain who shows a clear difference in the reference frames used between the programming of intra-word refixational movements and inter-word scanning movements. As Beauvillain points out, these findings require a capacity to "store" a saccadic movement in terms of a motor error signal. The motor error signal contains the information required to bring the eyes to the new position of the target following the first movement (as discussed briefly in sect. 3.3.1 of the target article).

This leads to the important issue of single versus multiple salience maps. Our model focused on the level of the individual saccadic movement and we postulated a single salience map, although of course with multiple inputs. **Frens et al.** suggest that additional maps are unlikely, yet other commentators (**Kramer et al., Taylor**) argue for multiple salience maps. **Thompson & Bichot** support the consideration of the frontal eye fields in salience map terms and present evidence showing that this map receives an "intrinsic salience" signal in a search pop-out situation. We agree with Taylor that maps here and in other cortical areas will be organised so as to resolve conflict resolution processes and we were, of course, at pains to point out that our model at this level was functional rather than anatomically sited.

R6. Cross-modal interaction effects

Commentaries by **Colonius & Arndt** and by **Crawford et al.** discuss situations in which stimuli from both visual and auditory modalities are presented. A robust effect is the facilitation in visually guided saccade latency with spatially co-incident auditory stimulation. Meredith and Stein (1986) have demonstrated an increase in collicular neuronal activity in this situation. Some other relevant findings are less robust. Similar results (centre of gravity effect, express saccades, remote distractor effect) can occur with auditory and visual combinations of stimuli. However, in contrast to the visual–visual situation, these results are less automatic and are absent if instructions are given to ignore the auditory stimulation. Furthermore, auditory distractors in the opposite hemifield do not produce the remote distractor inhibitory effect on saccade latency (Colonius & Arndt). A number of factors may be involved here. First, auditory stimuli are difficult to localise and it may be important to obtain measures of subjects' estimates of the perceived location of auditory distractors. Second, the perceived location of auditory distractors may be influenced by the location of a visual stimulus due to a form of ventriloquism effect. Third, auditory stimuli facilitate latency due to a general warning signal effect (Reuter-Lorenz et al. 1995; Ross & Ross 1980; 1981). Finally, the peripheral processing of auditory stimuli is more rapid than for visual stimuli. The remote distractor effect between visual stimuli is reduced, and may even reverse, when the stimuli are not simultaneous (Walker et al. 1995). Thus, as Colonius & Arndt suggest, the respective time of arrival of visual and auditory signals is likely to be important (see also **Chou & Schiller**). However, other factors such as the contribution of a generalised warning signal effect must also be taken into account and we prefer not to discount the possibility that a remote auditory stimulus may, under appropriate conditions, act like a remote visual stimulus.

R7. Binocular considerations

Two interesting commentaries consider the issue of binocular eye control. The view, generally held implicitly, that saccades are conjugate movements has never been totally in accord with observations. The new observations by **Zhou & King** show that a control system largely coding monocular movements exists at the level of the brainstem excitatory burst neurons (EBNs) as well as at the level of oculomotor neurons. Zhou & King describe our model as assuming that visual information from the two eyes is integrated to form a coherent representation of the visual world. We did not feel we had made this claim and indeed welcome the increased emphasis on separate control of spatial programming in each eye. This is both in accord with results on saccadic disconjugacy and provides a potential link to the differences in eye control shown by strabismics (Kapoula et al. 1997; Maxwell et al. 1995). However a rather basic aspect of our model concerns the single WHEN pathway. In their commentary, Zhou & King support the view that the timing of saccades in each eye are co-ordinated by a common pool of pause neurons but their own result reporting occasional monocular saccades during REM sleep is then puzzling (Zhou & King 1997). An issue for future research will be to discover how the relevant visual information reaches these lower level centres. Results showing that disparity information reaches the superior colliculus is cited in **Van Gisbergen & Chaturvedi.**

How might these results be reconciled with the general conjugacy shown by the saccadic system? One possibility is that conjugacy is maintained through the target selection process. **Van Gisbergen & Chaturvedi** report convincing evidence from their recent work that target selection occurs in a three dimensional framework. In recent work we have studied an individual with total ophthalmoplegia (Gilchrist et al. 1997; 1998). This individual shows patterns of scanning in visual tasks where the head is moved in a saccadic fashion, albeit with a substantially slower velocity than that of saccadic eye movements. Saccadic scanning of the visual world would appear to be a general property of active vision and not exclusively an oculomotor manifestation.

R8. Learning and memory

In the target article, we outlined some suggestions about the way that short and long term learning processes might be incorporated into higher levels of the model. We believe that study of these processes will offer a challenging area for future research on the saccadic system and welcome the contributions of commentators who offered elaborations and additions to our suggestions. In our account, we stressed the carry-over effects in visual search experiments when a particular search target is used repeatedly. **McPeek et al.** cite recent work on the "priming of pop-out" phenomenon. **Olivers et al.** highlight a second type of carry-over, in which a particular search dimension is similarly repeated. We see the suggestion of Müller et al. (1995) in which multiple-dimension maps feed into a supra-dimensional salience map as quite consistent with our own account and offering the capacity for both intra-dimensional and inter-dimensional learning. **Jüttner** described further spatially specific form of short term learning. We believe that these processes constitute the "rudimentary mechanistic influences" which **Latimer** requests although we concede that there is still a large gap between our current state of knowledge and his requirement of a system with a capacity to survive in a hostile environment.

Latimer takes us to task for dealing rather superficially with high level learning and other processes affecting salience. The criticism that we are more concerned with the how than the why is justifiable, although we would point out the statement in our introduction that our framework was intended to be an account of low level influences on saccade generation in a way which was upward-compatible rather than a full life-encompassing approach. Latimer uses the fall off in visual acuity away from the fovea to argue for a dissociation between covert and overt attention. Interestingly, one of us has argued elsewhere (Findlay & Gilchrist 1998) that the fall off in visual acuity is consistent with the primary of the overt over the covert attentional system.

R9. Attention

We anticipated that our treatment of attention would be contentious and a number of commentators have homed in on just this point. We wish to reiterate two reasons why we wish to avoid attentional terminology. First we feel that certain implicit assumptions are likely to arise from the use of attentional terminology in explanations. We argued against the disengage-move-engage view of attention, which we believe is misconceived and arises from a plausible but mistaken use of the spotlight metaphor. With the possible exception of **Fischer,** no commentator has objected to this rejection of an influential viewpoint (**Radach** welcomes its rejection). It is likewise very easy to make the implicit assumption that attention is a limited resource. Our second reason for avoiding attentional terminology is that it is also easy to allow an homunculus to slip in through the back door (**Latimer**'s "temptation to believe that gaze is self-directed") and we feel that the view that covert attention selects a target for the saccadic movement does not always avoid this danger. We realise that in some ways, we are here dealing with an issue of terminology only. We discuss the role of executive control in a subsequent section and the spatial selection window of our model operates in many ways like an attentional spotlight.

An example of the difficulties raised by reliance on attentional terminology is illustrated by one point made by **Fischer,** who revisits the finding by Mayfrank et al. (1986) that attention allocated to a peripheral target suppresses express saccades. This finding contrasts with other work (Walker et al. 1995) showing that attentional instructions do not increase or substantially decrease saccade latencies in the attended direction (but do considerably increase those in the nonattended direction) and also the work described in the commentary by **Dorris & Munoz** concerning target predictability. This raises an immediate question of what "attention" meant in Mayfrank's experiment and the conflict of findings is indeed puzzling if attention is regarded strictly in a spotlight manner. However, in terms of our model, we are quite ready to believe that giving a certain type of instruction to attend to a peripheral location will have a dual effect, leading both to increased fixate centre activity as well as to a spotlight-like change in the spatial selection window.

Pollatsek & Rayner accept the general outlines of our model and indicate that it provides a parsimonious account of a considerable amount of data. Their classic work on the perceptual span raises the key issue about attention. Material in the visual periphery around the forthcoming destination of a saccade target is more effectively processed than at other locations. We have no quarrel with this important finding. Perceptual selection and oculomotor selection accompany one another. Attentional explanations generally treat perceptual selection as the primary phenomenon, in part because the dominant tradition in vision is to emphasize the passive, image processing, nature of the process. More recently an alternative "active vision" approach has gained ground in which a more piecemeal approach to visual processing is emphasized rather than perceptual selection per se. One critical area is visual search, where recent work (Belky & Motter 1998; Findlay & Gilchrist 1998; Motter & Belky 1998) has queried the need to invoke covert attentional scanning.

Kramer et al. report a set of intriguing new studies and argue that they show a need for covert attention to be incorporated into the picture. In their first experiment, a novel target appeared at the same time as a colour change cue indicated the target to be fixated. As we would predict from the privileged access at level 3 from target onsets, this target often captured the forthcoming saccade. They argue that the failure to find saccades to an "average" location invalidates the concept of a single salience map. Two comments must be made about this finding. First, the angular separation of target and distractor is about at the limit of the relatively narrow sector of the visual field where averaging occurs (Ottes et al. 1985; Walker et al. 1997), and in the plot shown in Figure 2 of Theeuwes et al. (1998), some saccades do apparently show a small effect of averaging. The second problem is that, as shown in Findlay (1997) and also apparent in Figure 3 of Theeuwes et al. (1998), endpoints of saccades to a colour singleton target are rather widely scattered (possibly because the pop-out resulting from a colour singleton relates to a difference signal between the singleton and its neighbours). Assuming that this reflects a broad peak in the salience map, such a peak would be less effective in promoting averaging. The occurrence of a short latency subsequent movement is discussed in section R5.

In the second experiment, it was demonstrated that the occurrence of this novel stimulus augmented processing of a subsequent letter form (a potential physiological correlate is reported by **Thompson & Bichot**). **Kramer et al.** argue that this shows a rapid covert attentional scan. When we rejected covert attention scanning in section 4.6, we had in mind scanning endogeneously. Although our general approach is to avoid attentional terminology, the ingenious results of Kramer et al. lead us to accept that if peripheral cueing is to be interpreted attentionally, then an exogeneously driven attention "scan" may occur during a fixation.

Crundall & Underwood apparently welcome our standpoint on attention, and raise some thought-provoking further points. They draw an interesting parallel with the attentional theory of Logan (1996) which is based on distributed spatial representations of visual target. Indeed Logan's "reduced threshold" would appear to have considerable operational similarity to our spatial selection process. Crundall & Underwood argue that our suggestion of learned salience effects results in a paradoxical loop whereby stimuli in peripheral vision may have modified salience weighting before identification. However as they themselves go on to point out, this is only a problem if identification is treated as an all or none process. Undoubtedly some stimulus properties can be identified in peripheral vision. The final important suggestion in their commentary concerns whether decline in activity in the fixate centre should be viewed in energetic or informational terms. In our formulation, based on results such as those of the gap experiment, we emphasised a fixation centre affected by stimulus physical properties. We also emphasise that our model can be implemented in the actual nervous system, and thus such an interpretation seemed most appropriate. Nevertheless we are intrigued by the suggestion here which also occurs in other commentaries and will be discussed more fully in section R13 on reading.

R10. Executive level and the frontal lobe

A number of commentators have highlighted the need for "executive" high level control processes in saccade generation (**Quaia & Optican, Gooding, Crawford et al.**) and some have attempted to attribute these to specific brain regions (Gooding, Crawford et al.). It is fair to say that the higher-level control of saccade generation is less well understood in terms of process and underlying neuroanatomy than is the case for reflexive saccades. Our attempts to draw parallels between known physiological findings is greatest at the lower levels 2 and 3, and decreases as one moves up to levels 4 and 5. However, having tried to avoid incorporating at attentional homunculus, we are somewhat cautious in adding an extra level of "executive" control which is open to many of the same criticisms (Rabbit 1997). **Crundall & Underwood** want the effects of learning to be incorporated to account for effects such as the greater salience of incongruent stimuli that may be quickly fixated.

Although we would rather rely on the low-level visual explanation of such effects (Henderson & Hollingworth 1998) we do not accept that our model relies as heavily on bottom-up processing as suggested. In section 4.5, we discuss processes of competitive interaction operating in the search selection process, which may incorporate factors such as learning. In the following section 4.6 on "covert attention," we note similarities with a model proposed by Henderson which relies on weighting stimulus locations to bias search selection (Logan's variable thresholds provide a plausible alternative to weighting). The notion that attention is the mechanism that sets the level of thresholds has little additional explanatory power and raises the question, What mechanism controls the high-level controller?

Gooding discusses the increase in pro-saccade errors made by schizophrenic patients on the anti-saccade task in terms of so-called "executive functions" of the dorsolateral prefrontal cortex (DLPFC). Such "executive processes" are thought to include components such as "inhibition," "planning," "monitoring," and "control" required in various high-level cognitive processes such as working memory (Baddeley 1992). Some of the evidence implicating a role of executive processes in the production of anti-saccade errors was discussed in section 4.2.1. It was noted that the process of "goal redefinition" proposed by Hallett may share some functional similarity with processes involved in tasks of spatial working memory (suppressing a prepotent response, manipulating target position, maintaining a goal on-line). Whilst accepting that the frontal lobe is implicated in increased anti-saccade error rates and also working memory we are cautious in attributing these specifically to the DLPFC. A recent review of the anti-saccade literature found that a wide range of cortical and subcortical brain regions have been implicated in functional imaging studies (Everling & Fischer 1998). In addition, in a recent case study by one of us, a profound anti-saccade and working memory deficit was found following damage largely restricted to ventrolateral prefrontal cortex, VLPFC (Walker et al. 1998).

The increase in anti-saccade error rates in schizophrenic patients has been attributed to a "central executive" deficit (**Gooding, Crawford et al.**). The term executive function is, however, poorly defined and the tests designed to examine executive function have been criticised as having low test-retest reliability and validity. Furthermore, the executive processes under investigation appear to be no more than a further description of the task demands (Rabbitt 1997). The incorporation of a "central executive" may contribute little additional explanatory power to our framework. A degree of caution is also required in the interpretation of increased pro-saccade errors in some neurological and psychiatric populations. Everling and Fischer (1998) found that although many studies of schizophrenics have reported increased numbers of pro-saccades, this is not found in all patients. They also questioned the interpretation of high error rates in this patient group and concluded that "based on these few controversial studies, it is hard to decide whether schizophrenic patients really have a general deficit to inhibit reflexive saccades to distracting stimuli" (p. 893). They emphasised that the "dual-task" demands of target transformation could be a factor involved in error rates.

Crawford et al. specifically suggest that the mental representation of the target may be associated with an abnormally high level of activation in the WHERE system of schizophrenics that leads to increased saccadic distractibility. This is at odds with our proposal that only activity in the nonspatial channel can directly influence saccade triggering, and in the absence of empirical evidence for such over activity there is no obvious reason why it should be accepted. Crawford et al. also report that the secondary corrective saccades of schizophrenics have short latency. Similar observations have been made in normal subjects in the anti-saccade (Hallett 1978) and double step paradigms (Becker & Jürgens 1979) – see section R5 on programming two saccades.

R11. Neurological and psychiatric conditions

We are pleased to see that some commentators appear to have found the framework useful in accounting for abnormal saccades following a wide range of different pathologies. Although we limited our account to cases of unilateral neglect following parietal lobe damage, some commentators have described abnormal saccades in cases of other disorders in both man and monkey that they would like to see integrated into the framework. This is a challenging problem, but we were pleased to find that the framework has provoked this level of analysis.

In this context, we would note that "unilateral neglect" is a heterogeneous disorder and multiple patterns of behavioural dissociations have been observed. Neglect can arise following damage to a range of different brain damage including the posterior parietal lobe and also regions of the frontal cortex, but it has also been observed following damage to subcortical structures such as the thalamus. The manifestations of neglect are different in cases with parietal and frontal damage (**Heide et al.**; see also Husain & Kennard 1997). Furthermore, neglect is difficult to induce in monkey, although the less severe deficit of "extinction" can be produced. In man, neglect is most typically seen following damage to the right hemisphere producing left neglect. Cases of right neglect following left hemisphere damage are rare and less severe, which further highlights the increased functional specialisation in man. Our account of saccade deficits in neglect can be criticised for not having accounted for these lateralisation effects and functional specialisation.

R12. Consequences of brain damage

The account of the saccadic deficits observed in patients with unilateral parietal damage was based on the idea of separate spatial channels for L and R saccades and the assumption that unilateral brain damage produces permanent underactivation of the (level 3) automatic ipsilesional peripheral detection system. This underactivation leads to a permanent underactivation of the salience map involved in encoding contralesional saccades. Thus, contralesional stimuli will produce low levels of activation within the salience map and would not de-activate the fixate system. We proposed that this underactivation can account for the increase in latency and hypometricity of contralesional saccades and the absence of an influence of contralesional distractors on the latency of ipsilesional saccades (see: **Fanini & Marzi**).

Fanini & Marzi describe interesting results from a study of patients with unilateral lesions and extinction who made unwanted saccades during a manual reaction time task. First, it is interesting to note that the ability to inhibit saccades under these conditions has been attributed to damage to the medial and ventrolateral frontal cortex (Paus et al. 1991) and so it would be interesting to know if these subjects had damage that included the frontal lobe. Unlike our neglect patients their extinction patients made equal numbers of left and right saccades with stimuli presented unilaterally (amplitude of contralesional saccades not mentioned). In common with our own findings, the latency of contralesional saccades was greater than that of ipsilesional saccades and there was no increase in ipsilesional saccade latency under bilateral target conditions. An intriguing observation was that the extinction patients made less unwanted reflexive saccades under bilateral stimulus conditions. This decrease in unwanted ipsilesional saccades is suggestive of some degree of an inhibitory influence exerted by contralesional visual stimuli possibly on the fixate system. If this was indeed the explanation, it is puzzling why there was no effect of the bilateral stimuli on saccade latency. In normal subjects the magnitude of the latency increase expected under these conditions is in the region of 15–20 msec and it is possible that such small effects may be swamped if the variability of latency is large for "unwanted" saccades under these conditions. It may be instructive to see if latency effects are observed when extinction patients are instructed to make saccades under distractor conditions.

Guillaume et al. demonstrated saccade deficits in the cat following unilateral inactivation of the caudal cerebellar fastigial nucleus (cFN) with similarities to those observed in cases of neglect. In this context it should be noted that the cFN, like the posterior parietal cortex, is thought to control saccades via efferent projections, including the deep layers of the superior colliculus (SC). Although Guillaume et al. accept our account of the latency increase in neglect patients, they note that the decrease in amplitude is difficult to explain without positing a change of location of activity in the salience map. One possibility is that in neglect patients these severely hypometric long latency saccades are not target elicited but reflect an impaired attempt to implicate a voluntary search strategy for a contralesional stimulus (Walker & Findlay 1996). Guillaume et al. also report an interesting relationship between hypometria and latency, which was taken as evidence for interactions between the WHERE and WHEN systems. We have not found a similar relationship in our parietal patients, however, and any contralesional saccades which are made were typically <2 deg in amplitude and showed little or no correspondence with target eccentricity. The cerebellum is typically thought to be unnecessary for the production of visually guided saccades, as latency and dynamics of saccades are often not influenced by cerebellar lesions. The specific contribution of the cerebellum is thought to be one of modulation of amplitude based on an internal estimate of current eye position (Keller 1989) and a degree of caution needs to be exercised before the present model is revised to account for this effect.

Chou & Schiller present a compelling argument that extinction may reflect a delay in the time required to convert contralesional stimuli into a motor output. In their study, extinction was produced by a unilateral lesion in the region of the frontal eye fields in monkeys (note damage to this region does not induce neglect/extinction in man; Rivaud et al. 1994). Following the frontal eye field (FEF) lesion, a saccade direction response bias was observed that depended on the stimulus onset between the onset of stimuli to the left or right of fixation (note, it would be of interest to know the effects on saccade latency and if they showed a similar shift so that the maximal inhibitory effect was not shown for simultaneous onsets). Specifically, the monkeys made contralesional saccades under conditions in which the contralesional stimulus was presented at long intervals before the ipsilesional one. This result is interpreted as reflecting a delay in the transformation of contralesional events into saccades. However, the temporal delay explanation may not provide a parsimonious explanation of the saccade deficits observed in human subjects with neglect and extinction. First, it is not clear why neglect patients do not make contralesional saccades to unilateral contralesional stimuli when the stimulus is presented for over a second (it is difficult to interpret long latency saccades as they could reflect poor fixation or a search strategy). Second, it is not clear how a temporal processing delay alone can account for the severe hypometricity of contralesional saccades. We agree, however, that such temporal delays may be a factor involved and note with interest that a similar finding has been made in human patients with extinction (Rorden et al. 1997).

Heide et al. illustrate the dissociation in saccade deficits in patients with parietal and frontal lesions. Contralesional "reflexive" saccades made by patients with parietal lesions were impaired, while those made by patients with FEF lesions were normal. Frontal neglect was observed, however, when the patients viewed visual scenes whereby they failed to explore the contralesional side of space and had increased fixations. Although Heide et al. state that the parietal patients performed the task "almost normally," it should be noted that other studies have demonstrated abnormal contralesional scene scanning in parietal patients (Karnath 1994; Walker et al. 1996). Although we are willing to take these findings as further support for our inclusion of separate channels for internally-triggered and visually triggered saccades, we are less convinced that these can be mapped directly onto the FEFs and parietal lobe respectively. As the frontal eye fields receive projections from the posterior parietal cortex (amongst other areas) there may be a downstream influence of parietal damage on FEF activity. Furthermore, Heide et al.'s proposal that the FEFs control the "intention to explore space," appears to overlap the view that the posterior parietal lobe encodes the intention to make a movement (Snyder et al., 1997). Thus, we are reluctant to assign these functions to either the FEFs or parietal lobe alone.

R13. Reading

Our article did not have as its primary purpose to address saccade control in reading, and discussion was restricted to a short part of section 4.5.1. However, we have been interested to receive so many commentaries from workers in this flourishing area. Characteristically, these commentaries focus on the issue of high-level versus low-level control and in the introduction we pointed out that it was a misinterpretation to treat our model as exclusively one of low level control. We shall start by discussing whether the area of reading might indeed require a radically different treatment, follow this with a review of individual commentaries and finally make some tentative steps towards a synthesis.

A problem in assessing whether our model will extend to reading is the fact that much work in reading places heavy emphasis on analysis at the word level. For example, **Radach** starts his commentary with the claim that every saccade is directed towards a target object, rather than a region. Similarly **Pollatsek & Rayner**'s E-Z computational model is mainly concerned with this level of analysis. Whilst trivially true that gaze cannot land on more than one object, it cannot assumed a priori that this object level representation is involved in the saccade programming and certainly, in reading, saccades do on occasion land in the blank spaces between words. Since word boundaries have no specific status in our salience map (although they will of course constitute one of various parallel inputs into the map), it is not always easy to compare our approach with those that start with the problem of selection of a target word.

Pollatsek & Rayner raise the possibility that saccade control in reading requires different considerations from those that apply in other areas but rapidly argue against such proliferation. We would also hope that a general model could encompass both the processing of symbolic material in reading and more naturalistic visual material. However caution may be in order. The crucial question seems to be how the process of lexical access, which as **Doré-Mazars** points out is highly automatized in adult readers, can generate signals that influence the oculomotor system. One possibility is that lexical access is no different from other forms of visual recognition, but an alternative is that each time lexical access occurs, some additional signal ensues, perhaps relating to the formation of a serial linguistic representation. This second suggestion is implicit in some theories about the process, for example, the suggestions by **Vitu** discussed below. Speculations on the neurophysiological correlates of lexical access are unlikely to be directly testable for many years to come, but no alternative to excitatory and inhibitory patterning of neural activity is yet forthcoming as the way in which all information is represented in the brain.

Radach refers to the important result of Rayner et al. (1996) showing that an upcoming word is slightly but consistently more likely to be skipped if it is a high-frequency, common word (see also Gautier et al. 1998). Radach, in discussing his "indirect influences," makes a plausible and useful elaboration of the way in which implicit learning and memory might operate at level 4. Radach argues that our routes for top-down influences on the target selection process cannot account for this finding. This is certainly true with his restricted view of the intrinsic salience route (visual salience through atypicality), but if, as we suggested, learning and automaticity can modify the salience weightings, the results could be accommodated. This is of course at the expense of rendering our account much more complex and less predictive.

Vitu makes several interesting and welcome suggestions about how high level processes might contribute to the salience map in the same manner as the processes we have labelled search and spatial selection. We are puzzled though by the detailed suggestion that an unidentified word provides an inhibitory influence over other target words. An unidentified word in the fovea should provide an inhibitory influence on the fixate system (cf. the suggestion by **Crundall & Underwood**) but in contrast, it would be desirable for an *identified* word to exert an inhibitory influence on the salience map. The suggestion that this interplay of activity might remove the need for a spatial selection process during reading is interesting but not totally convincing. There are additional unidentified words in the line below that currently fixated, which without some further influence would form equally good saccade targets. Finally, intra-word regressions raise some interesting questions. Vitu uses their properties to argue that saccade direction might be computed separately from saccade amplitude. We are loath to accept this radical change to our modelling philosophy and refer to the suggestion of **Beauvillain** that they are examples of a double saccade program (see earlier section).

R14. Conclusions

Our original aim in the target article was to provide a framework that we believed adequately accounted for results from experiments looking at saccadic responses to simple target configurations, and which we hoped might also be a useful general approach to saccade control when considering the viewing of complex material. Surprisingly few commentators have raised problems with the work on simple target configurations. In contrast, many commentators have concentrated on the role of higher level processes and offered suggestions for revised and alternative approaches. In this area, we concur with **Frens et al.**'s hope that refinement of the framework, which in a number of instances has been forthcoming from the commentaries, will lead to an integrative view of the saccadic system.

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

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