orbitofrontal cortex. These same structures are also central to Adolphs' (2001) neurobiology of social cognition and Schore's (1997; 2000; 2001) and Davidson et al.'s (2000) circuits of emotion regulation. In two recent books (Schore 2003a; 2003b), I have documented a growing body of research on the experience-dependent maturation of these three limbic structures over early stages of development, which ontogenetically evolve in a subcortical to cortical sequence over discrete critical periods of postnatal brain development. These studies demonstrate that increasingly complex emotional communications embedded in attachment experiences imprint a fixed ontogenetic sequence of early maturing amygdala, then ventral anterior cingulate, and finally orbitofrontal levels of the limbic system (Helmeke et al. 2001; Nair et al. 2001; Neddens et al. 2001; Poeggel et al. 2003; Ziabreva et al. 2003). The organization and increasing interconnectivity of these limbic structures over the stages of postnatal development (the first 2 years in humans) allows for the appearance of more complex systems for appraising emotional value and regulating psychobiological states.

Lewis's fertile model brings the following questions to mind. Could this developmental information about the sequential-stage, experience-dependent maturation of a three-tiered limbic system offer clues about the sequence of psychoneurobiological operations of the trigger phase, self-amplification phase, and self-stabilization phases of self-organizing emotional appraisals in the adult human brain? Could these three amygdala, cingulate, and orbitofrontal limbic levels produce separate subcortical-cortical implicit appraisals (and visceral responses), and would their vertical integration across multiple levels of the vertical limbic neuraxis be involved in what Lewis calls "emergent wholes"? Could "flows of activation" among these subcortical and cortical systems be linking energetic (excitatory and inhibitory synaptic) pathways that are originally sequentially imprinted in critical periods of development of these corticolimbic structures? Would these patterns of energy flow follow the rostral-to-caudal development of expanded arousal-energy systems in the maturing brain? Could each component level process a trigger, self-amplification, and self-stabilization phase, with information reciprocally moving bottom-up and top-down between and within levels of the neuraxis, with such synchronized dynamic adjustments allowing for what Lewis calls "an ongoing state of engagement with the world." Does this mechanism describe Lewis's "vertical integration," and could this more complex interconnectivity of higher and lower components of the limbic system optimally adapt on a moment-to-moment basis to a rapidly changing environment?

Although Lewis makes an important contribution emphasizing lower subcortical mechanisms that regulate the arousal (and energy metabolism) of the higher cortex, I suggest the current appraisal literature has largely overlooked a key contributor to bottom-up emotion processes, the energy-expending sympathetic and energy-conserving parasympathetic components of the autonomic nervous system, and thereby the body. In other words, vertical circuits also include "limbic-autonomic circuits" (Schore 2001). Craig (2002) provides evidence that the right orbitofrontal cortex, the hierarchical apex of the right limbic system, processes information from the ANS and generates the most complex subjective evaluation of interoceptive state, the highest representation of the sense of the physiological condition of the body. This line of research suggests that the higher corticolimbic centers appraise not just exteroceptive information, but also interoceptive information that is critical to adaptive function (see Schore 2003a; 2003b). Furthermore, studies indicate that this same right frontal area is dominant for the appraisal of biologically meaningful exteroceptive and interoceptive self-related information in contexts of threat (Sullivan & Gratton 2002). These data clearly suggest that appraisal mechanisms need to be studied in more than the non-stressed or artificially stressed state, and in states of low and high arousal.

In the target article Lewis also offers some brief thoughts on the roles of the right and left hemispheres in appraisal processes. There is now compelling evidence that the right hemisphere develops in early infancy, before the left, and that the rapid emotional communications and appraisals embedded in attachment transactions imprint the right limbic system (Schore 2003b). I agree with Lewis's conclusion that right hemisphere processing of somatic-affective information precedes left hemisphere semantic processing. In recent work (Schore 2003a; 2003b) I suggest this may reflect early implicit appraisals of the ventral processing stream dominant in the right hemisphere, antecedent to the explicit appraisals of the dorsal stream dominant in the left. This left lateralized (dorsolateral prefrontal cortex) processed explicit information may then be callosally fed back to right orbitofrontal implicit systems. The right orbitofrontal cortex, centrally involved in affect regulation, may then top-down relay this information to lower levels of the right limbic-autonomic neuraxis to cingulate and amygdalar limbic structures and to monoaminergic arousal and hypothalamic motivational centers, which in turn alter CNS arousal and ANS autonomic arousal. This bottom-up adjusted arousal state and somatic-affective information can then be fed back up the neuraxis, altering higher cortical processing. Resonance between the higher and lower levels of the right brain may then allow it to self-organize to an optimal level of complexity and act as "an emergent whole." The right brain has been suggested to be dominant for the ability to maintain a coherent, continuous, and unified sense of self (Devinsky 2000; Schore 1994).

The dynamic systems perspective of emotional processes presented by Lewis also suggests that longitudinal studies of a single system dynamically moving through state spaces may be of more value than averaging group measures. This experimental approach may offer a deeper understanding of emotion psychopathogenesis. Self-organization concepts can also be applied to the field of emotion communication and brain-to-brain intersubjectivity. This integration can lead to an emotion theory that can shift between a one-person and a two-person psychology.

The importance of inhibition in dynamical systems models of emotion and neurobiology

Julian F. Thayer[a] and Richard D. Lane[b]

[a]*National Institute on Aging, Intramural Research Program, Gerontology Research Center, Baltimore, MD 21224;* [b]*Department of Psychiatry, University of Arizona, Tucson, AZ 85724-5002.* **jt182f@nih.gov**
lane@email.arizona.edu

Abstract: Lewis makes a compelling case for a dynamical systems approach to emotion and neurobiology. These models involve both excitatory and inhibitory processes. It appears that a critical role for inhibitory processes is implied but not emphasized in Lewis's model. We suggest that a greater understanding of inhibitory processes both at the psychological and neurobiological levels might further enhance Lewis's model.

Lewis has made a very important contribution by arguing that antecedent and consequent processes are one and the same. For too long appraisal processes and cognitive consequences of emotional arousal have been considered separate academic domains. It is refreshing to reevaluate this long-held assumption in light of modern neurobiology and to consider the implications of this insight for future research. Lewis's framework also incorporates individual differences within a single model that addresses antecedent and consequent processes. This unifying vision has great potential for expanding our understanding of emotional processes.

A major conclusion of this target article is that traditional distinctions between cognition and emotion break down and no longer appear valid when one considers the neural substrates and the dynamic interactions of the processes in question. This was in fact the fundamental thesis of the volume *Cognitive Neuroscience of Emotion* (Lane & Nadel 2000). It is refreshing to see this fundamental thesis, which breaks from centuries of academic tradition, taken seriously.

In our neurovisceral integration model we too have proposed dynamical systems as a unifying framework in which the boundaries between emotion and cognition are brought down (Thayer & Lane 2000). Lewis certainly has incorporated many aspects of our model into his work. Thus, our models share many similarities including the integration of emotion theory with neurobiology, and the use of a dynamical systems framework. However, there are some important differences as well. One important difference is our emphasis on the role of inhibitory processes. Whereas we share the idea that emotions may be viewed as attractors or points of stability in an emotional state-space, we argue that inhibitory neural processes are critical for the phase transitions that allow a system to move adaptively from one attractor or emotion to another in the state-space. In fact, we would propose that inhibitory processes are crucial for all of the phases that Lewis states make up an emotional interpretation. As noted above, inhibitory processes are associated with phase transitions and are therefore involved in Lewis's trigger phase. We have noted previously that what Lewis calls the self-amplification phase is a result of disinhibition, that is, a release or sensitization of excitatory processes as a result of decreased inhibition. Lewis clearly notes the importance of inhibition for his self-stabilization phase and we have noted elsewhere the importance of inhibition for learning (Thayer & Friedman 2002). Therefore, to complete the connection between emotion theory and neurobiology we feel that an understanding of the role of inhibitory processes is essential. Inhibitory processes provide for the sculpting of neural action at all levels of the neuraxis. The features that make inhibitory processes critical have been progressively explored in neurobiology.

Constantinidis et al. (2002) have recently detailed the role of inhibition in the temporal flow of information in the prefrontal cortex. Using simultaneous single cell recordings in monkeys, they demonstrated inhibitory interactions between neurons active at different time points during the course of a complex working memory task. They noted that the influence of inhibition was particularly evident at transition points in the action sequence, thus supporting the idea that inhibitory neurons are critical for behavioral state changes. Similarly, it has recently been demonstrated in humans that enhancement of GABA-related inhibition may be a very efficient mechanism for synchronizing larger neuronal populations (Fingelkurts et al. 2004). These findings and others (Waldvogel et al. 2000) suggest that a little inhibition at the right time can have a large influence on the behavior of the organism, highlighting the nonlinear nature of the inhibitory control.

At the psychological level, we have also argued for the importance of inhibitory processes. We have noted that perseverative behavior, including worry and rumination, may represent the breakdown of inhibitory processes (Thayer & Lane 2002). Again, neurobiology supports such an idea. For example, in a murine model of anxiety, decreased GABAA-receptor clustering was associated with harm-avoidance behavior and an explicit memory bias for threat cues (Crestani et al. 1999). Mice with reduced GABAA-receptor clustering showed enhanced reactivity to threat stimuli (an effect that was reversed by diazepam), a facilitation of trace conditioning in a fear conditioning paradigm, and a deficit in ambiguous cue discrimination. These findings are remarkably similar to the HR acceleration to and explicit memory bias for threat words, and failure to habituate to neutral words, found in generalized anxiety disorder patients in a conditioning paradigm (Friedman et al. 2000; Thayer et al. 2000).

It should also be noted that whereas GABA is usually an inhibitory neurotransmitter and Lewis states that "GABA is always inhibitory" (sect. 5.2, para. 2), GABA like many neurotransmitters is functionally complex and hence can have excitatory actions (Köhling 2002). Therefore, recognition of the complexity of the neurobiology is also needed and is in fact called for in dynamical systems models.

Taken together, however, it appears that an understanding of the role of inhibition is critical if one is to fully integrate emotion theory, or behavior in general, with neurobiology. In the end we feel that Lewis has made an important contribution by outlining this general framework. It will definitely serve as a catalyst for additional theoretical and empirical work.

Mechanisms of the occasional self

Don M. Tucker

Electrical Geodesics, Inc., Eugene, OR 97405. **dtucker@egi.com**
www.egi.com

Abstract: Considered in relation to the component brain systems of appraisal-emotion interactions, dynamical systems theory blurs the divisions that seem obvious in a psychological analysis, such as between arousal, emotion, and appraisal. At the same time, the component brain mechanisms can themselves be seen to be incomplete as units of analysis, making sense only in the context of the whole organism.

In a time when powerful new methodologies are applied to studying human brain activity, the growing evidence base calls for more complex theoretical models. It is time to begin training theoreticians, generalists who forego methodological or empirical specialization to acquire the scholarship, intellectual discipline, and conceptual flexibility necessary for understanding both psychological and neural mechanisms. In this target article, Lewis explores the form that a comprehensive theoretical analysis might take when it is applied to cognition-emotion interactions in the brain.

Perhaps the major point of the article is that the evidence points to complexity in causal relations among the psychological functions of emotion and cognition, and a corresponding complexity in the causal relations among the brain mechanisms underlying those functions. Dynamic systems theory provides metaphors for complex cybernetics, including positive and negative feedback, self-stabilization, and emergent properties. Perhaps more important is that, through Haken's (1977) insights, this line of reasoning shows that the causality in part-whole relations is not always best understood through reductionism, toward mechanistic parts from superordinate wholes. Rather, the functional role that a mechanism plays within an integrated system becomes the embedding context that is also a kind of explanation. Certainly there are proximal causes that can only be understood as originating from the body's physico-chemical substrate. Yet, in a systems explanation, this functional role of a mechanism's operation is as important an explanation as the more elementary physiological and physicochemical processes from which it emerges. In the psychological analysis of appraisal and emotion, Lewis provides important examples of the causal complexity that makes one-sided accounts (emphasizing linear cognitive or emotive causality) unsatisfying.

In the application to neural systems, the theoretical analysis faces a more daunting challenge. The brain systems currently understood to be integral to motivation, emotion, and cognition are not only complex but multiple. With patient scholarship, Lewis surveys the relevant landscape of brainstem, diencephalic, striatal, and corticolimbic circuits, and even here the review is illustrative rather than comprehensive. Nonetheless, it soon becomes apparent that, in every circuit or system surveyed, we find no separation, causal or otherwise, between emotional and motivational functions and cognitive functions. Apparently, psychological function and physiological function are not aligned in any simple harmony, at least not in the way we approach them in psychological theory. The conclusion, then, must be unsettling for psychologists. Whereas the separation of emotion and cognition seems to be obvious to a functional analysis, the complexity of interactions among multiple systems, for arousal, for specific action tendencies, or for more general attentional and memory biases, leads to great difficulty in saying what is cognition and how it differs from emotion. Is this what we expect from a theoretical analysis of complexity,