

that we begin to lose the meaning of the functional questions that seemed so clear in the beginning?

Maybe it is. Maybe it could even become a necessary step toward sophistication in neuropsychological theory.

More than the loss of familiar functional distinctions, neurophysiology shows us the scope of constituent mechanisms. Lewis's review of neural circuits and processes leads us to confront a scope of phenomena – arousal, drives, memory organization, attentional control – that is much broader than the mental functions that were considered relevant in psychological appraisal theory. Even in his selective illustration of the brain's control systems, each system seems to cross multiple functional levels, leading to the remarkable conclusion that functions such as motives or emotions that we would isolate so clearly in a psychological analysis turn out to be embedded within a larger neurophysiological landscape.

What if we take this embeddedness of mechanisms back to the psychological theory? We would have to conclude that our isolation of emotions as separable functions, or of cognitions as distinct causal entities, may be psychological fictions – fictions that may be useful for academic psychological theory, but are of limited use for a neuropsychological theory that attempts to span both brain and mind of actual people. Rather, we need to fit any mechanism within the appropriate part-whole relations, where the organism-in-environment is the context, the whole that explains the mechanisms. Neither cognitions nor emotions are discrete causal agents that can be separated from the whole of the biological context. This context is formed both by the immediate physiological exigencies, such as environmental threats or visceral need states, and by the enduring residuals of the person's developmental history. In neural terms, the whole of the organism's cognitive-emotive matrix is achieved by vertical integration of multiple systems of the neuraxis. In psychological terms, the embedding whole represents the superordinate construct of the personality, the self.

On the other hand, when we instantiate an organismic construct, like the self, within neurophysiological terms, this construct becomes more tentative than when expressed only in psychological terms. Both cognitive and emotional components of the self are dependent upon their constituent physico-chemical substrates. As a result, the self cannot be assumed as an organizing principle for all mental or neural processes. Rather, it forms a context for only those processes that operate when the constituent self mechanisms are activated. Again, the discipline of thinking in both psychological and neurophysiological terms raises new challenges for the theorist. Not only does it complicate familiar functional distinctions, but it makes clear that dynamical psychophysiological systems are indeed dynamic, such that the embedding context of the ongoing self is an occasional state, emerging only to the extent that the constituent mechanisms are recreated in the continual flux of psychophysiological processes.

Dynamic brain systems in quest for emotional homeostasis

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Abstract: Lewis proposes a solution for bridging the gap between cognitive-psychological and neurobiological theories of emotion in terms of dynamic systems modeling. However, an important brain network is absent in his account: the neuroendocrine system. In this commentary, the dynamic features of the cross-talk between the hypothalamic-pituitary-adrenal (HPA) and gonadal (HPG) axes are discussed within a triple-balance model of emotion.

Lewis's dynamic systems approach on the interaction between brain, emotion, and cognition provides a timely contribution to

heuristic reasoning in the field of affective neuroscience. However, his notion that psychologists and biologists cannot communicate on the issue of emotion misses ground. Admittedly, theories are still in their infancy but the first steps towards psychobiological theories of emotion have been set (e.g., Damasio 1998; Davidson 2003a; Panksepp 1998a).

This commentary mainly concentrates on a pivotal emotional network underexposed in Lewis's framework: the endocrine system. Attention is given in particular to the dynamic cross-talk between the hypothalamic-pituitary-adrenal (HPA) and the hypothalamic-pituitary-gonadal (HPG) axes (Viau 2002) and the antagonistic effects of their end-products, cortisol and testosterone, on motivation and emotion (e.g., Van Honk et al. 2003; 2004). Our discussion is framed in a triple balance model (TBM) of emotion, a heuristic which suggests that reverberating neurodynamic affective maps, created on different anatomical levels of the brain, depend in their continuous quest for emotional homeostasis on the fine-tuned action of the steroids cortisol and testosterone (Van Honk & Schutter, in press).

Emotional homeostasis is crucial for survival and a prerequisite for balanced reactions to reward and punishment (Ressler 2004). This homeostasis depends on (1) *Subcortical balance*: The primordial responses of reward and punishment are approach or withdrawal, and in simple animals they are classically illustrated by fight or flight, which is initiated in subcortical affective circuits and controlled by endocrine-autonomic nervous system interactions (Decatanzaro 1999). Millions of years of evolution have sculptured these primordial flight or fight machines into primates with highly complex social emotional brains. (2) *Cortical balance*: In humans, approach and withdrawal provided the rudimentary building blocks for the development of the emotions anger and anxiety. These occur in the behavioral hiatus when actions are delayed and provide for more flexible behavioral tendencies in which the neocortex is heavily implicated. In particular, the left and right prefrontal cortices are subsequently involved in these sophisticated forms of behavioral approach and withdrawal (Davidson 2003a). (3) *Subcortical-cortical balance*: Finally, to secure complete homeostatic emotion regulation, this layered subcortical-cortical system necessarily needed integration, therefore the expansion of the neocortex was accompanied by the emergence of one of evolution's finest yet most vulnerable adaptations, a loosely-coupled brain communication pathway (MacLean 1990). This TBM of emotion is an evolutionary inspired psychobiological heuristic that not only aims to scrutinize the neurobiological mechanisms behind adaptive homeostasis in human social-emotional functioning, but also sets out to predict the maladaptive, pathological consequences of particular imbalances in emotion (Van Honk & Schutter, in press). A crucial hypothesis in the model is that the end-products of the HPA and the HPG axes, the steroid hormones cortisol and testosterone, are pivotally involved in homeostatic emotion regulation through their *antagonistic* action on the balance between the sensitivity for punishment and reward.

This antagonism begins with the mutually inhibitory functional connection between the HPA and HPG axes (Viau 2002). Cortisol suppresses the activity of the HPG axis at all its levels, diminishes the production of testosterone, and inhibits the action of testosterone at the target tissues (Johnson et al, 1992). Testosterone in turn inhibits the stress-induced activation of the HPA axis at the level of both the hypothalamus and the pituitary gland (Viau 2002). The same steroids are also suggested to act by binding to amygdaloid-centered steroid-responsive neuronal networks (Wood 1996) where they regulate and facilitate neuropeptide gene-expression, which changes the likelihood of approach (testosterone) or withdrawal (cortisol) when confronted with particular emotional stimuli (Schulkin 2003).

The antagonistic involvement of cortisol and testosterone in the sensitivity for punishment and reward can be traced on the three balances of our psychobiological model of emotion. (1) *Subcortically*, animal evidence demonstrates that at the amygdala, cortisol-

facilitated CRH-gene expression versus testosterone-potentiated amygdalar vasopressin gene-expression results in the expected reversed shift in the balance between the sensitivity for punishment and reward (DeVries et al. 1995; Schulkin 2003). Concurring antagonistic effects of cortisol and testosterone have been observed in humans during implicit or unconscious measures of approach and withdrawal-related emotions that predominantly depend on subcortical processing (Van Honk et al. 1998; 1999; 2003; 2004). (2) Although the steroids primarily target subcortical affective regions, there is evidence for a relationship between cortisol and dominant right-sided *cortical* asymmetry in young children and nonhuman primates, which accompanies punishment-sensitive characteristics of behavioral inhibition (Buss et al. 2003; Kalin et al. 1998). Contrariwise, recently we found that testosterone administration induces reward-associated left prefrontal cortex activation during the display of erotic movies (unpublished observation). (3) Our *subcortical-cortical* evidence builds on a theory wherein the phylogenetically different brain systems relate to the subcortically generated delta (1–3 Hz) and cortically generated beta (13–30 Hz) oscillations in the electroencephalogram (EEG). Relative increases or decreases in subcortical-cortical cross-talk are computed by correlating the change in power between these bands, and it has repeatedly been demonstrated that elevated subcortical-cortical cross-talk as indexed by EEG is accompanied by elevated punishment sensitivity (Knyazev & Slobodskaya 2003; Knyazev et al. 2004). On the endocrinological level, increased levels of cortisol have been associated with enhanced punishment relative to reward sensitivity and are evidently accompanied by increased subcortical-cortical cross-talk (Schutter & Van Honk 2005). In an opposite fashion, reductions in subcortical-cortical cross-talk after administration of testosterone have been observed in healthy volunteers (Schutter & Van Honk 2004). This *decoupling* of subcortical and cortical processing is argued to indicate a shift in motivational balance from punishment towards reward sensitivity (Schutter & Van Honk 2004).

In sum, an increasing body of evidence suggests that the steroid hormones cortisol and testosterone are antagonistically involved in the modulation of emotional homeostasis on the different phylogenetic levels of the brain. Importantly, this emotional homeostasis is not only subcortically controlled by bottom-up inter- and intra-axes negative feedback mechanisms, but also cortically through top-down psychological regulatory processes (Mazur & Booth 1998). This dynamic steroid hormone regulation of social emotional behavior provides a bridging principle between the psychological and biological domains, and might well prove to be an important neurobiological mechanism in motivation and emotion.

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A dynamic duo: Emotion and development

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Abstract: A dynamic systems (DS) approach uncovers important connections between emotion and neurophysiology. It is critical, however, to include a developmental perspective. Strides in the understanding of emotional development, as well as the present use of DS in developmental science, add significantly to the study of emotion. Examples include stranger fear during infancy, intermodal perception of emotion, and development of individual emotional systems.

Lewis presents a dynamic systems approach to emotion with an emphasis on self-organization of small neurological units and

larger social wholes. As is typical of self-organizing systems, he proposes that large complex emotion systems arise from oscillating interactions among smaller and often simpler forms that may have emotional potential. We also have argued that the study of emotion must not veer into a barren, reductionist landscape in which a set of boxes fixed in a linearly organized fashion sit waiting to be opened. We wish only to add some examples from our work that expand Lewis's call and also reintroduce the critical need to include development in any study of emotion, and especially in a dynamic systems (DS) approach to emotion (see also Lewis 2000b). Some of the most outstanding research on emotion is developmental (Izard et al. 1995; Malatesta & Izard 1984; Nwokah and Fogel 1993; Witherington et al. 2001), as is some of the best work using DS principles (Magai & Haviland-Jones 2002; Thelen & Smith 1994). This is no accident: During particular age periods of rapid change (e.g., infancy), one can observe the coaction of a number of systems in real time within a reasonable research time frame. However, across a life span the DS principles are applicable.

A decade ago, we proposed a multicomponent systems approach for understanding the origins and development of emotion (Haviland & Walker-Andrews 1992). Our primary focus was on the socialization of emotion, and our primary example was the emergence of fear of strangers. We argued that stranger fear was not an additive growth function built with "more" cognition, but, in DS terminology, a phase. Further, stranger fear is expressed (or not) due to a number of initial conditions, including the typical infant-caregiver communication patterns that have emerged over time. Since that first article we have added other examples that could both benefit from a DS perspective and contribute support to DS principles.

One example arises from research on infants and their self-organizing patterns of emotion perception. The environment is replete with multimodal and co-occurring information for objects, events, and personal experience. An observer moving through the world sees occluding surfaces, hears transient sounds, may touch rigid objects, and smell and taste various substances concurrently. Information for emotion is available multimodally as well. An angry person may scowl, raise his voice, gesture abruptly, and tense his muscles. The perception of the emotional expression is not merely the sum of each of these components. Rather, the observer perceives a unified multimodal pattern that has unique communicative affordances. Moreover, the presence of multimodal information may facilitate the perception of an event (Bahrick & Lickliter 2000; Walker-Andrews & Lennon 1991). The detection of meaning in an expression develops as the observer's perceptual skills develop, as she gains experience, as she becomes more familiar with a particular person and eliciting situations. Consequently, an adult may recognize that someone is angry by observing gestures alone or attending to the situation, but the young infant appears to need the redundant, extended information. Similarly, the experience of emotion is multifaceted, including kinesthetic, somatosensory, and other modality-specific information. According to Stern (1985), such experience may provide for infants a feeling of *deja vue* that allows the infant to develop a sense of self as an extended emotional agent. The perception of multimodal information for emotions of the self and of others is an example of how "individual elements or groups of elements lose their independence and become embedded in a larger regime" (sect. 3.2.3 of the target article).

In a second example, fractal patterns have emerged in studies of life-span emotional development (Magai & Haviland-Jones 2002). The social-cognitive emotion system at a point in time shows features of fractal geometry or self-similarity of emotion pattern replicated at lower and higher orders of magnification. Individuals reproduce their unique emotion organizations psychologically. Without examining long-term development of individual change, as is required by DS, such fractal structures would not become apparent. Once established, the fractal patterns tend to organize new sensory information to form a "growing" system that