



Self-organizing individual differences in brain development

Marc D. Lewis

University of Toronto, 252 Bloor St. West, Toronto, Ont., Canada M5S 1V6

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Abstract

Brain development is self-organizing in that the unique structure of each brain evolves in unpredictable ways through recursive modifications of synaptic networks. In this article, I review mechanisms of neural change in real time and over development, and I argue that change at each of these time scales embodies principles of self-organizing systems. I demonstrate how corticolimbic configurations that emerge within occasions lay down synaptic structure across occasions, giving rise to individual trajectories that become entrenched with age. Emotions have a powerful influence on this process. This is because the neural processes mediating emotion consolidate patterns of activation across the brain, through their enhancement of inter-regional coordination in real time and their contribution to synaptic shaping over development. The loss of corticolimbic plasticity with age is an unfortunate fact of development, but it is compensated in part by transitional phases and individual learning experiences through which habits are modified or replaced. I emphasize variations in inter-systemic coupling as a key mediator of developing individual differences, and I discuss the acquisition of anxious/depressive appraisals as an example.

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Brain development has come to be conceptualized by many investigators as a process of self-organization. This view is based on a number of features: feedback between neural regions promoting long-term coupling and synchronization (Edelman, 1987), func-

E-mail address: mlewis@oise.utoronto.ca.

tional selection of cells or synapses through competition and elimination (Changeux & Dehaene, 1989), interplay between growth and elimination in the sculpting of cortical tissue (Greenough & Black, 1992), the convergence of structure from initial plasticity through corticolimbic resonance (Tucker, 1992), and recursive cycles of cortical coherence corresponding with developmental stages (Thatcher, 1998). Some of these processes and phenomena have been studied through sophisticated modeling techniques. These include neural network models that demonstrate the development of concepts over repeated trials (e.g. Elman et al., 1996). Some of these models specifically highlight mechanisms of feedback, synchronized oscillations, and other neurally inspired concepts (e.g. Grossberg & Somers, 1991). Other network-type models informed by neural plausibility are predicated on emergent cognitive phenomena such as conceptual coherence (Thagard & Verbeurgt, 1998). Some theorists conceptualize neural development in terms of constructivist ideas that cross the line, either implicitly or explicitly, into fundamental precepts of self-organizing systems. For example, Johnson (2000) identifies broad structural constraints in cortical tissue as the basis for progressive specification of structure through interactive processes. Still others integrate constructs from cognitive science and philosophy with critical mechanisms of biology and/or evolution to specify a role for self-organization in the neural basis of cognition (Thompson & Varela, 2001; Varela, Thompson, & Rosch, 1991). Finally, a few neuroscientists integrate the basic language of dynamic systems theory with detailed research on brain activity (Bressler & Kelso, 2001; Freeman, 1995).

These theorists have made immense contributions to our understanding of mechanisms of neural function and neural development at a variety of scales and across a wide spectrum of neural entities from synapses to macroscopic systems. Yet, few of them speak to issues of direct relevance to developmental psychologists, and none focus primarily on individual differences in development. Neuroscientists and those in related disciplines are most concerned with modeling basic mechanisms of coordination among multiple units, the biological or computational properties of the units themselves, and the general principles by which brains and artificial networks learn and evolve. In keeping with this focus, their interest in development is mostly restricted to normative processes, shared by all humans and often by nonhuman animals as well. The present article is intended for developmental psychologists, particularly those interested in social, emotional, and personality development. Moreover, it attempts to explain the vast proliferation of individual traits, capacities, styles, and even pathologies that characterize the socioemotional domain. Developmental trajectories have been modeled as self-organizing processes for nearly 20 years (e.g. Fogel, 1993; Keating, 1990; Lewis, 1995; Magai & Haviland-Jones, 2002; Thelen, 1990). It seems important to integrate this perspective with current knowledge about the brain, to specify a realistic biological foundation for detailed modeling of developmental processes.

In the following sections, I look at data on brain function and brain development acquired from neurobiological research, and integrate and interpret these data in relation to principles and mechanisms of self-organization, broadly conceived. In doing so, I pay particular attention to the role of emotion in organizing activity patterns spanning multiple neural systems, both within occasions and over development. Neural substrates of emotion can be seen to influence structural changes underlying all domains of development. However, the study of social and personality development demonstrates their power most clearly.

Principles of developmental self-organization for neuroscience

Self-organizing processes—or, more broadly, the activities of any complex adaptive system—become easier to conceptualize once we sort them out into “micro” and “macro” time scales. Thelen and Ulrich (1991) provided an important heuristic for this kind of analysis by demonstrating how real-time processes such as infant stepping fit developmental trajectories such as learning to walk. Thelen and colleagues went on to show that behavior converged to attractors in real time while development could be described as the formation and disappearance of those very attractors (Thelen & Smith, 1994). A number of theorists discuss reciprocal influences between microscopic and macroscopic time scales. Specifically, real-time processes give rise to developmental trajectories, and developmental trajectories constrain the activities of a system in real time. How does this work? In the first case, real-time activities converge to a particular pattern that *lays down traces* that facilitate the emergence of the same pattern in the future. To lay down traces is to permanently alter the structure of the system. For example, streams of rainwater that self-organize during each thunderstorm create trenches through one’s flowerbed over weeks and months. In the second case, developmental structuration—that is, the consolidation of structure over development—alters the elements in a system and their relation to each other. These alterations determine the system’s propensities—what it can and cannot do, and what it *tends* to do, on each occasion. In dynamic systems terms, we can say that developmental structure determines the *state space* of possibilities in the moment—in real time. The contours of the flowerbed, sculpted over many thunderstorms, constrain the movement of rainwater as it begins to flow and pool during each storm.

Brain activities can also be divided into time scales. In real time (milliseconds, seconds) the firing patterns of diverse neuronal assemblies become synchronized, cell groups transmit information to each other, and the activities of the brain literally cohere as a particular cognitive or behavioral act emerges from multiple possibilities (e.g., Lutz, Lachaux, Martinerie, & Varela, 2002; Thompson & Varela, 2001). In thermodynamic terms, real-time self-organization couples the metabolic activities of many component neurons, maximizing the flowthrough of energy in a far-from-equilibrium system (Prigogine & Stengers, 1984). I have modeled real-time neural self-organization in detail elsewhere (Lewis, 2005). But how should we characterize neural self-organization at the developmental scale? Like other developmental processes, brain development constitutes the increasing specification of structure, permitting activities that are more organized, more efficient, and more complex. For this process to be described as self-organizing in a strong sense (unlike, say, the development of one’s nose), neural development must achieve forms that were initially indeterminate, based on the (real-time) activities of the brain itself. There are parts of the brain that change little from infancy to old age. However, the cerebral cortex changes massively: the cortex is continually reorganized through the activities of daily living (Nelson, 2000), and the laying down of cortical structure is highly individualistic rather than prespecified (Johnson, 1998). Developmental change in the cortex constitutes a literal reorganization of the connections (or synapses) between neurons, and these connections evolve and stabilize based on the activities of the neurons themselves. Hence, cortical development truly is self-organizing, and the massive changes that take place in the cortex alter activity and structure across all other brain regions that interact with it. In this sense, the entire brain self-organizes with development.

There are several other principles of developmental self-organization that can be applied to the brain. First, the formation of structure through self-organization means that systems *lose degrees of freedom* as they develop. This concept can appear difficult, but it is really very simple. When you move into a new house and look at the empty living room, you can imagine many ways for that room to take shape. Once the movers have put down the furniture, there are fewer possible rooms that can be imagined. Then, when the sofa is placed against a particular wall, there are fewer still; and finally when the carpet is laid down and the book shelf put up, there may be only one configuration that “works,” despite ongoing minor variations. All developmental processes work this way. A 4-year old child has not yet developed a learning style, but that same child at 14 has already crystallized habits for attending, learning, and remembering. Personality development epitomizes the loss of degrees of freedom with development. Parents cannot predict what their child will be like as an adult. But meet an adult friend after several years and she will be much as you remembered her in college. The degrees of freedom in her personality development have been mostly used up. Note that this does not imply a loss of flexibility in real time! There are many ways to play a baseball game, but the rules of the game change little from season to season. In the cortex and limbic system, the stabilization of developmental structure is achieved through synaptic sculpting. As will be detailed later, synaptic structure is self-perpetuating and hence increasingly determinate (as opposed to indeterminate). Moreover, synaptic *pruning* consolidates developmental stability, by getting rid of the vast, proliferate web of under-used fibers that provided all those degrees of freedom in the first place. By getting rid of what is not being used, pruning stamps a special kind of permanence on the synapses that remain.

A related principle is what I call *cascading constraints* (Lewis, 1997). The emergence of a structure (e.g., a schema, skill, or belief) at any point in a developmental sequence constrains the characteristics of the structure to emerge next, and so on. Learning habits that emerge in elementary school constrain the academic functioning of the child in high school, and study habits in high school constrain ambitions and accomplishments in university. Putting the sofa against one wall constrains the available locations for the bookshelf. The idea of cascading constraints helps make sense of developmental trajectories. Structures appearing early in development limit the possible features of later structures, then development selects from among those features, further narrowing the path of possibilities. Cascading constraints are ubiquitous in brain development. For example, prolonged stress in infancy leads to excessive glucocorticoid activity, resulting in synaptic reduction and even cell death in the hippocampus and other structures. The resulting decrements in self-regulation, memory, positive mood, and other functions can never be completely undone, but they can be partly ameliorated by maternal nurturing in a subsequent phase of development (Heim & Nemeroff, 2001; see Nelson, 2000, for a review). These cascading constraints, self-organizing in their own right, constitute a set of markers along the route of a developmental trajectory, and each plays its part in fashioning and refining that trajectory.

A final principle is that of developmental transitions. Developmentalists with a dynamic systems orientation have shown that transitions are periods of increased fluctuation or instability (Ruhland & van Geert, 1998; van Geert and Steenbeek, this volume; van der Maas & Molenaar, 1992). Behaviors become unmoored from their entrenched habits, a variety of new forms proliferate for a while (temporarily *increasing* degrees of freedom *developmentally*), then some subset of those forms stabilizes, providing new

habits for the next stage of development. An example is the proliferation of sentence types shown by toddlers when they first learn to talk at about 18–24 months of age. Following that period, speech settles down to more predictable forms, based on the dominant linguistic environment. Developmental transitions are explained as reorganizations of the structure of the system, and this is nowhere clearer than in brain development. As detailed later, a developmental transition may take the form of a wave of synaptogenesis followed by a wave of pruning. However, pruning itself can reorganize the brain, by forcing it to utilize more efficient routing for its synaptic traffic. The increased variability in thought and behavior in early adolescence has been associated with massive pruning at this age.

In this section, I have outlined principles of self-organization that can be applied to any domain of development and demonstrated their instantiation in neural development, at least with broad brush strokes. However, to appreciate individual differences in neural development in finer grain, it is first necessary to describe how the brain works in real time. The following section provides an account of brain function that is consistent with a dynamic systems view, whereby configurations of neural coherence self-organize rapidly, in the moment, with each cognitive or behavioral act. Following Freeman and Tucker, I will suggest that emotion is a critical arbiter of neural self-organization in real time, and hence the forge for neural change and stabilization over development.

Brain function in real time

The brain is the ultimate self-organizing system. In the cerebral cortex alone, approximately 20 billion cells, each with thousands of connections, provide a massive population of interacting units in a state of continuous flux. Despite its potential for immense noise, chaos, or disorder, this system converges rapidly to highly ordered, synchronous states (e.g. Thompson & Varela, 2001). Each of those states taps enormous cooperativity across the elements in this system. In fact, this cooperativity can take the form of literal *phase synchrony*, whereby the waveform of voltage fluctuations in one part of the brain is locked in step with the waveform produced by another part of the brain. Corresponding with neural self-organization, but at a different level of description, the components of cognition and attention can be said to converge and form into coherent thoughts and plans. The various sensory, motor, and executive systems become linked, working memory becomes engaged, actions are selected and refined, and so forth. Some scientists have studied the parallels between neural coherence and cognitive coherence (e.g. Engel, Fries, & Singer, 2001; Skarda & Freeman, 1987; Thompson & Varela, 2001), and most studies of neural coherence indeed focus on phase synchrony in the cerebral cortex (usually at the frequency range of gamma oscillations). However, as neuroscientists become increasingly interested in emotion, they have begun to examine coherence or synchrony across subcortical as well as cortical systems (e.g. Kocsis & Vertes, 1994; Paré, Collins, & Pelletier, 2002). They have discovered evidence for spontaneous coupling or synchrony (at the theta frequency range) across brainstem, hypothalamic, limbic, and paralimbic systems when animals are motivationally engaged (see Lewis, 2005, for a review & synthesis). Thus, we can assume that neural self-organization in real time is embodied by phase synchrony across multiple systems, providing a mode of communication by which diverse brain regions can couple together to form a coherent whole.

To think about neural synchronization across multiple subsystems, and to establish its importance for emotion as well as cognition, I will review the functional anatomy (with some major pieces missing) of each of the hierarchical levels of the neuroaxis. A more complete analysis would include bodily processes as well, though these go beyond the scope of the present article. We can roughly divide the brain into four levels, each more advanced and appearing later in evolution than the previous one. Fig. 1 provides a sketch of the hierarchical arrangement of these levels. Fig. 2 provides anatomical detail for many of the systems included.

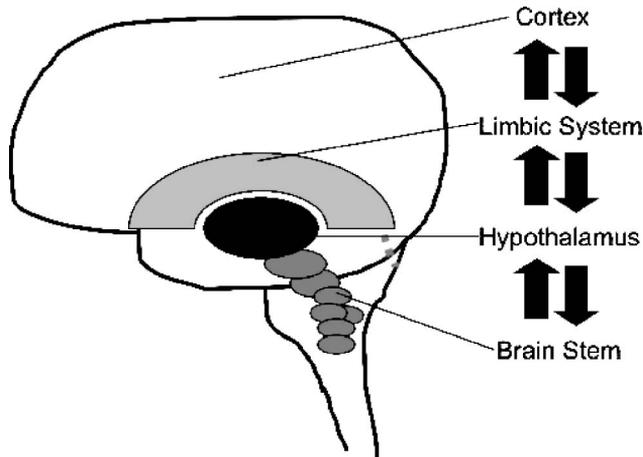


Fig. 1. Vertical integration across four levels of the neuroaxis. This sketch highlights the bidirectional flow of information that integrates functioning over the entire brain.

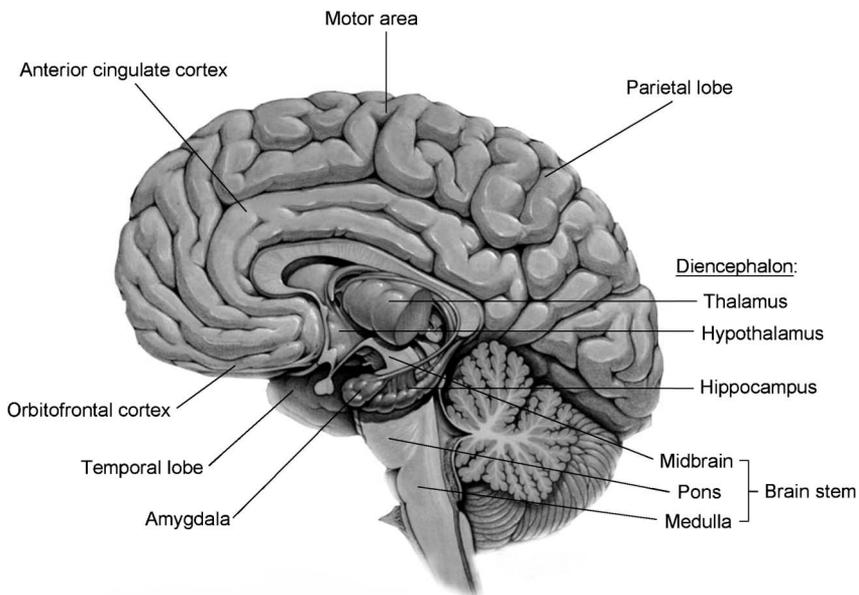


Fig. 2. Some of the major anatomical structures of the human brain (Lewis, 2005; used by permission).

1. *The brain stem.* The shaft of nerve tissue at the core of the brain (divided into midbrain, pons, medulla) contains sets of nuclei for programmed responses to internal and external events. These nuclei control relatively primitive, packaged response patterns (e.g., defensive and attack behavior, vigilance, feeding, freezing, sexual behaviour, facial expressions), each highly independent and stimulus-bound, and many of which go back to our reptilian ancestors. Brainstem systems orchestrate emotional behavior even in the absence of higher brain systems. For example, animals without a forebrain display “sham rage”, which has the behavioral appearance of rage. Panksepp (1998) argues that there is nothing “sham” about this rage: it exemplifies a basic emotion system functioning without cortical inhibition. He emphasizes that partially independent brainstem (and striatal) circuits can be identified for anger, fear/anxiety, love/attachment, interest/excitement, sadness, joy, and sexual desire—hence the brain stem is the seat of many basic emotions, and the behavioral propensities it orchestrates may be considered the *action tendencies* discussed by emotion theorists (e.g. Frijda, 1986). Critically, the brain stem and nearby structures also produce a variety of neuromodulators (e.g., dopamine, norepinephrine) that modulate activity in the cortex and virtually all other brain systems. Many of these chemicals also affect bodily systems, such that bodily responses are prepared to correspond with brain changes.
2. *The hypothalamus.* In higher animals, the actions of many brainstem systems are coordinated by or synchronized with activity in the hypothalamus, which sits just above them. The hypothalamus controls the internal milieu, including the organs and vascular systems, partly through its output to the autonomic nervous system via direct axonal pathways and partly through the release of hormones into the blood. It also receives information from these systems in return, thus functioning as a central regulator of bodily responses to relevant environmental events. At the same time, the hypothalamus complements the neurochemical output of the brain stem. It produces neuropeptides that set body and brain systems into coherent goal-directed states, such as territorial aggression, scavenging for food, courting and mating, and so forth. Each neuropeptide has parallel effects on body and brain. For example, the endogenous opiates inhibit various physiological processes to protect the animal from physical stress while providing analgesia and soothing through their actions in paralimbic areas (areas at the interface between the cortex and limbic system). Neuropeptide-induced states are organized at a higher level than the more elementary and diffuse modes elicited by brainstem neuromodulators. Moreover, the extended release of neuropeptides and the comprehensive action orientations they effect may help maintain lasting emotional states or moods (Panksepp, 1998; Potegal, Hebert, DeCoster, & Meyerhoff, 1996).
3. *The limbic system.* This is a rough semicircle of structures that grew out of the diencephalon and evolved profoundly in mammals. These structures mediate learning and memory, whereas lower structures control perception and action according to fixed “programs” that required no learning. This is a critical distinction, especially when it comes to development. Limbic and higher structures may be considered “open” in that they change with development on the basis of experience, whereas lower structures are considered “closed” because they change little or not at all (Panksepp, 1998). The progression from sensory input to motor output is slowed down in the limbic system, so that responses can be fit more precisely to the learned aspects of situations (Tucker, Derryberry, & Luu, 2000). According to Tucker and colleagues, this slowdown corresponded with the evolutionary advent of emotions, whose motivational force works by

maintaining the focus of attention and action rather than by *rapidly instigating* some “fixed action pattern.” Indeed, the limbic system mediates emotional states that orient attention and action to whatever is presently meaningful. The amygdala, a key limbic structure, tags neutral stimuli with emotional content (LeDoux, 1995; Rolls, 1999), thereby creating chains of associations based on emotional experiences. Connections from the amygdala to lower (hypothalamic and brainstem) structures activate motivational response systems given current stimulus events, and connections from the amygdala up to the cortex entrain perception and attention to these events. While the amygdala mediates emotional memory, the hippocampus organizes episodic memory and allows for the monitoring of one’s movements through space and time. The hippocampus interacts with the prefrontal cortex (possibly through the mediation of the cingulate cortex—Barbas, 2000) to allow volitional cognitive activities to recruit specific memories in the service of planning and strategizing. The amygdala and hippocampus appear to function in synchrony, such that emotional associations pull for explicit memories as animals pursue plans to achieve their goals.

4. *The cerebral cortex.* The layers of the cortex surround the limbic system, and the recently evolved cells that inhabit these layers are the locus of what we normally call cognition, perception, and attention. In the cortex, the time between stimulus and response appears to be greatly stretched out (Tucker et al., 2000). Inputs from the world and potential actions connect with each other through a matrix of associations, comparisons, synthesis across modalities, planning, reflection, and sometimes, but not always, conscious control. These operations take time, and emotions maintain a coherent orientation to the world during that period of time. For example, deliberate action is guided by attention to alternative plans, and anticipatory attention is constrained by emotions concerning the pursuit of particular goals. Thus, cortically mediated actions are functional, not only at the level of some phylogenetically ancient blueprint, but also at the level of a continuously refined model of the world, achieved by selecting, comparing, and pursuing particular plans while integrating the information fed back by the world. The cortex is also a key system for the cognitive control of emotional responses—often referred to as “emotion regulation.” In particular, the prefrontal regions execute sophisticated perceptual and cognitive activities (including attention, monitoring, decision-making, planning, and working memory) that are recruited by (and that regulate) the emotional responses mediated by the amygdala and lower structures (Barbas, 1995; Bechara, Damasio, & Damasio, 2000; Davidson & Irwin, 1999).

There are two cortical systems that are especially important for integrating the cognitive and emotional aspects of psychological functioning: the anterior cingulate cortex (ACC) and the orbitofrontal cortex (OFC). Both regions serve as interfaces between the prefrontal cortex and limbic system. They are therefore called “paralimbic,” and they appear to mediate cognitive activities relevant to emotional states (Barbas, 2000; Rolls, 1999). As shown in Fig. 2, the ACC is located on the medial surfaces of the PFC. ACC activation has been associated with monitoring and evaluating potential actions, monitoring and resolving conflicts, and selective attention more generally (Carter et al., 2000; Gehring, Goss, Coles, Meyer, & Donchin, 1993; van Veen, Cohen, Botvinick, Stenger, & Carter, 2001). The executive system mediated by the dorsal ACC is characterized by voluntary choice and is central for directed attention and for learning (Frith, Friston, Liddle, & Frackowiak, 1991; van Veen et al., 2001). However, the more ventral regions of this complex system have been

closely linked with emotional processing. The OFC, on the ventral surface of the PFC (see Fig. 2), appears to encode and hold attention to threatening or rewarding aspects of the environment (Rolls, 1999). Such processes are thought to extend or build onto the more basic conditioning functions of the amygdala (Cardinal, Parkinson, Hall, & Everitt, 2002). The OFC is responsive to changes in the hedonic valence of anticipated events (Hikosaka & Watanabe, 2000; Rolls, 1999), and it is activated when “implicit appraisals” of motivationally relevant situations are held in mind (Schore, 1994). Its downstream connections to the amygdala, hypothalamus, and brain stem are also integral to emotion, and its activity has frequently been implicated in the activation and regulation of emotional states (Davidson, Putnam, & Larson, 2000; Hariri, Mattay, Tessitore, Fera, & Weinberger, 2003; Lévesque et al., 2003).

Mechanisms of neural change in real time

How do these neural structures interact with each other as the brain goes about its business in real time? The hierarchy of brain levels is often construed in terms of domination or control of lower levels by higher levels. Indeed, the cerebral cortex subordinates the more primitive functions of the limbic system, which subordinates functions in the brain stem. However, as emphasized by Tucker et al. (2000), the downward flow of control and modulation is reciprocated by an upward flow of synaptic activation and neurochemical stimulation (see Fig. 1). The brain stem and hypothalamus entrain limbic structures by means of neuromodulators and neuropeptides, locking in perceptual biases and associations, and they also recruit cortical activities to ancient mammalian and even reptilian agendas. Primitive agendas and requirements thus flow up the neuroaxis from its most primitive roots at the same time as executive attention, planning, and knowledge subordinate each lower level by the activities of the cortex. If not for the bottom-up flow, the brain would have no energy and no direction for its activities. If not for the top-down flow, recently evolved mechanisms for perception, action, and thought would have no control over bodily states and behaviour. It is the reciprocity of these upward and downward flows that links sophisticated cognitive processes with basic motivational mechanisms in a rapid process of synchronization called “vertical integration” (Tucker et al., 2000). Vertical integration is hypothesized to occur whenever a significant change in internal or external events triggers an emotion and thus demands the initiation of a cognitive or motor response. Moreover, as noted earlier, this convergent activity may be mediated by phase synchrony (e.g., in the theta band), as diverse systems begin to resonate with each other at the same or related frequencies, thus maximizing their communication.

The principle of vertical integration helps explain how multiple neural structures become coordinated in a coherent configuration—a unified whole—in a matter of moments. This is the essence of real-time self-organization. But it is important to briefly describe the connections between neural structures that make this possible. Two kinds of connections can be distinguished: the flow of information from one neuron to the next through normal synaptic processes, and the action of neuromodulators and neuropeptides that enhance or inhibit these events.

Synaptic communication takes place between neurons at all levels of the nervous system. Axons from a sender neuron release “intrinsic” neurotransmitters (primarily glutamate and GABA) that cross the synapse and either increase or decrease the voltage of the receptor neuron. This change in voltage increases or decreases that neuron’s tendency to

fire. Excitatory neurons increase the firing tendency (which translates to the firing rate) of the receptor neuron, while inhibitory neurons decrease it. These influences are always juxtaposed with the influences of many other neurons, such that the impact of one neuron on another is relatively small. However, neurons belong to populations that work together, and the compilation of excitatory or inhibitory signals from populations of neurons have a powerful impact on the firing rate of receptor neurons. Thus, firing rates of neuronal populations influence the firing rates of neurons downstream from them, which influence the firing rates of neurons further downstream, and so on, in a synaptic chain, and such changes in firing rates are the fundamental currency of neuronal communication. In addition, the tendency for neurons to fall into phase synchrony with each other allows their influences to compile more efficiently, and that is why phase synchrony constitutes a basic mode for neuronal coherence and self-organization.

The kind of neurotransmitter that supports normal synaptic transmission is manufactured in each neuron and functions locally at nearby synapses. However, neurotransmitters and neuropeptides manufactured in the brain stem and hypothalamus are released in larger volumes, at many synapses simultaneously, far from their sites of origin. These neurochemicals, which I will lump together under the term “neuromodulators,” travel to sites all over the brain, including all limbic, striatal, and cortical areas (Fuster, 1996; Izquierdo, 1997). There they alter the influence of one neuron on the next, modulating firing rates upward or downward. Thus, the effects of a small number of cells in the brain stem and hypothalamus radiate outward to many synaptic sites, producing a one-to-many effect—a fountain of modulation. These effects are global rather than local, and they provide a key mechanism by which motivational concerns influence cognitive and perceptual processes. For example, acetylcholine has often been linked to motivational enhancement of attention through the activation of cortical neurons (Gu, 2002). Dopamine activates approach and exploratory behavior through its effects on synapses in the orbitofrontal cortex and striatum (e.g. Depue & Collins, 1999). Opiates have multiple effects on different brain regions, but their overall impact is to make the animal less responsive to dangers in the environment. Critically, these neuromodulatory effects are often triggered by emotional associations or perceptions mediated by limbic and paralimbic structures. For example, amygdala responses mediating emotional associations send activation down “descending” pathways to brainstem and hypothalamic centers, which in turn produce their global effects through “ascending” fibers to these and other brain regions. In this way, emotions greatly affect information processing throughout the entire brain.

Finally, the flow of information among neuronal populations generally assumes the structure of feedback loops. Receptive populations of neurons send axons back to the neurons from which they receive information, both locally to their immediate neighbours and distally to structures far away across the brain. This design feature of neural tissue is critical because it promotes self-organization and vertical integration. Feedback circuits tend to amplify small changes in a self-enhancing manner, and then, as more elements are recruited to a particular pattern, to settle down into steady states of activation. Thus, messages from one neuronal population can recruit other assemblies to “join along,” eliciting massive change given small perturbations. However, once enough populations of neurons participate in the new pattern, they exert a stabilizing influence on each other, such that the whole pattern endures for a prolonged period of time. Critically, the amygdala and paralimbic cortex (ACC and OFC) are at the crossroads of all important synaptic traffic along the neuroaxis. And it is these systems, intimately involved in processing emotion, that gen-

erally trigger the fountain of neuromodulation originating from the brain stem and hypothalamus. As a result, emotional processes enhance and extend neural feedback. Specifically, incipient emotional responses are capable of promoting sudden changes in global neural patterning, causing a rapid switch in appraisals; emotional responses then lead to global stabilization, causing appraisals to become entrenched for seconds, minutes, or even hours. That is why emotions grab our attention, direct our thoughts and perceptions, and hold them in place until some activity (either physical or mental) intervenes and reduces emotional activation.

The role of emotion in neural self-organization thus functions as a double-edged sword. On one hand, *self-augmenting* feedback, orchestrated by limbic and paralimbic structures with the help of ascending neuromodulators, promotes synaptic activity *and hence initiates synaptic change*. In this respect, emotional processes yield novel synaptic configurations. On the other hand, *self-stabilizing* feedback, orchestrated by the same structures and neuromodulators, but lasting longer and recruiting additional subsystems, consolidates patterns of synaptic activity *and hence minimizes synaptic change*. In this respect, emotional processes are central to the maintenance of synaptic patterning. Thus, emotional processes cut both ways: they generate synaptic change and they maintain synaptic sameness. Earlier I suggested that developmental self-organization relies on four principles: progressive reorganization based on the system's own recursive activities, increasing self-specification and predictability (loss of degrees of freedom), cascading constraints that narrow the range of future options, and transitional phases. In the following sections I will show how the double-edged sword of synaptic change and stabilization serves each of these principles, thereby carving out individual trajectories of development.

Mechanisms of neural change in development

Some aspects of brain development are highly universal. For example, increased myelination and pruning of prefrontal cortex in early adolescence is thought to usher in the capacity for abstract thought. However, some aspects of brain development are highly individualistic. Even the localization of language varies among individuals, and functions such as emotion regulation show immense variety in regional activation even in young children (e.g., lateral asymmetries in prefrontal activation in response to emotion-eliciting events, Fox & Davidson, 1987, 1991). As discussed in more detail later, functional differentiation increases with development. A greater number of viable trajectories become possible and variability becomes increasingly conspicuous. What remains a mystery, however, is the growing inertia that each developmental path accumulates over time—the eerie manner in which developing humans become increasingly crystallized versions of themselves. Why does this occur? A “brain’s eye view” of development shows that change and consolidation of synaptic patterning is responsible for all psychological development—both the laying down of normative functions such as vision, object permanence, and theory of mind, *and* the laying down of individual pathways, for example the continuous branching of unique trajectories of personality development. Work by Johnson, Nelson, and their colleagues provides an excellent inroad to understanding the neural basis of normative development (e.g. Johnson, 2001; Nelson, 2000). In this article, I focus instead on the development of individual variations.

Synaptic elaboration (proliferation and strengthening) and synaptic pruning are the two forces that sculpt neural networks and thus shape development. These forces are deeply

complementary, because synaptic elaboration increases the use of some synapses over others while pruning gets rid of synapses that are under-used. In this section, I go on to describe these and related processes as instruments of self-organization, highlight their dependence on motivational mechanisms, and extend a model of normative cortical development to a discussion of emerging individual differences.

Earlier I reviewed the dynamic systems principle that the flow of activity among the elements of a system lays down traces, changing the structure of the elements and their connections, and thereby enhancing the probability that the same patterns of activity would recur on future occasions. Hebb (1949) applied a similar principle to explain brain plasticity and learning, whereby the co-activation of neurons produced structural changes at synapses between them, increasing their probability of becoming co-activated in the future. An important class of candidate mechanisms for this kind of learning includes long-term potentiation (LTP). In LTP, particular frequencies or durations of firing of the pre-synaptic neuron produce long-term chemical changes in the post-synaptic neuron, permanently altering the structure of the synapse to potentiate transmission in future. For this to occur, the post-synaptic neuron must be activated, glutamate from pre-synaptic terminals must travel to a specific class of receptors in the post-synaptic neuron, and then protein synthesis must take place for a period of time (up to hours). It is generally thought that these events must also take place across occasions for changes in synaptic structure to endure. As a result of these events, it takes less activation to produce the same response in the post-synaptic neuron on future occasions. Amazingly, such changes in synaptic sensitivity are the basis of all learning and development, both normatively and individually. But what is the role of emotion in this fundamental mechanism of change?

In fact, emotion and motivation figure strongly in LTP and related mechanisms, not only in “social” learning but in all learning. The state of excitability of the receptive neuron and the time course of its activation are crucial determinants of LTP. For many authors this implies that the neurochemical excitation that accompanies emotional states is essential for synaptic modifiability and learning (Freeman, 1995; Post et al., 1998; Tucker, 2001). Research demonstrates that neuromodulator arousal facilitates LTP (e.g. Centonze, Picconi, Gubellini, Bernardi, & Calabresi, 2001; Izquierdo, 1997; Izumi & Zorumski, 1999) and that neuropeptide action consolidates synaptic change and enhances memory formation (Adamec, Kent, Anisman, Shallow, & Merali, 1998; Flood, Baker, Hernandez, & Morley, 1990). The amygdala may be critical to memory consolidation in various systems, because of its facilitation of brainstem/hypothalamic neurochemical release (Packard & Cahill, 2001) and its direct projections to the hippocampus (Hamann, Ely, Grafton, & Kilts, 1999). Moreover, phase synchrony between the amygdala and hippocampus is thought to mediate emotional influences on memory formation and consolidation (Paré et al., 2002). ACC activation, which I have described as integrating cognitive and emotional aspects of attention, is thought to be critical for learning new contingencies (Cardinal et al., 2002; Gemba, Sasaki, & Brooks, 1986). These and related findings suggest that events that are not emotionally significant may not maintain arousal or attention long enough for learning to take place (cf. Gallagher & Holland, 1992; Lewis, 2005; Rolls & Treves, 1998). Finally, LTP has been observed in limbic, paralimbic, striatal, and cortical structures, but lower brain systems do not show plasticity of this kind. As a result, the information that consolidates through LTP must derive from the attentional and evaluative contents of the cortex and its limbic underpinnings, and these, as already discussed, are highly influenced by present emotional states.

But what exactly is self-organizing about synaptic shaping? The key point is that synapses are strengthened the more they are used, and they are more used the more they are strengthened. Moreover, emotional arousal functions as a catalyst for this cycle, enhancing *use* within occasions and hence *strengthening* across occasions. This fascinating mechanism constitutes a feedback cycle that works in developmental time rather than real time, or, more precisely, that links real time and development. Change initiates more change and in this sense is self-augmenting. This is how new habits get a leg up. (And note that even learning to count to ten is a new habit, fueled by emotional states of interest and excitement.) But as long as many of the same synaptic activities recur across occasions—as they must, given synaptic strengthening—change is self-stabilizing, which means that new habits quickly begin to gain inertia, and hence to win out over competing forms that are yet to come along. This is the double-edged sword of change and stabilization to which I referred earlier. And it is the means by which individual developmental paths self-organize—that is, differentiate in unpredictable ways, based on novel structure, and then consolidate, crystallizing that structure. More generally, the same double-edged sword cuts trenches in the flowerbed when it rains. Recursive activity creates new trenches, almost haphazardly, but then bestows on them the mantle of permanence just because they are there. Recursive modification is thus the “blind gardener” of diverging trajectories (a takeoff on Richard Dawkins’ “The Blind Watchmaker”). However, there is at least one important difference between brains and flowerbeds. Despite its increasing tendency to flow into established channels, the rainwater still has other options for its flow. In developing brains, pruning eventually gets rid of the other options, so the pathways that are strengthened and elaborated become the only game in town.

Pruning is also a mechanism of synaptic shaping—and thus developmental change—in and of itself. Pruning is often thought of as a complement of synaptic elaboration, because it does indeed get rid of under-used synapses, thus entrenching patterns created by synaptic elaboration. In this sense, pruning brings up the rear: synaptogenesis builds new roads through the jungle, synaptic strengthening (e.g., via LTP) paves them, making them more efficient, and pruning gets rid of the under-used dirt roads that have now become obsolete. However, synaptic pruning can work to sculpt neural circuits on its own. Selectionist theories (e.g., Changeux, Edelman) posit an initial repertoire of synaptic overproduction, or else continued overproduction, which is whittled down by experience or other factors to a greatly-reduced but much more efficient network of connections. Changeux and Dehaene (1989) propose a “Darwinian” model stipulating an endogenously determined overabundance of synapses, some of which regress and disappear whereas others endure and become stabilized (see Johnson, 1998, for a review). Thelen and Smith (1994) review this account in some detail because it so nicely matches their basic developmental tenet: that self-organizing processes in development rely on selection from initial variability. Less research is available on the specific mechanisms of pruning, and it is not known to what extent emotional processes contribute to pruning. However, there are several possibilities. First, some mechanisms of synaptic change diminish rather than potentiate synaptic transmission, including long-term depression (LTD). Like LTP, LTD is influenced by neuromodulation as well as by the frequency and duration of synaptic activity, and it is thus bound to be influenced by emotion. Second, Schore (2003a) has developed an elaborate model based on evidence that emotional stress dysregulates neural activity in infancy. By truncating prefrontal activation during social exchanges, excessive stress results in the shutdown of circuits for processing social information, leading to lifelong tendencies for

blunting socioemotional behavior and avoiding novelty (Schoore, 2003a). Pruning could be one contributor to this shutdown. Third, and conversely, we can infer that more normal levels of emotion contribute to pruning simply by strengthening synaptic pathways that end up *not* getting pruned.

One particularly influential account of developmental change (Greenough & Black, 1992) points to two different kinds of complementarity between elaboration and pruning, depending on whether the change is normative or driven by individual experiences. In the first case, *experience-expectant* change involves the overproduction of synapses in anticipation of a species-general class of experiences that are particularly important to “learn” at a certain stage of development. Leading up to this developmental window, the overproduction of synapses allows for maximal sensitivity to the impact of this class of experiences—for example the development of stereoscopic vision in the first few months of life and of speech perception in the second half of the first year. The formation of synaptic connections in a particular region of cortex encodes the most systematic or salient experiences within the new domain, and then pruning gets rid of the left-over synapses. With *experience-expectant* learning, synaptogenesis is prespecified, and experience—though of a particular sort—is responsible for selecting the connections that will remain for a lifetime. The other kind of relation between synaptic elaboration and pruning is called *experience-dependent*. In this case, synapses are formed in response to experience rather than in anticipation of experience. Synapses grow as needed to incorporate relations inherent in new experiences, gleaned from the environment, but potentially unique to the individual learner. This growth process is then followed by pruning which crystallizes the most relevant associations and gets rid of those which are extraneous or unreliable. As a result of *experience-dependent* synaptic change, developmental trajectories can be characterized as “a quiltwork of small blooms that may further regress on individual schedules” (Greenough & Black, 1992, p. 175). Note that *experience-expectant* change lends itself to a model of sensitive periods in neural development, whereas *experience-dependent* change is independent of any normative developmental timing.

The impact of motivational factors on both *experience-expectant* and *experience-dependent* synaptic change has not been systematically evaluated. However, it seems likely that *experience-expectant* changes are mediated by endogenous differences in neuromodulator systems that may be associated with temperament, and that *experience-dependent* changes make use of neuromodulator activity to promote and establish synaptic networks encoding experiences that are emotionally compelling (Collins & Depue, 1992). Collins and Depue model a sequence of synaptic shaping guided by individual differences in neuromodulator activity. First, a greater endogenous endowment of dopamine-producing cells augments synaptic shaping in cortical regions devoted to reward-seeking during sensitive periods (*experience-expectant* learning). The resultant greater connectivity in synaptic networks in these regions, for these individuals, would then enhance the capacity for (*experience-dependent*) learning about particular rewards, which would again rely on dopamine reception. In this scenario, primitive impulses to seek rewards create and elaborate a lattice of maximal specificity over several phases of development, demonstrating the intrinsic role of motivational processes in neural self-organization. For example, an energetic and sociable (and dopamine-rich) infant may not only become a language user earlier in development, but may also use his linguistic fluency to entertain and engage adults, thereby increasing opportunities for social rewards and social learning. Alternatively, dopamine-supported surgency during the “terrible twos” may facilitate skills for coercing others to

satisfy one's frustrated goals, leading to the consolidation of an assertive or aggressive personality style.

The notion of experience-expectant change implies normative periods of synaptic proliferation and synaptic pruning. These periods may serve not only as sensitive periods for normative acquisitions, but also as phases of pronounced plasticity in which developmental trajectories can be established or altered. For example, [Schore \(1994, 2003b\)](#) has written a great deal on the establishment of infant attachment patterns based on the plasticity of the right orbitofrontal cortex in the first year of life. Changes in grey-matter volumes are the principal means for studying normative trends in synaptic proliferation and pruning. Yet, age-related increases and decreases in grey-matter volumes vary tremendously across the cortex ([Gogtay et al., 2004](#)). For example, synaptic density in the visual cortex is at its peak toward the end of the first year and then begins to decline steadily toward adult levels. However, grey-matter volumes in some parts of the PFC (e.g., dorsolateral PFC) continue to increase up to pre-adolescence, with maximum thickness occurring around 11–12 years of age, followed by a decline that lasts into early adulthood ([Giedd et al., 1999](#)). Levels of glucose metabolism, which may also reflect synaptogenesis and pruning, rise and fall in frontal cortex on a roughly parallel timeline ([Chugani, 1994](#)). It thus appears that very rapid pruning in the PFC—up to 10,000 synapses per second ([Spear, 2000](#))!—finally overtakes synaptic elaboration by early adolescence. Indeed, the transition to adolescence has been described as a massive reorganization of PFC allowing increasing efficiency in the circuitry of decision-making, self-regulation, and abstract thinking ([Steinberg et al., in press](#)). However, this may also be a period in which individual differences in interpersonal capabilities, emotion regulation skills, and personality structure are at peak sensitivity and most vulnerable to environmental influence ([Granic & Patterson, in press](#)). The consolidation of these characteristics over the years of adolescence (the final phase of prefrontal pruning) may represent a loss of degrees of freedom in individual development that can never be regained.

Modeling the nature and timing of synaptic change is crucial for understanding developmental pattern formation. But it does not provide an overarching picture of neural self-organization. Such a picture may be glimpsed in [Johnson's \(1999, 2000\)](#) “interactive specialization” approach. This model explains the development of cortical organization on the basis of interconnections within and among cortical regions. The first claim is that the specialization of cortical regions (e.g., areas of the fusiform gyrus for face processing) is not built in. Rather, it develops through usage, specifically the interaction of cortical cells with each other and with other sources of sensory information (e.g., the thalamus). Given slight intrinsic differences in the properties of different cortical tissues, patterns of feedback among cells are biased toward the processing of particular types of information (e.g., linguistic information, visuospatial information). These differences in efficiency set up inter-regional competition. Consequently, particular functions gravitate to regions that mediate them most efficiently. The second claim is that the emergence of new skills depends, not on the recruitment of new regions of cortex, but on the coupling of activities across regions that are already functioning. Thus, new cognitive acquisitions are mediated by the functional integration of regions that have already become specialized through competitive processes. With respect to both claims, on-line neuronal interaction leads to network elaboration, giving rise to new capabilities in normal development. Although Johnson is not specific on this point, it would seem that this process must depend in large part on the mechanisms of synaptic shaping discussed earlier. What is unique to this model, however,

is that the dedication of cortical activities to particular functions emerges within regions initially and then across regions subsequently. Thus, the actual real-time activity of interacting neurons is responsible for the initial organization and progressive reorganization of the cortex.

Johnson's model embodies several key principles of developmental self-organization. The first is the emergence of structure through recursive interactions among the elements of the system. Though Johnson sometimes refers to his model as constructivist in nature, the emergence of higher-order organization or complexity through recursive processes is central to a self-organizational account (e.g. Lewis, 2000b). Second, the model specifies that structural reorganizations are typical of development, with new skills subserved by new patterns of interaction among existing structures. Structural reorganization is a key feature of developmental self-organization, as highlighted earlier. Third, while Johnson is more interested in normative than individual pathways, Johnson, Halit, Grice, and Karmiloff-Smith (2002) speculate that developmental disorders such as autism and Williams' syndrome result from the progressive emergence of unique patterns of cortical specialization rather than preexisting brain anomalies. They propose that these disorders result from the laying down of unique configurations of intra- and inter-regional interactions that build on themselves over the time course of development. This kind of emergent trajectory exemplifies cascading constraints, resulting in the loss of degrees of freedom, and I will revisit these notions in greater detail later. Finally, Johnson et al. (2002) claim that their model of cortical specialization is consistent with evidence that the same functions are subserved by smaller, more localized regions of cortical activation as children develop. Indeed, neuroimaging research has shown that the same tasks elicit less cortical activation in adults than in children (Casey et al., 1997; Durston et al., 2002), and our own research (Lewis, Lamm, Segalowitz, Zelazo, & Stieben, *in press*) reveals decreasing magnitudes of cortical activity across five developmental waves from age 7 to 16 in a task tapping emotion regulation. We also find increasing "frontalization" (localization of function to prefrontal regions) with age, consistent with other research (e.g. Bunge, Dudukovic, Thomason, Vaidya, & Gabrieli, 2002; Rubia et al., 2000). Thus, Johnson's claims about increasing specialization seem to apply very neatly to emotion regulation capacities.

It is clear from this discussion that the cortex is highly plastic and malleable. But to what degree do subcortical structures change with experience? The hippocampus and amygdala show neuronal branchings and synapse formation. Like the cortex, these organs are functional only insofar as they are able to change structurally in response to experience. They are designed for structural elaboration so that mammals can anticipate and interact flexibly with a changing world on the basis of learning. However, sublimbic levels of the neuroaxis (e.g., the hypothalamus and brain stem) are not designed for learning of this sort. Their contribution is to anchor the fine-tuned interface with the world, elaborated in the cortex and limbic system, with the age-old requirements and functions of the body. This is not to say that cells in these structures do not change at all with activity. Hypothalamic synapses change functionally in response to over- and understimulation and become more or less responsive to physiological inputs, resulting in modifications of neuromodulator release and other functional changes. As far as is known, brainstem nuclei show little if any plasticity. Their functions are set in place prenatally and change little in response to experience. As reviewed earlier, brainstem nuclei can be considered the seat of basic emotions such as anger and fear. When stimulated by perceptual, cognitive, and memory functions mediated by the cortex and limbic system, these groups of cells orchestrate behavioral

impulses and neurochemical activities that implement the action tendencies ascribed to basic emotions (e.g. Panksepp, 2003).

Thus, the brain consists of multiple systems that are highly diverse in their structure and function and yet become rapidly synchronized in real time, when situations are emotionally compelling. In developmental time, however, these different systems show very different patterns. The cortex and limbic system go through massive structural organization and reorganization in response to experience. They literally self-organize with development. These changes are partly determined by normative schedules of synaptic shaping and functional specialization and partly by the playing out of unique interactions between the individual and the world. However, the basic wiring of the hypothalamus and brain stem changes little or not at all with experience. Thus, these systems provide a kind of anchor or fundamental constraint to developmental self-organization. They ensure that, whatever corticolimbic patterns are sculpted by experience, they continue to be bound by emotional agendas to serve organismic goals and requirements. This would imply that corticolimbic patterns supporting normative acquisitions, such as language, and individual acquisitions, such as aggressive behaviour, shyness, and suspicion, are constrained by the requirements of food, mating, protection, exploration and so forth embodied in basic emotion systems. Yet the question remains: how are these constraints implemented? I suggest that they are implemented through the requirements of vertical integration—that is, synchronization across multiple levels of the neuroaxis—in real time. Corticolimbic configurations that stabilize in real time do so because they provide a way for thought, behavior, and emotion to work together in pursuit of a viable goal or strategy. What doesn't "work" doesn't cohere—not even for a moment. Because the hypothalamus and brain stem are key players in vertical integration, only synaptic activities that serve emotional requirements cohere in the first place. Hence, it is only *those* patterns that become articulated and consolidated, through synaptic elaboration and sculpting, in development. To return to the rainwater in the garden, many differently shaped rivulets may appear, leading to many different patterns of trenches over time. However, all viable rivulets must satisfy one basic requirement—that the water flows downhill. The following section maps out a model of individual differences in personality and social development based on these premises.

Self-organizing individual differences

In the previous section, I described the shaping of synaptic networks through elaboration and pruning, normative timelines of developmental plasticity, and Johnson's model of increasing cortical specialization, complexity, and consolidation. I also proposed a role for emotional contributions to each of these processes and noted their implications for individual differences. In this final section, I speculate on the neural bases of self-organizing individual differences in socioemotional and personality development. This account incorporates aspects of a model that was first introduced several years ago (Lewis, 2000a), but it sticks closer to what we know about the brain. The fundamental proposition is simple: corticolimbic configurations that last longer and recur more frequently in real time are those that become entrenched in development. In other words, the cognitive–emotional states we inhabit the most, in childhood and adolescence, sculpt the neural parameters that determine who we are as persons for the rest of our lives. I have already discussed the processes of elaboration and pruning that translate real-time synaptic configurations into developmental structure. These processes depend on emotional activation in a variety of ways, also

discussed earlier. To review, emotional states constrain the patterning of synaptic activities in real time, the neurochemical correlates of emotion are necessary for synaptic strengthening and memory consolidation, and the motivational functions of lower brain systems provide a relatively constant anchor for self-organizing processes in development.

Neuroscientists are just beginning to map out the neural underpinnings of personality. Some personality differences have been attributed to differences in neuromodulator systems such as the ventral tegmental area, a source of dopamine for motivated attention (Depue & Collins, 1999). Others have been associated with differences in the amplitude or latency of cortical responses to stimuli. For example, event-related potentials (ERPs) that tap response inhibition and self-monitoring are larger than usual for anxious, obsessive individuals (Gehring, Himle, & Nisenson, 2000) and smaller than usual for undersocialized individuals (Dikman & Allen, 2000). Because these ERPs are thought to originate in the ACC, and because they generally appear in motivationally relevant conditions (Luu & Tucker, 2002), these differences have been hypothesized to reflect individual differences in emotion regulation (Lewis & Stieben, 2004). In a recent fMRI study, higher scores on extraversion and neuroticism correlated with greater activation in various cortical regions, and in the amygdala in the case of extraversion, in response to positive and negative stimuli respectively (Canli et al., 2001). Finally, neural correlates of mood and behavior disorders have been studied through lesion studies as well as imaging research. Davidson and colleagues (e.g. Davidson, 1998) have related asymmetries in frontocortical activation to depressive tendencies, and they have hypothesized, based on these results, that left-frontal activation is crucial for overcoming negative emotional states mediated by the right PFC. Fox (1992) discovered similar associations between lateral asymmetry and avoidant behavioral styles in infants, suggesting a neural correlate of early differences in temperament. One particularly interesting set of studies finds that individuals suffering with anxiety and/or depression show increased activation of ventral prefrontal cortex (e.g., OFC) (Drevets & Raichle, 1998). In contrast, individuals with reactive aggression tend not to activate ventral prefrontal regions such as the OFC (Blair, Colledge, & Mitchell, 2001). All of these studies, and many others not reviewed here, come to a similar conclusion: the neural underpinnings of sociopersonality and clinical differences involve regions that are centrally involved in emotion or its regulation. However, these studies have almost nothing to say about the *development* of these individual differences. How might this be conceptualized?

Let us take as a model problem the finding that increased ventral prefrontal activation appears to accompany anxiety and depression. Neuroimaging research indicates that anxious or depressed individuals utilize ventral prefrontal regions such as the OFC and ventral ACC on various neuropsychological tasks more than normal controls. For example, a variety of studies have shown that cerebral blood flow, measured by PET technology, is higher in the orbitofrontal cortex, and higher in ventral ACC when controlling for volume differences, in depressed than normal subjects. This research area is complex, and it includes some contradictory findings. However, there are three particularly important discoveries to emphasize. First, successful treatment (e.g., with antidepressive drugs) can decrease activation in ventral PFC (Drevets, 1999; Mayberg et al., 1999). In other words, individual differences in ventral activation are functionally malleable, and not completely entrenched, even in depressed subjects. Second, normal subjects who undergo sad or anxious mood induction, and anxious or obsessive subjects exposed to anxiety induction, both show increased activity in these regions (see Drevets & Raichle, 1998, for a review). Thus, negative emotion helps to induce this pattern of cortical activation for both normal and atypical

populations. Third, increased *ventral* prefrontal activity corresponds with decreased *dorsal* prefrontal activity (including dorsolateral PFC and dorsal ACC) for depressive subjects, and this pattern can also be reversed by successful treatment (e.g. Bench, Frackowiak, & Dolan, 1995; Mayberg et al., 1999). Moreover, as with ventral overactivation, dorsal underactivation can be induced experimentally when normal subjects are exposed to anxiety-provoking stimuli.

The tradeoff between ventral and dorsal prefrontal activation has been of interest to neuroscientists of many stripes. Dorsal prefrontal regions, including the dorsolateral PFC and the dorsal ACC, are known to mediate “cool” cognitive processes involved in tasks that require comparing alternatives, selecting among potential strategies, working memory, and so on (Zelazo & Mueller, 2002). Conversely, ventral prefrontal regions such as the OFC and ventral ACC are commonly recruited for “hot” cognitive tasks, that require judgements with emotional consequences, and for establishing a response mode (approach or withdrawal) in reaction to immediate emotional contingencies such as threat or reward (Rolls, 1999). Moreover, these ventral regions are densely connected with the amygdala, hypothalamus, and brain stem structures, all of which are involved in different levels of emotion processing. Thus, depressive or anxious individuals somehow turn off cortical systems that would permit the calm evaluation of present circumstances and turn on systems that hold attention to the emotional aspects of the environment, surely amplifying and extending their anxiety-related appraisals. Why do they do it?

At first glance, the answer may appear simple. Heightened anxiety recruits these cortical regions in real time, through vertical integration. Vertical integration ensures compatibility in the activation patterns of regions up and down the neuroaxis. If the brain stem and hypothalamus are presently mediating anxiety states, then they would entrain the activity of cortical regions that mediate appraisals of threat and prepare the organism for escape. However, emotions do not always recruit appraisals. Sometimes, perhaps most of the time, appraisals of particular aspects of the world recruit emotions, and in fact this is the party line in emotion theory (Lazarus, 1999; Scherer, 1999). In keeping with a dynamic systems perspective, I would revise this story to say that tendencies to appraise situations in particular ways induce or augment incipient emotional states that feed back with cognitive processes which enhance or stabilize these appraisals. Hence, a tendency to process information ventrally rather than dorsally would begin to elicit anxiety in otherwise neutral or at least novel situations, limbic and lower-brain circuits mediating this anxiety would become increasingly activated, and this activation would feed back to ventral cortical systems that increasingly attend to the anxiety-relevant aspects of the present situation (Lewis, 2005). Feedback and coupling among these cortical and subcortical systems can thus explain the emergence of anxious appraisals in real time. But how do these tendencies become habitual for characterologically anxious or depressive individuals? An answer is provided by the phenomenon of recursive synaptic modification, or what I have referred to as *developmental* feedback (feedback between real-time processes and developmental processes). Each time vertical integration turns on ventral prefrontal regions, and consequently turns off dorsal prefrontal regions, synaptic shaping in the cortex increases the probability of similar activation patterns on future occasions. Because ventral systems have dense reciprocal connections with the amygdala and lower brain systems, recurrent firing patterns in the amygdala would ensue from the same epoch of vertical integration, leading to synaptic shaping in the amygdala that parallels the sculpting of ventral cortical networks. The coupling of activation across these systems in real time would be very likely

to elicit negative emotion, and this emotional coloring would maintain stable patterns of activation in real time and enhance synaptic shaping over developmental time. Thus, ventral networks that monitor threat would become more and more elaborated, and more readily called upon to assess uncertain situations. They would also hold an increasing advantage over dorsal networks for responding to novel situations.

Let us look a little more closely at the development of these corticolimbic habits for anxious or depressed individuals. Synaptic shaping over development would serve to elaborate and strengthen threat-related circuits in ventral prefrontal cortex, but it would do so at the expense of alternative circuits in dorsal regions—circuits that would remain less sculpted and less efficient as a result. The on-line synchronization of ventral and dorsal regions might in turn remain more difficult, especially in the presence of negative emotion. This description is close to Schore's (2003a) model of orbitofrontal consolidation in circumstances of insecure attachment, when high levels of stress reduce the flexibility of networks for appraising and responding to interpersonal challenges. The evolution of a multi-site ventrofrontal-limbic "infrastructure" would also epitomize Johnson's notion of interactive specialization. Following Johnson, this infrastructure could be said to support the development of a new "skill"—in this case, a cognitive set for expecting and being prepared for the worst. Within the cortex itself, this infrastructure might couple orbitofrontal systems for directing attention and preparing a response with posterior circuits attuned to aspects of the environment rich with threat-related information (e.g., the fusiform gyrus for attending to facial information). Johnson does not discuss interactions with limbic structures, but ventral prefrontal activity would likely recruit amygdala circuits mediating threat-related associations as well. The notion of corticolimbic coupling was introduced by Tucker (1992). He hypothesized a state of "resonance" between the cortex and limbic system whenever gist-like cognitive appraisals recruited emotional meaning. This idea foreshadows an account of vertical integration based on phase synchrony (in the theta band) across the entire neuroaxis (Lewis, 2005). In any case, individual corticolimbic "infrastructures" simply imply that cortical specialization consolidates along with limbic proclivities for expressing and regulating emotional responses.

I have suggested that a consolidating infrastructure across corticolimbic circuits becomes increasingly ingrained over occasions through emotional enhancement and synaptic shaping, mediating the self-organization of an anxious or depressive disposition over development. This picture of developing individual differences is consistent with a loss of degrees of freedom, as personality or clinical patterns become more deeply entrenched in neural tissue. However, this somewhat pessimistic account should also be tempered by consideration of resilience in development. For some individuals, corticolimbic plasticity remains a potent antidote to consolidating habits of appraisal and behavior. In fact, Barbas (1995) suggests that the plasticity of paralimbic systems is the key to both risk and resilience, supporting both lifelong flexibility and vulnerability to psychiatric disorders. This picture is also consistent with the principle of cascading constraints. The increasing elaboration or consolidation of one set of circuits reduces the viability of another set. This differentiation helps determine whether subsequent experiences will be influential or inconsequential, or whether they will be processed as threats or opportunities. Thus, as in any self-organizing system (and in contrast to entropic systems), differences are created rather than used up, and each newly established difference fans out to subsequent differences down the line. Finally, this picture remains compatible with the principle of developmental transitions. Let us imagine that the consolidation of an orbitofrontal "bias" emerges at one

of three ages: middle childhood, early adolescence, or late adolescence. We could make sensible predictions that this processing habit would remain in place for several years if it started in middle childhood, would be highly transitory if it appeared in early adolescence, and would endure for a lifetime if it emerged in late adolescence. Experience-expectant waves of synaptic elaboration and synaptic pruning would result in a different balance between sensitivity and entrenchment for different regions of cortex at each of these ages. In this way, the roadmap of individual developmental pathways will always be synchronized with a normative timeline of synaptic plasticity.

Finally, I have used data on ventral overactivation to demonstrate competition between cortical regions. This was intended to show how a personality or clinical disposition could consolidate through the recursive elaboration of circuits in one region at the expense of another. However, I think this represents a very coarse example of developing individual differences. Brain science is nowhere close to identifying differences in the wiring of small subregions—populations of cells within the OFC or ACC—that could mediate more subtle differences in appraisal styles. At an even finer grain of analysis, the content of individual appraisals, or conceptual categories for making sense of the world (e.g., associations among women, fire, and dangerous things, following Lakoff, 1987), should also correspond to dominant patterns of network activation established through experience. However, the same principles should apply. At any spatial scale, the elaboration and efficiency of particular synaptic networks will have grown at the expense of alternative networks, through repeated experiences, thus increasing the probability that these networks would be recruited on future occasions. In young children, these synaptic competitions, and the full throttle of emotional activation that supports them, may ingrain particular tendencies until other powerful learning experiences reorganize the synaptic landscape. Luckily, fear of the dark and suspicion of the opposite sex are usually among these transient tendencies. However, by late adolescence, when pruning has surpassed synaptic growth in all prefrontal regions, such reversals should be increasingly difficult to achieve. By this age, the overall reduction in corticolimbic plasticity will have entrenched a repertoire of interpretations, beliefs, and habitual emotional responses, many of which will endure for a lifetime. Yet the cortex maintains substantial flexibility long beyond childhood. This flexibility resides in ongoing opportunities for synaptic reorganizations, as exemplified by the reduction of ventral prefrontal activation in adults treated for depression. Moreover, recent research has demonstrated the growth of new neurons in the human hippocampus, well into adulthood and middle age, providing additional possibilities for reconfiguring cortical networks (e.g. Gould, Tanapat, Hastings, & Shors, 1999). Nevertheless, as emphasized by Freeman (1995) and Tucker (2001), emotions are necessary for learning, change, and plasticity at any age. Thus, at any age, strong emotions may be required for retooling the machinery of personality that was set in place by strong emotions in the first place.

To conclude, the divergence and consolidation of developmental trajectories demonstrate that brains do in fact self-organize at a developmental time scale. Differences in brain development are dependent, in part, on initial conditions (i.e., temperament and other endogenous factors). But much of this divergence is a product of experience, and here *experience* is a short form for the ongoing stream of activity by which the brain teaches itself what to learn. Because each episode of real-time cognitive–emotional activity leaves some degree of synaptic change in its wake, we can say that brains develop by elaborating and extending the outcomes of their own activities. And synaptic alterations are recursive, which means that these activities tend to repeat themselves, forming lineages of individual

patterning that progressively elaborate their own emergent themes. These features of neural development epitomize self-organization in natural systems. Moreover, because brain activities also change the interpersonal environment (e.g., aggression promotes isolation, independence promotes mastery and admiration), this sequence of self-elaboration occurs in the context of a social world that becomes progressively more shaped to the features of the individual brain. If our minds were not inscribed in flesh, we would not have to worry about the properties of complex dynamic systems. But our minds are greatly dependent on our brains, and brains are designed by evolution to self-organize rapidly under the sway of experiences and the emotions that color them. Therefore, to understand developing minds, we need to understand developing brains, and the principles of self-organization provide a foundation for doing so.

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