The Brain as a Cultural Artifact
Concepts, Actions, and Experiences within the Human
Affective Niche

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"Culture" can be defined as a cohesive set of mental representations (ideas, beliefs, and values) and their manifestations (behavioral practices, artifacts, and institutions) shared by a group and acquired by new generations through social learning. This far-reaching definition implies that the worlds that people navigate, and their experiences in those worlds, are *inherently* cultural. Efforts to understand the implementation and generational transmission of human culture can be improved by considering the development, architecture, and dynamics of the human brain: How does the brain wire itself to model and engage with the physical and social surroundings that matter to survival? How does one brain interface with another (each of which is situated within a body)? And how does the brain guide action and create experience in a situated fashion? Attempts to answer these questions lead to the striking insight that human brains are cultural artifacts (e.g., Mithen & Parsons, 2008; Taylor, 2006). Brains implement culture, transmit culture, and are wired by culture.

In this chapter, we discuss the hypothesis that people help to regulate each other's bodies (for better or for worse), and this is a main mechanism through which culture wires a human brain. Specifically, we suggest that the process of regulating a body's internal systems, called *allostasis* (Sterling, 2012; Sterling & Eyer, 1988), drives the bidirectional relationship between the brain as a generator of culture (in concert with other brains) and a product of culture (Barrett, 2017a). This perspective is consistent with the view that culture becomes "embrained" (Kitayama & Salvador, 2017) and considers physiological regulation as a primary driver. That is, throughout a person's life, the brain becomes wired to run a model of the world that will control the body in an efficient manner through *predictive* processes. There is an emerging research consensus that actions, and their accompanying mental events, begin as top-down representations in the brain, fashioned from prior experiences (i.e., priors) that are then tested against the state of the world for correctness (Hutchinson & Barrett, 2019). This emerging internal model

will be tuned to the physical and sociocultural features of recurrent situations (and stressors) that an individual encounters. Cultural transmission (in the form of past experiences captured and reimplemented within the brain's wiring) prepares the individual for meeting these recurrent demands, thereby supporting the development of an internal model that is sufficiently tuned to the environment. In a typically developing brain, the result is an internal model that optimizes the balance between cost-effective predictions and more costly learning (i.e., modifying the internal model; Theriault et al., 2019). This hypothesis is informed by a multilevel framework for understanding culture that integrates research and theorizing on predictive physiological regulation (Sterling, 2012; Sterling & Eyer, 1988), predictive processing (Adams et al., 2013; Barrett, 2017b; Barrett & Simmons, 2015; Chanes & Barrett, 2016; Clark, 2013; Friston, 2010), cultural evolution (e.g., Boyd et al., 2011; Henrich et al., 2010; Heyes, 2018), cultural niche construction (Laland et al., 2003), and cultural affordances (Kitayama et al., 2006; Markus & Kitayama, 1991; Ramstead et al., 2016; for a broader discussion, see Barrett, 2017a).

We begin with the insight that humans are social animals because we assist one another with the necessary physiological regulation to meet the changing demands of the physical and social environment - that is, humans help one another to establish and maintain allostasis. For humans, allostasis is supported by the physiological dependencies that arise during early social contact. (Of course, humans can also make it harder to maintain allostasis, increasing one another's allostatic burden in various ways related to neglect, adversity, cruelty, power, hierarchy, and marginalization, but these are issues for another chapter). In this chapter, we focus on how humans' extended period of physiological dependency on caregivers provides the necessary conditions for infant brains to wire themselves to their physical and social surroundings. As the infant brain bootstraps a set of experiences into its wiring, it develops a model for how to best regulate its body in a given set of contexts (i.e., within the constraints of their culturally shaped world). The "outside" conditions of this world offer affordances or "possibilities for action" that establish and maintain the brain's internal model, which is inherently culturedependent.

We then discuss a hypothesis for the workings of a brain's internal model. Specifically, we propose that the brain maintains allostasis by continually engaging in on-the-fly, dynamic concept construction. The brain functions by continually constructing culturally shaped embodied concepts that predictively categorize sensory inputs in a given context, guiding action and creating experience in a highly situated manner. In this view, an internal model is not exclusively "inside" the head of the individual.

Furthermore, we suggest that one brain's internal model guides behavior, which creates a set of affordances that impact others' allostasis, shaping their behavior and experiences in turn. Eventually, allostatic regulation shifts away from primary caregiving relationships, which are supplanted by self-regulation based on a set of learned concepts that are continually reinforced by the social structuring of the environment. This social dependency across the lifespan further ensures the transmission of culture across generations. The particulars of what internal models are generated, and how they are realized in action, language, artifacts, institutions, and so on, are as varied as the ecological and historical contexts that characterize human existence.

We then discuss diversity of conceptual systems for emotion, that is, the psychological representations that are most intimately tied to allostasis, as an example of how profoundly culture tunes internal models to the context. We propose that emotional events, as cultural artifacts, may be learned and transmitted without the need for inherited biological causes such as dedicated emotion circuits. Finally, we consider the profound implications of our framework for the processes that support acculturation, when individuals move from one cultural context to another (including traversing social contexts in the course of a single day).

Social Regulation of the Body

Humans are a social species in many ways – even ultrasocial by some accounts (Tomasello, 2014). We form long-term pair bonds. We live in groups. We care for offspring over an extended period of time. We cooperate with each other and we reciprocate. In this chapter, we integrate the additional hypothesis that members of a social species regulate one another's physiological states in an anticipatory manner (Atzil et al., 2018; Atzil & Gendron, 2017; Barrett, 2017a; Schulkin, 2010), that is, they contribute to one another's *allostasis* (Sterling, 2012).

Allostasis

Allostasis involves continually anticipating the needs of the autonomic nervous system, the immune system, the endocrine system (i.e., the internal milieu), and the motor system – all within a dynamically changing environment (Sterling, 2012; Sterling & Laughlin, 2015). Allostasis meets the body's needs before they arise: It is not a condition of the body, but a set of processes employed by the brain to keep the body's systems in balance, regulating the various systems according to costs and benefits. These continual adjustments promote survival, growth, learning, and reproduction (transferring genes to the next generation). A brain must keep its body in balance in two senses. First, the energy expenditures of all bodily systems must be balanced at any given

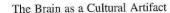
moment.¹ These expenditures are required to learn, plan, and execute the physical movements necessary to acquire those resources in the first place (and to protect against threats and dangers). Second, resource intake and expenditures must be balanced over the longer term to avoid running a deficit. The latter means that depletion of immediate resources in the short term must be balanced with a long-term return on energy allocation. Animals thrive when they realize a return on their energy allocation, yielding sufficient resources to explore the world. They consolidate the details of experience within the brain's synaptic connections, making those experiences available to guide later decisions about future expenditures and deposits.

The Brain System Implementing Allostasis

It is useful to think of a human brain as a single structure composed of billions of neurons. From a graph-theoretical perspective, neurons cluster into groups (or "nodes") that are strongly interconnected (via "edges") and that themselves interconnect in various arrangements to create broadly distributed sets of nodes or subnetworks (Sporns, 2011; Yeo et al., 2015). Within this structural arrangement, and with the help of other biological agents (such as glial cells, neurotransmitters, neuromodulators, and so on), neurons pass information back and forth to one another with varying degrees of ease, continually shifting from one pattern of information flow to others. Much of this activity occurs in the absence of any inputs from the surrounding world, referred to as "intrinsic activity" (intrinsic activity is very likely related to brain's control of the body, as it is always receiving sensory inputs from the body; e.g., Rebollo et al., 2018). The brain, as a single structure, can take on trillions of different patterns as sensory information from the body and the world modulate its intrinsic activity (Mitra & Raichle, 2016). Intrinsic activity is best described as an internal model of a person's body in the world (Barrett, 2017b; Barrett & Simmons, 2015). Modification of intrinsic activity patterns by sensory inputs is best described as *learning* (Hutchinson & Barrett, 2019).

The brain, as a network of neurons, is traditionally parsed into subnetworks of regions that are widely distributed across the brain, two of which are

Sometimes allostasis involves dynamically regulating resource allocation (i.e., diverting glucose, electrolytes, water, etc., from one system to another) to meet the body's spending needs. For example, in advance of standing up, the heart beats stronger and faster, blood vessels constrict, and blood pressure raises to ensure that the brain continues to receive the blood (and oxygen). Sometimes allostasis involves signaling the need for resources before the body runs out (e.g., drinking before dehydration occurs) or preparing for the intake of resources in advance of their ingestion. For another example, saliva in humans and some other mammals is made of alphaamylase, an enzyme that breaks down glucose. When the body needs glucose, saliva is preemptively secreted (even before anything is ingested). Even just imaging food causes glucose secretion.



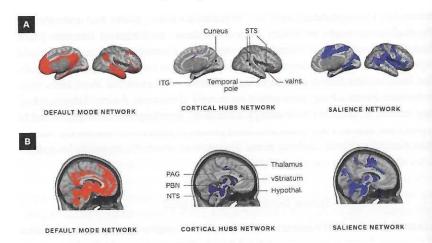


Figure 6.1 Default mode and salience subnetworks. The default mode subnetwork (shown in red) and the salience subnetwork (shown in blue) are interconnected by several "rich club" hubs (i.e., densely connected nodes shown in purple). Hubs belonging to the "rich club" are labeled. vaIns, = ventral anterior insula; MCC = midcingulate cortex; PHG = parahippocampal gyrus; PostCG = postcentral gyrus; PAG = periaqueductal gray; PBN = parabrachial nucleus; NTS = the nucleus of the solitary tract; vStriatum = ventral striatum; Hypothal = hypothalamus.

From L. F. Barrett, "The Theory of Constructed Emotion: An Active Inference Account of Interoception and Categorization," *Social Cognitive and Affective Neuroscience*, 2017, 12(1), p. 13 (https://doi.org/10.1093%2Fscan%2Fnsw154), by permission of Oxford University Press

important for maintaining allostasis: the "default mode" and "salience" subnetworks (e.g., Buckner, 2012; Seeley et al., 2007; see Figure 6.1). The default mode subnetwork is routinely involved in a variety of psychological tasks such as processing information about the self or any other concept, when mindwandering, when remembering autobiographical details, during emotion, and during context effects in perception. It has also been implicated in regulating cardiovascular function and other autonomic activity. The default mode subnetwork is thought to be important to the brain's ability to construct an internal model of the world. The salience subnetwork is also routinely involved in a similar range of psychological tasks, including regulating attention, remembering, emoting, integrating multimodal information, and regulating autonomic nervous system activity (for discussions, see Barrett & Satpute, 2013, 2017; Kleckner et al., 2017). Together, these two subnetworks make up an integrated system that implements allostasis, meaning they control the internal organs of the body, called viscera, associated with autonomic, metabolic, and

immunological functions. They anticipate the needs of the body and adjust how the internal systems of the body deploy resources to deal with the anticipated sensory world.

Allostatic changes in heart rate, blood pressure, respiration, temperature, and so on cause sensory changes, which are referred to as interoception (Craig, 2014). Several recent papers have suggested that the brain regions concerned with visceromotor regulation of the body within the salience and default mode subnetworks not only maintain and adjust allostasis, but also predict the anticipated interoceptive consequences of the allostatic changes (Barrett & Simmons, 2015; Kleckner et al., 2017; for related discussions, see Pezzulo et al., 2015; Seth, 2013; Seth et al., 2012). These interoceptive predictions are part of the brain's internal model of the world (as we discuss more in the section "Prediction, Concepts, and Categorization"). Regions implementing interoception, in contrast, such as the mid and posterior sections of the insular cortex, ultimately receive interoceptive prediction signals (i.e., the expected sensory consequences of visceromotor commands) and compare them to the actual ascending sensory inputs from the organs and systems within the body's internal milieu, correcting predictions when necessary (Kleckner et al., 2017; discussed in more detail in Figure 6.2). This suggests that the default mode and salience subnetworks are also important for establishing and maintaining the brain's interoceptive representations of the state of the body.

Together, the default mode and salience subnetworks are also important for establishing affective *feelings* (Lindquist et al., 2016). Interoceptive sensations are made available to consciousness as lower dimensional feelings of affect, that is, as feelings of relative activation or deactivation (arousal) and pleasant or unpleasant (valenced) feelings (Barrett & Bliss-Moreau, 2009). The brain is always maintaining (or attempting to maintain) allostasis, and as a consequence interoceptive signals are always being represented, suggesting that affective feelings can be thought of as a general barometer of allostasis. This hypothesis further suggests that affective feelings are not specific to episodes of emotion, but are properties of consciousness. It further suggests that psychological concepts like "stress," "reward," and "motivation" can be understood in terms of allostasis and its temporal dynamics.

As already noted, the default mode/salience system is also at the core of many other psychological phenomena, including memory, decision-making, theory of mind, attention, and a host of others (for discussion, see Kleckner et al., 2017). In fact, the regions that maintain allostasis not only send interoceptive prediction signals, but they also send sensory prediction signals to all sensory systems, in effect helping to establish the brain's internal model (as discussed further, below; see Figure 6.2; see also Chanes & Barrett, 2016; Hutchinson & Barrett, 2019; e.g., Keck et al., 2013). In addition, the network for maintaining allostasis contains more than 50 percent of the most connected

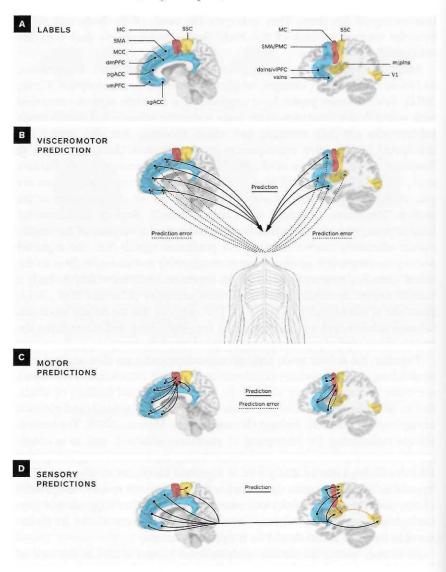


Figure 6.2 A depiction of predictive coding in the human brain. (A) Key limbic and paralimbic cortices (in blue) provide cortical control the body's internal milieu. Primary motor cortex (MC) is depicted in red, and primary sensory regions are in yellow. For simplicity, only primary visual, interoceptive and somatosensory cortices are shown; subcortical regions are not shown. (B) Limbic cortices initiate visceromotor predictions to the hypothalamus and brainstem nuclei (e.g., periacquiductal gray, parabrachial nucleus, nucleus of the solitary tract, etc.) to regulate the autonomic,

cortical regions, called rich-club hubs, that together form a high-capacity backbone for synchronizing neural activity to integrate information across the entire brain (van den Heuvel & Sporns, 2013). This backbone may also be important for establishing and maintaining consciousness (Chanes & Barrett, 2016). These observations prompt the intriguing hypothesis that, whatever else a brain is doing – thinking, feeling, perceiving, preparing for action – it is doing so in the context of regulating the systems of your body (your internal milieu) as energy resources are spent during learning, play, self-protection, reproduction, and when searching for more resources. This balancing act – allostasis – is a fundamental feature of the nervous system (Barrett & Finlay, 2018).

For the purpose of understanding how culture becomes embrained, these insights offer some important hypotheses: the default mode and salience subnetworks, working together as a system for maintaining energy balance, continually anticipate the needs of the body and attempt to meet those needs

Figure 6.2 (cont.)

neuroendocrine, and immune systems (solid lines). The incoming sensory inputs from the internal milieu of the body are carried along the vagus nerve and small diameter C and Ad fibers to limbic regions (dotted lines). Comparisons between prediction signals and ascending sensory input result in prediction error that is available to update the brain's internal model. In this way, prediction errors are learning signals and therefore adjust subsequent predictions. (C) Efferent copies of visceromotor predictions are sent to MC as motor predictions (solid lines) and prediction errors are sent from MC to limbic cortices (dotted lines). (D) Sensory cortices receive sensory predictions from several sources. They receive efferent copies of visceromotor predictions (black lines) and efferent copies of motor predictions (red lines). Sensory cortices with less well-developed lamination (e.g. primary interoceptive cortex) also send sensory predictions to cortices with more well-developed granular architecture (e.g. in this figure, somatosensory and primary visual cortices, gold lines). For simplicity's sake, prediction errors are not depicted in panel D. sgACC = subgenual anterior cingulate cortex; vmPFC = ventromedial prefrontal cortex; pgACC = pregenual anterior cingulate cortex; dmPFC = dorsomedial prefrontal cortex; vIPFC = ventrolateral prefrontal cortex; MCC = midcingulate cortex; vaIns = ventral anterior insula; daIns = dorsal anterior insula and includes ventrolateral prefrontal cortex: SMA = supplementary motor area; PMC = premotor cortex; m/pIns = mid/posterior insula (primary interoceptive cortex); SSC = somatosensory cortex; V1 = primary visual cortex; and MC = motor cortex.

Figure and caption reprinted from L. F. Barrett, "The Theory of Constructed Emotion: An Active Inference Account of Interoception and Categorization," *Social Cognitive and Affective Neuroscience*, 2017, *12*(1), p. 10 (https://doi.org/10.1093%2Fscan% 2Fnsw154), by permission of Oxford University Press

before they arise (i.e., they contribute to allostasis). In so doing, they play a role in predictively regulating action and in constructing the brain's representation of the body's state (as discussed in Barrett, 2017b; Hutchinson & Barrett, 2019). Simultaneously, these subnetworks send signals to other systems in the brain that anticipate the sensory changes consequent to visceromotor and skeletomotor control. These prediction signals constitute the brain's internal model of its body in the world. In this view, a brain does not perceive the world and then act. Instead, seeing, hearing, feeling, and perception as a whole are a consequence of anticipating the needs of the body when preparing to act or learn.

The Infant Brain

To run an internal model of the body in the world that guides efficient allostasis, a brain must contain certain structural connections. But an infant brain is not a miniature adult brain and is not up to the task of allostatically regulating its own body. At birth, most of the long, thick (and metabolically expensive) axon pathways that create the brain's subnetworks are incomplete, such that the connectivity most responsible for allostasis is not yet fully developed (Dubois et al., 2014; Fransson et al., 2007, 2011; Gao, Lin, et al., 2009; Gao et al., 2011, 2017; Gao, Zhu, et al., 2009; Geng et al., 2017; Smyser et al., 2011). As a consequence, a human infant is almost totally dependent on her caregivers to regulate her body, teaching her how to nurse and eventually eat solid food, how and when to put herself to sleep, how to regulate her temperature and so on. As we discuss below, these allostatic activities, along with attention regulation and other social activities, provide opportunities for learning that drive brain development and allow her brain to wire itself to the physical and social realities of her surroundings (see also Atzil et al., 2018; Barrett, 2017a).

This early brain development can be described as growing a contextually relevant model of one's body in the world. Caregivers engage their infants in very different activities across cultures, creating culture-specific opportunities to learn (Greenfield et al., 2003; Shweder et al., 1998). In this way, a human brain, built from one general genetic plan, can become wired to create more than one internal model, depending on the physical and cultural context in which it develops. For example, cultures are highly divergent in the degree to which experiences involving close bodily contact (co-sleeping, continual wearing of infants) are expected. These divergent activities function to shape brain wiring, providing the experiences that eventually equip a person with a culturally tuned, embodied conceptual system within the first years of life. This system, eventually, constitutes the brain's internal model that maintains allostasis, constructs experience, and guides action.

As a consequence of experience, axons grow, myelinate, and organize into fiber tracts, producing a considerable increase in neural connectivity during infancy and childhood (Cao et al., 2017). Neural connections are also pruned, producing substantial changes in neural connectivity (Low & Cheng, 2006), meaning that brain networks develop slowly. The integrated allostatic/interoceptive system (consisting of the default mode and salience subnetworks) remains immature even at two years of age and becomes more developed later in childhood. The human brain does not reach an adult-like structural organization until a person is in their early to mid-20s (Cao et al., 2017; Dosenbach et al., 2010). Correspondingly, from infancy through to adulthood, the brain is able to bear more of its own allostatic burden.

The highly plastic infant brain grows within an extended, dynamic period of allostatic support (Finlay & Uchiyama, 2017) that is culturally prescribed and socially delivered. The long window for brain development in humans allows cultural influences to sculpt brain architecture via the interaction with caregivers and environment. It is now well established that there is tremendous individual variation in the structural aspects of brain development during infancy and childhood, particularly at the front of the brain where circuitry important for allostasis, motor function, and various social functions resides. This anatomical variation is influenced by the epigenetic context (for discussion, see Cao et al., 2017; Gao et al., 2017), including, we hypothesize, social and cultural input. The considerable individual differences and plasticity in brain development in response to environmental factors (including broadly cultural factors like socioeconomic status, SES), coupled with evidence of cultural influences on psychological development, together suggest that cultural practices and structure encourage the infant brain along particular developmental trajectories.

The human brain's structural architecture is the foundation for its complexity, that is, the patterns of information flow within the brain (Deco et al., 2011; Hermundstad et al., 2013; Honey et al., 2009; van den Heuvel & Sporns, 2013). Throughout each day, the human brain rapidly and efficiently shifts its pattern of information flow – that is, its spatiotemporal patterns of neural activity – within this fixed structural architecture. In its adult form, the brain functions as a complex system, able to implement trillions of patterns of information processing; it is also an information-gaining system because it learns from its environment and is able to combine past experiences in novel, generative ways.

The Affective Niche

Early interactions with caregivers and other members of a cultural group, and the way the life of a group is organized, form the basis for learning what aspects of the immediate environment are important to allostasis (the signal) vs. those that are irrelevant to allostasis (the noise). That is, these interactions shape the development of the individual's *affective niche*.

The idea of an affective niche derives from an embodied understanding of how a brain works. A body must be watered, fed, and cared for, so that it can grow, thrive, and ultimately, reproduce and care for its young. Growth, survival, and reproduction (and therefore gene transmission) depend on the near continual intake of energy resources (metabolic and otherwise). Further, the physical movements necessary to move around in the world and acquire those resources in the first place (and protect against threats and dangers) require upfront energy expenditures which in mammals include spending resources such as glucose, water, oxygen, electrolytes, and so on. To flourish, an animal must balance energy expenditures with deposits and see a return on its resource investments, not just in the quality and quantity of resources acquired, but also in having enough surplus energy to encode and consolidate the details of experience, making those experiences available within the brain's synaptic connections to guide future decisions about expenditures and deposits. From the brain's perspective, then, its body and the world beyond are a system within which the body's overall metabolism and energy regulation must be managed. Choices about when and how to move, as well as when and how to encode (learn) new information, are economic choices about energetics and other biological resources. All potential actions and learning have an energy cost, and a human's brain (like all animal brains) weighs costs against potential rewards and revenues in the service of balancing its global energy budget via allostasis. Information and the objects/experiences that are obtained with energetic investments (such as movements or learning) are said to have value – they are signal (rather than noise) in the person's niche (i.e., they are parts of the physical environment that are meaningful and relevant to a person's well-being; Barrett, 2017a; Barrett et al., 2016).

An affective niche, therefore, can be said to include everything in the physical (including other social agents and their affective/behavioral repertoire) and psychological environment (including simulations of future, past or imagined events) that is relevant to an individual's allostasis. An affective niche should be considered on a momentary scale, such that anything included has the capacity to have an immediate impact on allostasis. (Note this is distinct from affective niche as defined elsewhere; Colombetti & Krueger, 2015; we conceptualize of an affective niche as anything having the potential to promote *or* disrupt allostasis.) As a result, what is within an organism's affective niche often, but not always, has ramifications for the long-term survival of an organism (individual fitness) or whether their genetic material will be passed on to another generation (inclusive fitness). The implication is that the affective niche of an organism is considerably broader than an

organism's ecological niche, which is traditionally defined based on consequences for fitness.

An affective niche is dynamic and constructed. Humans, like all animals, do not merely adapt to or die in a physical environment that they find themselves in. They *create* their environments by selecting and modifying what is inside their affective niche (and what can be safely ignored). Consider this example of niche construction from evolutionary biologist Richard Lewontin's *The Triple Helix* using two songbirds, the phoebe and the thrush (Lewontin, 2000). The phoebe, but not a thrush, builds a grass nest, so grass is part of a phoebe's ecological niche. A thrush uses rocks to crack open seeds, whereas a phoebe does not, so rocks are part of a thrush's ecological niche. Both phoebes and thrushes live in the same physical surroundings filled with grass and rocks within the northeastern United States, but their ecological niches, which are determined by their activities, are different. We would say that grass is important to allostasis in a phoebe and so is part of its affective niche; rocks are important to allostasis in a thrush and so are part of its affective niche.

But the affective niche expands beyond the ecological niche, to include aspects of the environment that may not be relevant to fitness but are relevant to allostasis in the immediate sense.³ Importantly, affective niche construction is not always beneficial. Just as modifications to the environment can be disruptive and impose new selection pressures on an organism (i.e., negative niche construction; Laland et al., 2000), so, too, affective niche construction can produce novel disruptions to allostasis. All classical conditioning experiments, which pair a neutral object with an object or event of value, so that the originally neutral object takes on value, are examples of niche construction, effectively expanding the affective niche of an animal well beyond what could be considered part of its ecological niche (for discussion, see Barrett, 2017a). For example, Rhesus macaques can learn to distinguish painting styles by Monet, van Gogh, and Dali when they are rewarded with juice or other food, bringing the paintings into their affective niche when otherwise the canvases

² Similarly, definitions of social and cultural niches also typically emphasize relevance for fitness, typically emphasizing inclusive fitness.

While we can understand the evolution of allostastic mechanisms in terms of their fitnesspromoting qualities (i.e., lending necessary flexibility to cope with novel stressors), learning
expands the scope of allostatically relevant events well beyond the original conditions under
which these mechanisms were originally invoked. For example, it is possible to extend grass to a
thrush's affective niche by rewarding the bird with food whenever it, say, picks up a piece of
grass in its beak. Various forms of conditioning are, in essence, expanding an animal's affective
niche. The consequence is that allostatic mechanisms (the HPA axis, catecholamines, and
cytokines) can also lead to "allostatic load" reducing the fitness of an organism, such as when
stressors become chronic (McEwen, 2005). That is, the functioning of these same systems that
can achieve allostasis can also result in "allostatic overload," the experience of being "stressed
out," and, in the long term, to disease and mortality.

would be noise (e.g., Altschul et al., 2017). In humans, this expansion is vast, and largely driven by experiences of social regulation of allostasis and the affordances of the environments that humans construct. We hypothesize that early caregiving experiences help to shape the affective niche of the developing infant, and in so doing create the conditions for a brain to develop a culturally shaped internal model of its body in the world (Atzil et al., 2018).

Caregiving Supports Affective Learning

We hypothesize that early caregiving experiences set the stage for representations of certain "outside" conditions of the physical and social worlds to be wired into the brain as an internal model of that world which, among other things, accomplishes allostasis for the particular body that it regulates. A caregiver's allostatic support is rewarding for an infant (and often the caregiver; Atzil et al., 2018; Barrett, 2017a; Feldman, 2017). While a caregiver is providing nutrition, comfort, and so on, she is, in effect, providing a reinforcement for whatever else is being learned in the moment. Each time a mother feeds her infant is a multisensory event with certain perceptual regularities (how the mother smells, looks, and sounds; the feel of her touch; the taste of her milk or formula; and the infant's interoceptive sensations associated with being fed and cuddled). An infant's brain captures this sensory context (including the interoceptive context), and the more successful the allostatic impact, the more rewarding the event, and therefore the better the learning. Each time an infant brain learns, it takes in a dynamic pattern of sensory inputs from the body and the world: sights, sounds, smells, and so on, and also the sensations from the inner core of the body. Little by little, and with surprising speed, an infant brain learns the regularities in these multisensory associations. This is how changes in light become sights, changes in air pressure become sound, changes in chemicals become smells and tastes, and so on.

Therefore, as a brain learns to represent aspects of the world that impact allostasis, it learns to distinguish those inputs that impact its body's metabolic demands from those that do not in a particular cultural context. This is crucial because brains are metabolically expensive and therefore cannot be frivolous; they do not have the resources to learn about everything. Aspects of the environment that are physically present but irrelevant for allostasis in a particular situation or context are not part of an organism's affective niche. As a result, these environmental features go unnoticed. Learning is a metabolic investment that must produce a return; the energy required to encode and consolidate the details of experience, making those experiences available within the brain's synaptic connections to guide future allostatic decisions, must allow a person to survive and thrive in the cultural context she inhabits.

In effect, an infant brain wires itself to an environment that is shaped by the humans who care for the infant. By supporting allostasis, caregivers shape an infant's affective niche and teach her to construct the environment in which she lives and grows (selecting aspects of the physical environment to attend to or ignore). In this way, the rewarding nature of caregiving provides the reinforcement that encourages the acquisition of behaviors and concepts (i.e., aspects of culture) that are necessary to be a competent member of the culture (Atzil et al., 2018; Atzil & Gendron, 2017; Barrett, 2017a). Ultimately, this allows the brain to bootstrap a set of experiences into its wiring that become its culturally relative internal model of its body in the world.

Prediction, Concepts, and Categorization

An Internal Model Is Predictive, Not Reactive

At the most basic level of description, the brain runs an internal model in order to regulate the body in the world as it uses and replenishes resources. An increasingly popular proposal is that the brain accomplishes this feat by implementing an internal model that is predictive. The proposal is that brains do not simply react to the world; instead they actively predict and test those predictions against incoming sensory evidence. That is, the intrinsic neural activity that implements the brain's internal model functions as prediction signals and incoming sensory input only perturbs this model when there is a mismatch (i.e., prediction error). This idea is called predictive coding (e.g., Clark, 2013; Rao & Ballard, 1999; Spratling, 2017), in which prediction signals, as representations constructed from past experiences, are compared with incoming sensory information to form prediction errors; prediction errors can be encoded and learned to update stored experience, which is then available for use in future predictions. Related approaches include the Bayesian brain (e.g., Vilares & Kording, 2011), which assumes that the brain performs (approximate) Bayesian inferences when computing predictions and prediction errors, belief propagation (e.g., Lochmann & Deneve, 2011), which proposes that predictions are anticipatory causal explanations for sensations that are mapped, inversely, to those sensations, and active inference (e.g., Friston et al., 2017), which hypothesizes that the brain's model of how sensations are caused is constrained by the need to minimize the cost of prediction error. Using the various sensations at a given moment in time, the

⁴ There is a well-known principle of cybernetics: anything that regulates (i.e., acts on) a system must contain an "internal model" of that system (Conant & Ashby, 1970). From a brain's perspective, the "system" in question includes its body and everything in the environment within its niche.

brain predicts what is to happen next; the sights, sounds, and other sensations, including interoceptions that are represented right now (i.e., the present situation) allow the brain to anticipate the physiological state, the specific motor actions, and the sensations (i.e., the demands) that are expected to result a moment from now.

A brain's internal model does not implement one prediction at a time. It is continuously implemented as multiple competing simulations, each of which has some probability of fitting the incoming sensory inputs. In effect, the brain is trying to answer the question, "what is this new, incoming sensory input most similar to, when compared to situated, past experiences?" You can think of a prediction as a partially completed pattern that classifies (categorizes) incoming sensory signals to guide allostasis and action based on prior (culturally constrained) learning.

Based on brain anatomy, physiology, and functional dynamics (Barrett, 2017b; Bassett & Bullmore, 2006; Chanes & Barrett, 2016; Hermundstad et al., 2013), we hypothesize that the default mode and salience subnetworks, also responsible for orchestrating allostasis and interoception (Figure 6.1), initiate prediction signals in the brain. Via cascades of intrinsic activity, these subnetworks modulate the firing of neurons in sensory and motor cortices to implement motor and sensory predictions; these predictions⁵ are partial neural patterns that prepare the brain to regulate the autonomic nervous system, the immune system, and the endocrine system; prepare the motor system for a set of muscular movements; and also prepare the sensory systems to perceive the sensory consequences of these upcoming physical changes (see Figure 6.2).

Incoming sensations from the body and the world either confirm these predictions (failing to modulate the intrinsic neural activity) or modify them (by changing the intrinsic neural activity so that the brain learns what it was not able to predict⁶). In this way, the brain uses prior knowledge implemented within its wiring to build representations – predictions –that are similar enough to the current situation for the brain to estimate bodily energy needs and prepare for action (i.e., allostasis). Prediction signals function as conditional, or Bayesian, filters for incoming sensory input, implementing allostasis, driving action, and constructing experience (Barrett, 2017b). Prediction errors, if they are deemed important for allostasis, will be encoded (i.e., learned) and will modify neural firing to modify the brain's internal model. Once prediction errors are minimized, the resulting representations also serve as inferences

about what caused the sensory events and associated actions (Hohwy, 2013; Lochmann & Denève, 2011).

On the hypothesis that prediction co-opts the same subnetworks, we propose that interoception and allostatic regulation are part of every mental event, whether people are aware or not (Barrett, 2017a). Indeed, interoceptive sensations made available affective feelings, with qualities that scientists describe using various features, such as valence and arousal (Barrett & Russell, 1999; Barrett & Simmons, 2015; Kuppens et al., 2013). These affective properties are not specific to emotion but are basic features of conscious experiences (Damasio, 1999; Dreyfus & Thompson, 2007; Edelman & Tononi, 2000; James, 1890/2007; Searle, 1992, 2004; Wundt, 1896/1897). A brain's internal model predicts not only the relevant sensory regularities in the external environment, but also the statistical regularities of the internal milieu (interoceptions) and their corresponding low-dimensional affective features (Barrett & Simmons, 2015).

Predictions Are Concepts

In every moment, the brain assembles a population of predictions. Each prediction is a partially completed neural pattern that has some probability of being the best fit to the current circumstances (i.e., Bayesian priors). In effect, this population is a concept (Barrett, 2017a, 2017b). A concept is a group of instances that are similar for some purpose (Murphy, 2002). The idea that predictions are concepts is similar to Barsalou's notion of "ad hoc" concepts (Barsalou, 1983) or situated conceptualization (Barsalou, 1999, 2008) - concepts are constructed as needed, using the sensory and motor systems (including those that represent allostatically relevant events; Kan et al., 2003; Kousta et al., 2011; Niedenthal et al., 2009; Wilson-Mendenhall et al., 2011). A concept is a group of distributed activation patterns across some population of neurons. So the human brain can be said to be engaged in dynamic concept construction for the purposes of maintaining allostasis and guiding action. Concept learning, then, is the encoding of sensory and motor prediction errors (i.e., whatever information was not anticipated or anticipated information that did not materialize). Within this framework, we can consider categorization as an instance of "good enough" fit between a given predictive pattern and the observed state of the world.

Of course, not all patterns are equally useful. A conceptual system must be sufficiently complex and context sensitive to maintain allostasis. That is, the conceptual system must support predictions about the upcoming state of the world so the individual can prepare in an efficient and effective manner. Prior knowledge enhances the complexity of a brain, and improves its ability to generate predictions, which in turn improves its efficiency. Culture provides a

⁵ Prediction signals are also called "simulations," "top-down" or "feedback" signals, "forward models" or memories that continuously anticipate bodily changes, motor actions, and events in the sensory environment.

⁶ Unanticipated sense data from the world and the body (prediction errors) function as feedback for predictions, also known as "bottom-up" signals, "feedforward" signals, or simply "learning" signals.

mechanism for promoting complexity via prior knowledge. Cultural transmission of concepts allows your brain to reconstruct/reassemble the information that has been useful to other people in your cultural context in the past without your having to invest the cost of obtaining that information by trial and error within a single lifetime. Further, building a conceptual system via personal experience alone is not only inefficient, but highly costly. Consider how costly (and dangerous) it is for one person to learn about allostasis in an inductive way, by trial and error. The goal is not to correct mistakes but to prevent them.

Humans have flourished as a species, in part because we can also learn from each other's experience. This arrangement of wiring each other's brains allows humans to expand across the globe, creating livable habitats by feeding, clothing, and learning from each other in otherwise inhospitable physical conditions (Boyd et al., 2011; Henrich et al., 2016; Richerson & Boyd, 2005). We transmit this learning across generations using stories, recipes, and traditions, and also via childrearing practices, shared attention, and other forms of interpersonal interaction (Muthukrishna & Henrich, 2016). This is how each generation shapes the brain wiring of the next, with the ultimate consequence of optimizing prediction within that cultural context. Other individuals in a person's culture(s) fine-tune the conceptual system for maintaining allostasis for a given set of constraints that are of concern to that particular group. That is, people regulate one another's nervous systems using shared concepts.

All social species regulate each other's allostasis, usually by chemical and behavioral means. But humans have this additional way: we influence the development of each other's conceptual systems by the words and expressions we use, the similarities we emphasize, and the ones we ignore. Words are critical elements in the maintenance of allostasis because they fine-tune a conceptual system, allowing it to be more agile and flexible by serving as social invitations to form concepts (Chen & Waxman, 2013; Ferry et al., 2010; Gelman, 2009; Waxman & Gelman, 2010; for an extended discussion, see Barrett, 2017a; Hoemann et al., in press).

Concepts for Body, Emotion, and Cognition

While all concepts, as instruments of culture, can be conceived of as tools for allostasis (Barrett, 2017a, 2017b), some anchor conceptual knowledge that more directly reflects how human culture organizes and expands the affective niche of the individual. In Western European and North American cultural contexts (comprising much of the psychological literature), allostatically relevant events are perhaps most directly captured by emotion concepts, like "sadness" or "disgust." These concepts foreground (and organize the meaning of) disruptions to the internal milieu (i.e., interoceptions), prescribe situationspecific actions, and facilitate communication. Further, emotion concepts serve as critical tools for social coordination and influence, often serving as bids for social regulation of allostasis. Emotion concepts (and the words used to name them) are transmitted early on in development in the context of caregiving relationships (Atzil & Gendron, 2017; Atzil et al., 2018; Xu & Barrett, 2019; Hoemann et al., 2020), and can provide a rich array of information for the individual to leverage or to deal with allostatically challenging situations. For example, conceptualizing a particular pattern of sensory inputs as "anger" guides the brain to prepare specific, situated actions. And indeed, individuals whose brains are able to construct more varied emotion concepts cope better with adverse life events and recover from illness more quickly than those who are less able to construct emotion concepts (for evidence and discussion, see Barrett, 2017a; Kashdan et al., 2015).

Divergent Concepts for Allostasis

Given the importance of the events that emotion concepts like fear and sadness capture, and the functions that they serve, dominant psychological approaches have assumed that such concepts sediment out from inherited biological circuits (what are referred to as *basic emotions*). Yet concepts for allostatically relevant events are not universal. There is remarkable diversity in what these concepts encompass and promote (Heelas, 1996; Lillard, 1998; Mesquita & Frijda, 1992; Russell, 1991). Here, we provide several examples of this diversity to illustrate how concepts likely reflect the wide variety of distinct genetic, environmental, and social contexts that humans inhabit and create (following Boyd et al., 2011). Emotion concepts can be considered a reflection of the tuning of systems of meaning to the context (Mesquita & Boiger, 2014), as well as a means of further reinforcing an affective niche that a culture inhabits.

For example, the English category of *anger* is associated with many goals, one of which involves overcoming an obstacle that someone blameworthy has put in your path. So, when one infant takes a toy away from another, sometimes she will cry, and her parents or caregivers might label this instance as 'anger'. Sometimes, the infant might swat the other child, and, again, her parents or caregivers might label this instance as 'anger'. When the infant spits her food out, or tips a bowl onto the floor, these events might also be labeled as 'anger'. So too when her play is interrupted to get ready for bed, and she stiffens her body as she is picked up. In each situation, the different motor actions are accompanied by different facial movements, different changes in the systems of her body (to support her motor actions) and correspondingly different bodily sensations, different sights, sounds, actions by adults, and so on, but they are all associated with the same goal: to remove an obstruction put there by someone else. We hypothesize that, across these dynamic, multimodal patterns, she also occasionally hears her parents uttering the word

^{&#}x27;angry'. Instances of word usage may be sparse at first (in particular, those directed at the infant; e.g., Beeghly et al., 1986; Dunn et al., 1987), but may help to agglomerate the category over time.

An obvious example of this "tuning" is when concepts for allostatically relevant events are lexically marked (i.e., with a distinct word or phrase) only in some cultural contexts but not others. Concepts that are often assumed to be core/universal are not lexically marked in all languages. For example, a translational equivalent for "sadness" was not noted in Tahitian culture (Levy, 1975; for further discussion, see Russell, 1991). Many terms for emotions also lack adequate translational equivalents in the English language. For example, the term hygge from Danish culture is often translated with English language concepts of "cozy," "friendly," and "snug" (Linnet, 2011). Yet these translations do not capture the relational aspect of hygge as a concept of social interaction (intimate socialization often involving storytelling, teasing) that promotes niche construction (creating a warm, informal environment) and certain affective consequences (pleasant, low arousal states). Instructively, attempts to export this concept outside of the Scandinavian context have led to simplifications of hygge as a décor scheme/lifestyle brand, limiting the potential interpersonal affordances of the concept that derive from hygge's connection to the value systems and consumption patterns of Danish culture (Linnet, 2011). Nevertheless, the popularity of recent popular science compendia of such "untranslatable" emotion terms does highlight the power of language to "spotlight" (Heelas, 1996) aspects of allostatically relevant events (and potentially expand an individual's affective niche), even when those terms are displaced from the original cultural and linguistic context.

Even more striking than variation in individual concepts is that allostatically relevant events are not always organized via concepts that highlight internal, mental experience. For example, distinctions between body states and mental states (Danziger, 1997; Lillard, 1998), or between emotions and other mental or physical states (Russell, 1991), are culture-bound. Little formal research has been undertaken to address the ramifications of making a distinction between emotions, body states, and actions. But evidence from neuroimaging studies reveals that inducing individuals to emphasize interoceptions versus external actions (Oosterwijk et al., 2015) or to experience physical states (more broadly) versus social perspectives (Wilson-Mendenhall et al., 2011) engages both distinct and overlapping circuitry in the brain. These data suggest that in cultural contexts where these distinctions are not made, individuals may routinely engage different sets of distributed neural patterns (potentially resulting in stable differences in subnetwork structure and organization).

While more evidence is needed, we can speculate that emotions are less likely to be treated as a distinct domain when they are not invoked as "causal" mechanisms for actions, experiences, and the grounds for prediction of other's behavior (i.e., essentialism), as they are in the Western folk model of emotion (Lillard, 1998; Lindquist et al., 2013). Consistent with this prediction, in our own research on emotion perception in small-scale societies in Africa where

the native languages (Otji-Herero and Hadzane) do not contain a word for the emotion domain, we observed that specific terms for emotional states were used less frequently than by American participants to describe other's nonverbal actions (e.g., a contracted zygomaticus). Instead, participants often generated language for situated *behaviors*, such as laughing at something (Gendron et al., 2018). These findings fit with the observation that multiple forms of categorization (e.g., group membership) are often a more functional means of generating predictions about our social worlds than mental state inferences (Hirschfeld, 2013).

Even when emotion is carved out as a distinct domain in a given language, the tendency to spontaneously use emotion concepts as explanations of allostatically relevant events appears to be culturally variable. Studies of maternalchild talk about impactful events in Chinese culture reveal more action-based language (and less mental state language like emotion term use) than is observed in American mothers (Doan & Wang, 2010). This finding fits more broadly with the observation that individuals from East Asian cultural contexts understand emotions as arising from the relationships between people (Uchida et al., 2009) rather than triggered by events in the environment. The locus of emotion is the roles that define interaction, not a mechanism within an individual, suggesting that emotions are generally less essentialized (i.e., defined by an unobservable and unspecified internal property; Medin & Ortony, 1989) in some cultural contexts. As a result, emotions are events that people enact together, such that allostatic regulation is occurring within the context of an interaction, as opposed to regulation at the individual level (Mesquita, 2001).

More broadly, we hypothesize that the cultural tendency to essentialize allostatically relevant events as emotions is related to sources of predictability – for others' behavior and one's own. Many cultures feature more highly scripted behavior that is defined by the situation and relationship between interaction partners (e.g., Gelfand et al., 2011). As a result, concepts will more readily highlight those sources of predictability (i.e., the cultural tasks) rather than internal experiences. Similarly, familiarity with others' action patterns (i.e., their habits) might also make it less likely that emotions are invoked as causal structures for behavior. We speculate that this may be more prevalent in small-scale societies where the range of individuals, situations, and possible behaviors are more constrained due to group size and complexity.

Convergent Concepts for Allostasis

While the discussion thus far has focused on diversity in concepts for allostatically relevant events, there are also clear examples of consistency. Linguistic concepts for "good" and "bad" or "pleasure" and "pain" (what are referred to

as concepts for the valence dimension of affect; Barrett & Russell, 1999; Russell, 1980) appear to be one such cultural feature. The ethnographic and linguistic records reveal at least some rudimentary concepts to represent experiences that are "pleasant" and "unpleasant" across cultures (see also Russell, 1991; for discussion of these concepts as "semantic primitives" that are in evidence across languages, see Wierzbicka, 1999).

Consistency in conceptual structures for allostatically relevant events may also be the product of convergent cultural evolution (Jablonka & Lamb, 2007; Lipo et al., 2006; Mesoudi et al., 2006; Richerson & Boyd, 2005). That is, different populations may independently develop (and pass on) similar concepts due to shared constraints. This convergence may be due to biological constraints of the human nervous system that make it more likely that certain concepts will "sediment out." For example, it is well documented that robust peripheral physiological changes occur in the context of "emotional" events, evidence of the mechanisms of allostasis at work. Importantly, these "changes" in the body are highly complex and variable both within and across different emotion categories (for meta-analytic evidence; Siegel et al., 2018). We can hypothesize that these properties such as "pleasure" and "displeasure" evolved across cultures to represent these changes, which are experienced as features of conscious experience. The affective features of experience, in this view, are like a simple barometer tied to the general state of the body (i.e., to allostasis). Affect is a core property of the neural architecture for representing visceromotor changes in the periphery (called interoception; Craig, 2009; Critchley et al., 2004; Kleckner et al., 2017); affective feelings are a low dimensional representation of the interoceptions that arise from allostasis. As a new instance of a concept is learned (i.e., prediction errors are encoded), information from multiple sensory modalities is integrated and compressed (Finlay & Uchiyama, 2015), creating multimodal summaries which are often called "abstractions" (Barrett, 2017a, 2017b). Affect, as an index of allostatic status, is hypothesized to be a universal and fundamental abstraction that human brains make. We hypothesize that valence (pleasure vs. displeasure/comfort vs. discomfort), is a low dimensional representation of the interoceptions that reflect whether an organism is successfully maintaining allostasis. As such, we suggest that affect is a feature of all concepts that the human brain constructs. Consistent with this hypothesis, all human languages have specific words to represent valence (Russell, 1991).

Convergent cultural evolution might explain similarities in concepts for more specific types of disruptions to allostasis due to similar environmental or biological constraints. For example, while we can point out examples of ethnolinguistic groups that lack an exact translational equivalent for an emotion like *sadness*, many ethnolinguistic groups do have highly similar concepts. The prevalence of concepts similar to *sadness* may be related to the experience of

loss (i.e., a core theme in English language conceptualizations of sadness; Smith & Lazarus, 1993) as an inevitable biological reality – mortality is a universal. Further, the core neurobiology of attachment includes systems involved in the maintenance of allostasis (i.e., dopamine function within a cortico-striatal-amygdala subnetwork; Atzil et al., 2017) and may be similarly implicated in the experience of broken attachment (Fisher et al., 2010). The experience of loss presents a significant disruption to allostasis across cultures, such that convergent concepts for that disruption, such as sadness and grief, likely evolved to meaningfully construct and regulate the experience of loss. Indeed, cultural systems for loss similarly involve complex forms of affective niche construction, via religious concepts (e.g., afterlife, ancestor worship) and cultural tasks as dictated by rituals (e.g., mourning practices like wearing black, ritualized crying), as well as structural changes in relationships (e.g., levirate marriage).

Emotion Acculturation

If the brain becomes wired with a conceptual system that fits environmental challenges that are specific to its cultural context(s), then moving to a different environment should challenge the maintenance of allostasis. We hypothesize that shifting into a novel cultural context places an enormous burden on the human brain. In the short run, this means that migration would come at a cost to well-being. In the longer run, continual allostatic load would lead to enhanced inflammation, creating a vulnerability to depression and anxiety disorders, along with a host of stress-related metabolic illnesses, including heart disease, diabetes, and cancer (for reviews, see Juster et al., 2010; Korte et al., 2005; see also Doamekpor & Dinwiddie, 2015; Peek et al., 2010).

Immigration is on the rise, and an increasing number of people experience a lack of "fit" between their internal model (and the concepts it enacts) and the environmental context (Mesquita et al., 2019). Consistent with our hypothesis that misfit comes at a cost, immigration has indeed been linked to acculturative stress as manifested by uncertainty, anxiety, and depression (Berry et al., 1987), as well as with problems in social adaptation, including relatively low school/work achievement and social competence (Sam & Berry, 2010). Results on the impact of immigration on physical health problems are not fully consistent (see below).

That it is important for a person to have an internal model that is wired to the physical and social environment is suggested by an increasing number of studies on cultural fit among natives. Natives who fit their culture's average levels of extraversion, promotion focus, emotional responses, and even religiosity were also found to have higher personal well-being and more relationship satisfaction, and even better reported health (De Leersnyder et al., 2014, 2015; Fulmer et al., 2010; Gebauer et al., 2012). A plausible inference from these

studies is that the fit between a person's internal model and their sociocultural context offers an advantage to maintaining allostasis.

Research on secondary acculturation of the conceptual system is in its infancy. This is because a tacit assumption in much acculturation research has been that while cultural affiliation and identity change, the 'psyche itself' remains untouched. Our approach challenges this view of acculturation (see also Mesquita et al., 2019). We hypothesize that, as immigrants engage in the new culture, new concept learning will take place to the degree to which concepts learned in the native culture fail to effectively regulate allostasis. For instance, an internal model that cannot predict social rewards in the new culture, or that does not allow for social coordination, will need to be adjusted, or else will come at a high cost. Importantly, when immigrant individuals come to share the conceptual system of the new culture, the majority of others can also help them regulate allostasis. Conversely, lacking social support will tax the person's ability for allostatic regulation.

An emerging body of evidence suggests that contact with a new culture may, in fact, result in a new and changed internal model of the body's relationship to the world (Mesquita et al., 2019; Pavlenko, 2009). In our own research on emotional acculturation, we have found that immigrant minorities' engagement in a new culture leads to better cultural fit of emotions with majority emotions (De Leersnyder, 2017; De Leersnyder et al., 2011; Mesquita et al., 2019). In this research, individuals from immigrant minorities and majority groups were asked to report their emotions in similar emotional situations. Minority emotional patterns were compared to the majority average in the same situation. Compared to first-generation immigrants, we found that second and later generations of immigrants had higher emotional fit with the majority's average emotions in similar situations. Furthermore, within the group of immigrants, the internal emotion models of immigrant minorities who frequently engaged in majority culture (e.g., spoke the majority language, had more majority friends) shifted more toward those of the majority members than the internal models of immigrant minority individuals who had less contact. This is an illustration of shifting internal models. Other research similarly suggests that engaging in a new culture brings about shifts in social cognition, self-esteem, self-concept, personality, and motivation, in the direction of the majority culture (Güngör et al., 2013; Heine & Lehman, 2004; Hong et al., 2000; Pouliasi & Verkuyten, 2012; Savani et al., 2011). Additionally, it seems that learning a language provides new concepts and, thus, itself is a shift in the internal model (Pavlenko, 2014).

Evidence that shifting internal models contribute to regulation of allostasis in the new cultural environment is scarce and inconsistent. Importantly, first-generation immigrants often have been found to be healthier than the general population (and when compared to their natal population), and also healthier than later generations of immigrants, something that has become known under

the term "immigrant paradox" (e.g., Hyman, 2004). At first sight, this finding is not consistent with our hypothesis that people with an internal model that cannot predict well in the new culture will fail to achieve allostasis. However, several factors may account for these relatively positive health outcomes for first-generation immigrants, and the research to date does not allow to distinguish among these explanations. One possible explanation for the immigrant paradox is a selection effect, with first-generation immigrants, especially those who voluntarily move, being the healthiest and most educated (Sam & Berry, 2010). It is also possible that many first-generation immigrant minorities live in neighborhoods and communities where their heritage internal models still predict their dealings with others well. Studies specifically connecting minority individuals' shifts in concepts to increases in well-being and health are rare and should be undertaken in future research. In a rare study connecting emotional experience with self-reported health, Consedine et al. found that immigrant women whose emotional experiences were more similar to those reported by their majority counterparts also reported better health (Consedine et al., 2014). One possibility is that healthier people are more able to make the necessary conceptual adjustments (i.e., the conceptual learning may pose less of a burden for the healthy than for those who must allocate resources to health maintenance and/or whose condition impairs capacity to adapt).

It is important to keep in mind that many bi- or multicultural individuals navigate different cultures. To predict their body's relation to each of their cultural worlds, these biculturals will need different internal models, plus the flexibility to apply the models matching the cultural environment at hand. Biculturalism, or the availability of multiple internal models, has been related to higher psychological well-being and better social adaptation (Nguyen & Benet-Martínez, 2013), although this finding may be constrained to those national contexts that favor multi-culturalism. In national contexts that require immigrants to assimilate, and thus fully change their internal models, immigrants seem to be better off if they choose segregation as an acculturation strategy (Mesquita et al., 2019). Segregation would allow immigrant minorities to largely sustain the predictability of their world, without changing their internal models, and to benefit from others from their heritage culture to help regulate allostasis. In a new country or culture, this strategy, while helping to maintain allostasis in the short run, may come at the cost of societal exclusion in the long run.

Immigration, and the shifts in internal models that it may entail, is not only important to study in its own right, but also forms a framework for understanding the predictive complexities with which many individuals in modern life must deal. Individuals traverse cultural boundaries on a daily basis, such as when leaving your family setting at home to enter your cultural context at work, when changing jobs, roles, etc. Even a relationship between two people can be thought of as microculture. A cultural neuroscience approach that offers

solutions for the daily challenges of acculturation must consider culture in these broader terms as well.

A Look Ahead

We have outlined a multilevel framework for charting the role that regulation of the body (achieved through allostasis) plays in the acquisition of internal models to organize experience and action within distinct cultural worlds. Neuroscience advances in our understanding of the structure and organization of the human brain (including evolutionary (dis)continuities) strongly suggest that human culture wires the brain with the necessary flexibility and complexity to contend with the expansiveness of the human ecological niche.

More research is necessary to bridge the gap between what we know about variation in internal models (including concepts for allostatically relevant events like "emotions") and how those models function. Questions about what leads a cultural group to develop a set of concepts for certain allostatic challenges and whether those concepts are functional for promoting allostasis are complex issues that require more empirical attention at multiple levels of analysis. But the evidence, thus far, suggests that there is a large variety of concepts surrounding allostatically relevant events, and, thus, it is reasonable to posit that a range of internal models are functional, depending on the context. More complex issues that warrant further empirical attention include the role that genetic variation plays in cultural diversity in emotion concepts (and related issues of culture-gene coevolution), how consistent versus divergent representations of emotion are within cultural groups, and how responsive concepts for emotion are within a culture to shifting sociodemographic factors (e.g., from rural to urban, from culturally isolated to interconnected, from subsistence agriculture to commerce, and so on).

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