

Language and emotion concepts in the predictive brain

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What does language have to do with emotion? The scientific answer used to be “not much at all,” but modern behavioral, physiological, and neural data suggest otherwise (see Hoemann et al., 2022; Lindquist et al., 2015a; Lindquist et al., 2016; Nook & Somerville, 2019; Shablack & Lindquist, 2019; Torre & Lieberman, 2018; for reviews). Collectively, these findings show that words naming emotion categories, such as “anger,” “disgust,” “fear,” “sadness,” and “joy,” help people acquire and use conceptual knowledge about their culture’s emotion categories throughout their lifespan.

In this chapter, we argue that language plays a mechanistic role in emotion because such emotion concept knowledge, once acquired, is used by the brain to predictively and adaptively regulate a person’s subjective emotional experiences and behaviors (Barrett, 2017; Lindquist et al., 2022). Building on predictive processing models of brain function (Barrett, 2017; Clark, 2013; Friston, 2010; Sterling, 2012), we argue that the emotion concepts learned via language during early development “seed” the brain’s emotional predictions throughout the lifespan. In support of this hypothesis, we briefly review constructionist theories of emotion (Barrett, 2017; Clore & Ortony, 2013; Lindquist et al., 2022; Nook & Somerville, 2019; Russell, 2003) and their support in behavioral, physiological, neuroimaging, and lesion data.

We then situate these constructionist predictions within recent neuroscience research that is revealing the functional neural architecture for emotions. Much research now suggests that this functional architecture routinely involves heteromodal association regions involved in semantic representation, abstraction, and predictive processing (Barrett, 2017; Lindquist et al., 2012; Satpute & Lindquist, 2019; Tottenham, 2020). These heteromodal association regions sit atop a predictive processing hierarchy in the primate—and especially human—brain and may therefore represent the mechanisms by which emotion concepts “seed” emotional experiences. We close

by looking forward to future affective neuroscience research that can continue to test hypotheses about the role of language in emotion.

The construction of emotion: Predictions and evidence for the role of language in emotion

The notion that language plays a role in emotion is most closely aligned with constructionist theories of emotion. Constructionist theories suggest that emotions are phenomena that emerge out of more basic, domain-general functions of the brain (see Gendron & Barrett, 2009 for a historical review; see also Chapter 1, Sander). Although they differ in specifics, many constructionist theories agree that concept knowledge about emotion categories such as (in English) “anger,” “disgust,” “fear,” “sadness,” “joy,” etc. are learned via socialization, honed over experience, and come to shape how sensory information from inside and outside the body is made meaningful over the lifespan (Barrett, 2006; Clore & Ortony, 2013; Lindquist et al., 2006; Lindquist et al., 2022; Nook & Somerville, 2019).

To form an instance of “anger” out of sensory information occurring within and outside the body is no easy task for the brain. Ample evidence shows that instances of an emotion category such as “happiness” are highly variable in their features—for instance, people may smile but also cry or do nothing when happy (Fernández-Dols & Ruiz-Belda, 1995). Meta-analyses show that there is no single peripheral physiological pattern (Siegel et al., 2018) or behavioral action repertoire (DeWall et al., 2016) that reliably differentiates happiness from other emotional experiences. Moreover, evidence for the dedicated central nervous system mechanisms for specific emotion categories is wanting; meta-analyses reveal that there is no happiness-specific center or network (or sadness, or fear, or anger, etc. center or network) within the brain that reliably and uniquely shows activation for a single emotion category (Lindquist et al., 2012; Touroutoglou et al., 2015). Studies that do claim to find functional brain

representations specific to a single emotion do not replicate the patterns of, e.g., “happiness” observed in other studies claiming the same. For instance, one study using multivoxel pattern analyses found that “surprise” mapped onto the mid and anterior cingulate cortex, bilateral anterior insula, bilateral mid-occipital cortex, bilateral thalamus, and bilateral cerebellum (Kragel & LaBar, 2015), whereas another study using similar classification methods found that “surprise” was classified by a different set of regions—the auditory cortex, supplementary motor area, and left insula (Saarimaki et al., 2018). Saarimaki et al. (2022) found that only functional connectivity in the default mode network could reliably differentiate between emotion categories, yet Touroutoglou et al. (2015) found that emotion categories were differentiated by connectivity between regions belonging to multiple intrinsic networks, such as the visuospatial network, the salience network, and the default mode network. Rather than functional representations in the brain specific to a single emotion, even experiences of the same emotion category (which occur in the same context and share features of intensity, valence, and arousal) are supported by distinct neural network patterns in different people (Doyle et al. 2021). As William Hunt wrote in 1941, “the only universal element in any emotional situation is the use by all the subjects of a common term of report (i.e., “fear”)” (p. 266). What Hunt was acknowledging was that emotion categories are abstract categories without strong statistical regularities to ground them. Different instances of say, happiness, are united by features that are more abstract than their objective manifestations.

In light of this evidence, the Theory of Constructed Emotion (Barrett, 2017; Lindquist, 2013) hypothesizes that concept knowledge binds together varied instances of an abstract category, such as “anger” (Lindquist & Gendron, 2013; Lindquist et al., 2022). Critically, evidence from cognitive science suggests that language is crucial for representing abstract

categories that lack strong statistical regularities in perceptual input (Borghi & Binkofski, 2014; Vigliocco et al., 2009). Because a person understands the category “anger,” they can experience frowning, an increase in heart rate, and yelling during goal obstruction as different from the same behaviors following the loss of a loved one (i.e., “sadness”). Meanwhile, knowledge of the category “anger” helps people understand frowning, an increase in heart rate, and yelling after someone violates a norm as similar to the first instance.

Evidence for the role of language in emotion

There is now ample behavioral, physiological, and neuroscientific evidence for the role of language in the acquisition of emotion concept knowledge during initial learning and its use during emotional experiences and perceptions. It is beyond the scope of this chapter to review these findings in full, although we briefly summarize them here (for comprehensive reviews of the behavioral and physiological findings, see Hoemann et al., 2022; Lindquist et al., 2015a,b, 2016; Lindquist, 2017; Nook & Somerville, 2019; Shablack & Lindquist, 2019; for reviews of the neuroscientific findings, see Lindquist et al., 2016; Satpute & Lindquist, 2019; 2021).

The Theory of Constructed Emotion is ultimately developmental (see Lindquist et al., 2022), and some of the most compelling evidence that language plays a role in emotion comes from studies of infancy and early childhood, where evidence suggests that learning words such as “anger,” “disgust,” “fear,” “sadness,” and “joy,” is associated with children’s subsequently more perceptually and experientially discrete and specific emotional experiences, emotion perceptions, and emotional understanding (see Nook & Somerville, 2019; Shablack & Lindquist, 2019; Widen, 2013 for reviews). For instance, one recent study found that the explicit labeling of new emotional facial expressions helped children understand them. When three-year-olds were asked to match emotional facial behaviors to particular emotional scenarios, specific, explicit

labeling of the emotion concept improved their performance, while broadly-valenced or irrelevant labels did not (Ogren & Sandhofer, 2022). Another recent study of parents' reports of children's emotions in daily life showed that as children develop over the first 5 years of life, the dynamics of their emotional experiences become more discrete and organized. Specifically, as children increase in age, the duration of their emotional states increases and transitions are more likely to occur from one state into another similarly- (versus differently) valenced state. That is, as children get older, they are more likely to be "in" an emotional state for a longer period of time, and they are more likely to shift from a state such as "anger" to "sadness" than "anger" to "pride." These more "mature" patterns of emotion dynamics were predicted by children's emotion vocabularies, such that children who produced more emotion words in daily life had more organized emotion transitions in daily life. Most critically, possessing a category such as "anger" and producing it in spoken language predicted greater organization in the dynamics of anger experiences in daily life, controlling for the child's age (Nencheva et al., 2023). These findings, although ultimately correlational, suggest that children's emotion word knowledge is related to the structure of their observed emotional dynamics in daily life.

Of course, emotion concept knowledge increases in complexity across childhood. There is evidence that emotion concept knowledge continues to become more complex and abstract throughout childhood and adolescence, a linear pattern that does not level out until around age 18 (Nook et al., 2020). This increasing complexity and differentiation of emotions is supported by neural evidence that children, compared to adults, have more similar (or less differentiated) neural responses to positive, negative, and neutral video clips in the ventromedial prefrontal cortex (vmPFC), amygdala, and nucleus accumbens (NAcc). These neural findings mirror the linguistic findings to suggest that the neural representations of different emotions become more

discrete across development (Mitchell et al., 2022). This neural similarity in children was particularly strong for negative stimuli, consistent with other research showing that most languages tend to differentiate amongst different negative emotions to a greater extent than positive emotions (Alves et al., 2017; Smidt & Suvak, 2015). The role of the vmPFC in the representation of emotion is especially interesting given work linking the vmPFC to the representation of semantic meaning, more generally (Shenhav et al., 2013).

In adulthood, individuals who use emotion words to report their emotional experiences more discretely in daily life also show more discrete clusters of peripheral nervous system activation during emotional experiences (Hoemann et al., 2021). Emotion perceptions become more categorical (versus dimensional) when adults have access to relevant emotion concept words (Nook et al., 2015), and learning novel emotion concepts induces categorical perceptions of facial behaviors (Fugate et al., 2010). When adults experience an unpleasant state, access to the word “fear” (but not other emotion categories, such as “anger”) causes them to experience behaviors typical of fear, such as risk aversion (Lindquist & Barrett, 2008) and the tendency to perceive others’ facial expressions as relatively more (versus less) threatening (Lee et al., 2018). Correspondingly, labeling one’s unpleasant affective states with an emotion word (e.g., “fear”) makes it more difficult to regulate that emotion via reappraisal or mindfulness, perhaps because the act of labeling one’s affective state causes it to become more discrete and “crystalized” (Nook et al., 2021).

In adults, the mere presence of emotion concept words (e.g., “anger”) in the instructions or as self-report options in neuroimaging experiments alters brain activation during the subsequent presentation of emotional stimuli (Brooks et al., 2017). Across hundreds of studies, a meta-analysis found that the presence of emotion concept words in behavioral neuroimaging

tasks is associated with increased activity within regions associated with semantic retrieval, such as the inferior frontal gyrus and lateral temporal cortex, during subsequent presentations of emotional stimuli. In contrast, the absence of emotion concept words in such experimental tasks is associated with increased activity within regions associated with arousal and uncertainty, such as the amygdala (Brooks et al., 2017). These findings are consistent with neuroimaging and psychophysiological work on “affect labeling” in which deliberately labeling an emotional stimulus or an emotional experience with a word such as “fear” or “anger” reduces amygdala activity (Burklund et al., 2014; Hariri et al., 2000; Lieberman et al., 2007; Payer et al., 2012; Taylor et al., 2003), emotional reactivity (Constantinou et al., 2014; Lieberman et al., 2011), and skin conductance level (Kircanski et al., 2012; Matejka et al., 2013; Niles et al., 2015; see Torre & Lieberman, 2018 for a review).

There is also evidence that individual differences in the conceptual representation and use of emotions are reflected in brain activity. One study assessed the degree of similarity between individuals’ conceptual, perceptual, and neural representations of “anger,” “disgust,” “fear,” “happiness,” “sadness,” and “surprise” (Brooks et al., 2019). Specifically, conceptual similarity of each emotion category was assessed with a conceptual ratings task in which participants rated how closely related each emotion was to a set of actions, bodily sensations, and thoughts. The perceptual similarity of the emotion categories was measured by categorization of emotional faces into each emotion category. Finally, neural structure was assessed as brain activation within the right fusiform gyrus (rFG) while viewing emotional faces. Representational similarity analysis (RSA) was used to determine the extent to which the structure of conceptual, perceptual, and neural representations was similar within individuals. Critically, the study showed that neural structure was predicted by conceptual structure, such that individuals who differentiated

more amongst emotion categories showed more specific neural representations of emotional faces (Brooks et al., 2019). These findings contribute to the evidence that top-down conceptual representations may shape how emotional percepts are represented in visual cortex.

“Emotional granularity” is a construct related to individual differences in the conceptual structure of emotions. Emotional granularity is a behavioral measure of the extent to which people tend to label their emotions using specific, nuanced language versus non-specific language. Research has found that the tendency to experience emotions in a highly precise, differentiated manner, as opposed to experiencing them as broad, general feelings, is related to diverse positive outcomes in mental health, emotion regulation, resilience, and other indices of well-being and adaptive health behaviors (see Kashdan et al., 2015 for a review). There is little research examining the neural mechanisms of emotional granularity, but one ERP study found that individual differences in granularity as measured during experience sampling in daily life were associated with differences in neural processing during emotional experiences in the lab. Specifically, individuals who were higher in granularity showed neurophysiological patterns that have been previously associated with semantic retrieval, working memory, and executive control during emotional experiences induced by evocative images (Lee et al., 2017).

Complementary to the neuroimaging literature, the lesion literature reveals that impairment in brain regions associated with semantic processing such as bilateral anterior temporal cortex and temporal poles is regularly accompanied by deficits in emotion processing (see Satpute & Lindquist, 2021 for a review). Patients with damage to the anterior temporal lobes had lower scores on a facial emotion recognition task than either healthy control participants or patients with frontal or parietal damage (Campanella et al., 2014). In another study, patients with focal lesions to the temporal pole reported experiencing fewer instances of emotions such as

anger, sadness, joy, etc. in their everyday lives than control participants (Grossi et al., 2014). Finally, patients with semantic dementia impacting their left temporal pole—a region routinely associated with concept representation (Lambon Ralph et al., 2009; Visser et al., 2010)—show deficits in emotional processing. One study showed that when tasked with sorting emotional faces into meaningful categories without the need to explicitly label them, semantic dementia patients only sorted faces into three categories, grouping by faces that appeared to them to be positive, negative, or neutral. This pattern contrasted with control participants, who sorted the faces into six or more categories corresponding to instances of anger, sadness, fear, disgust, happiness, and neutral emotion categories (Lindquist et al., 2014). In another study, emotion concept knowledge of semantic dementia patients was assessed by providing participants with emotion labels of “anger,” “pride,” “surprise,” and “embarrassment” and asking them to provide a synonym for the word, match it to the word it was closest to in another set of feeling words, provide an example of a context in which the emotion would be felt, and select a context example from a list of options. Patients’ facial emotion recognition was also assessed in a task in which they viewed faces displaying 10 different emotions and were asked to choose among 10 possible emotion labels for each face. Patients showed deficits in both emotion concept knowledge and facial emotion perception when compared to control participants. Moreover, emotion concept knowledge and perception ability were correlated, such that patients with greater deficits in emotion concept knowledge also had greater deficits in perception of facial emotions (Bertoux et al., 2020). Finally, Jastorff et al. (2016) found that reduced gray matter volume in the left temporal pole was associated with patients’ impairment in emotion perception when they were asked to detect whether dynamic emotional body expressions were either emotional or neutral.

Finally, patients with semantic aphasia also show impairments in emotion perception. Such patients have focal damage to the left inferior frontal gyrus or temporoparietal cortices, resulting in difficulties not with concept representation, but with conceptual retrieval (Souter et al., 2022). When instructed to freely sort emotional faces into categories, semantic aphasia patients differentiated between positive and negative emotions, but had trouble distinguishing different negative emotions from each other and were more likely than controls to make negative within-valence errors (e.g., to confuse an “angry” face with a “disgusted” face). They also benefited more than controls from the addition of emotion word examples such as “anger,” “disgust,” and “fear” that served as anchors for what the categories could be, facilitating access to emotion concepts (Souter et al., 2021). These findings are consistent with evidence that reduced gray matter volume in the left IFG in patients with dementia was correlated with deficits in the ability to categorize emotional body movements as “happy,” “angry,” “fearful,” or “sad” in the study by Jastorff et al. (2016).

Collectively, these findings suggest that language plays more than just a trivial role in the experience and perception of emotion—learning new emotion concepts, accessing those concepts, or being impeded in the access to those concepts—all shape emotional behavior, physiology, and the neural representation of emotions (see Lindquist et al. 2016a, b; Lindquist, 2017; Satpute & Lindquist, 2021). Yet questions remain about the mechanisms through which emotion words might alter emotional experiences and perceptions. The Theory of Constructed Emotion suggests that emotion concepts that are learned via language during early development may impact emotion because they help the brain to subsequently predict and organize the meaning of incoming sensations from the body and world as instances of emotion. These

findings are consistent with newer evidence for predictive processing models of brain function and newer understandings of the neural architecture of emotion.

Predictive processing models of brain function

There is mounting evidence that the brain evolved as a predictive processing system geared towards the task of making and updating predictions in order to meet the ongoing needs of the body's physiological systems (its internal milieu) as efficiently as possible (Adams et al., 2013; Clark, 2013; Friston, 2010). Predicting and preparing to meet these needs before they occur is more metabolically efficient than reacting to them, and thus optimal for survival. These predictions are made based on sensory information from outside the body (e.g., from the visual, auditory, olfactory, gustatory, and tactile modalities) and inside the body (e.g., from the interoceptive, proprioceptive, and vestibular modalities). To make accurate predictions of the consequences of these sensory signals and form appropriate motor response plans, the brain needs to make meaning of them, using learning from past experiences to interpret them in context. Predictive processing models have been applied to vision (Lupyan & Clark, 2015; Rao & Ballard, 1999), audition (Bendixen et al., 2012; Recasens et al., 2018), interoception and allostasis (Barrett & Simmons, 2017; Kleckner et al. 2017), and motor action (Adams et al., 2013).

In humans, language serves as a powerful source of prior knowledge with which to optimize prediction accuracy. Through language, humans are able to acquire and store knowledge of abstract conceptual categories, and this conceptual knowledge guides how incoming sense data is interpreted, serving to “seed” predictions about that data. This is thought to be the mechanism through which language can “penetrate” perceptions, cognitions, and actions (Lupyan & Clark, 2015). For instance, language has been shown to influence subjective

visual perception—hearing a verbal label of the category of an otherwise invisible image boosted that image into awareness (Lupyan & Ward, 2013). Access to linguistic information appears to adjust the predictive likelihood of a particular interpretation of the visual information being presented. We argue that the same principles apply to emotion.

The Theory of Constructed Emotion hypothesizes that emotions, like all subjective mental states (e.g., subjective visual perception), are a product of such predictive processes. Emotions can be thought of as predictive categories that are learned over time and that describe suites of motor actions, visceral actions, interoceptive sensations, and external sensations (sights, sounds, smells, tastes, etc.) that have co-occurred in the past in contexts sharing similar abstract themes (e.g., loss, threat). Of course, many animals engage in predictive processing by enacting motor and visceral actions that are adaptively tuned to the context at hand (e.g., freezing or fleeing in the face of a predator). Many of those animals can use learning to update those predictions, and many are able to experience interoceptive sensations (although see Craig, 2003 for differences in interoceptive processing in the primate v. non-primate brain). Yet the ability to represent diverse motor actions, visceral actions, interoceptive sensations, and exteroceptive sensations as related to one another by virtue of abstract themes such as “loss” is not likely to be possessed by all brains (see Bliss-Moreau, 2017; Lindquist et al., 2022). The Theory of Constructed Emotion hypothesizes that the human brain (and perhaps the brains of some other animals) can create categories in a unique way that is facilitated by language.

The role of language in emotion and predictive processing models of emotion are ultimately consistent with newer understandings of the neural architecture that supports emotions. Although emotions were once thought to be supported by dedicated neural structures (e.g., fear was thought to be generated by a subcortical network centered on the amygdala;

Panksepp, 2004), a century's worth of data has moved the science away from such models (see Barrett & Satpute, 2013; Lindquist et al. 2012; LeDoux, 2012; Hamann, 2012). Instead, recent network-based approaches to brain function consistently demonstrate that emotional experiences are associated with functional connectivity within sets of brain regions comprising domain-general brain networks such as the default mode network, salience network, frontoparietal network, dorsal attention network, and visual network (Doyle et al., 2021; Kober et al., 2008; Touroutoglou et al., 2015; Huang et al., 2018; Saarimaki et al., 2022; see Wager et al., 2015 for a meta-analysis) (see Figure 1 and chapter 2, Pessoa).

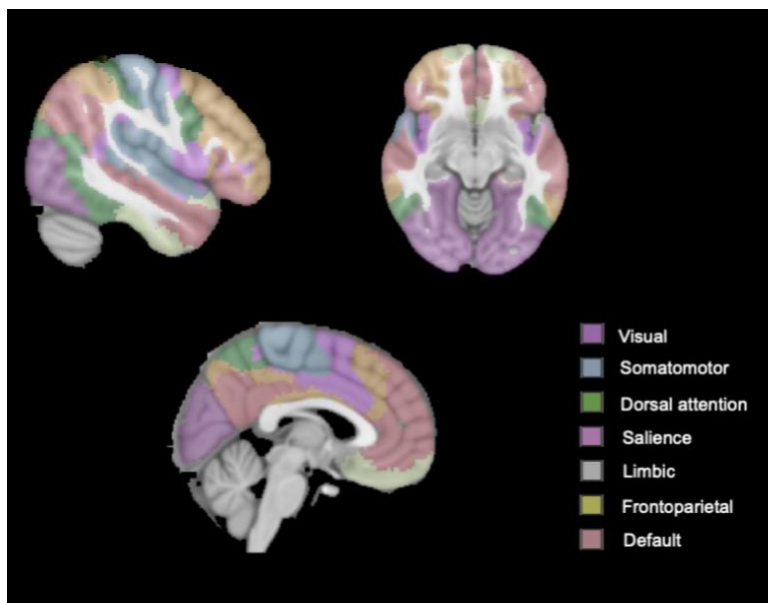


Figure 1. Intrinsic functional networks. Intrinsic functional networks from Yeo et al. (2011)'s analysis of resting state data. These "canonical" intrinsic networks have been replicated across many other studies using other methods and are thought to represent the functional organization of the brain (see Lindquist & Barrett, 2012).

In particular, experiences of emotion are consistently associated with the well-known default mode and salience networks (Barrett et al., 2016; Kleckner et al., 2017). The default mode network (pink, Figure 1) has been linked to semantic processing, conceptual knowledge and abstraction, self-referential processing, and autobiographical memory (Andrews-Hanna et al., 2010; Barrett & Satpute, 2013; Raichle, 2015; Satpute & Lindquist, 2019). The salience network (bright purple, Figure 1) has been linked to the detection of motivationally relevant

information and the representation of visceral sensations from the body (Barrett et al., 2016; Barrett & Satpute, 2013). Together, these networks are well-poised to make predictions about the internal and external sensations that are ultimately experienced as emotions. Indeed, these networks are themselves connected at rest, and the strength of functional connectivity between each of these networks is associated with the generation of skin conductance responses to evocative images (Kleckner et al., 2017). Via their connections to subcortical and brainstem structures as well as heteromodal association areas linked to abstract representation, these networks are thought to integrate incoming sensory information from the viscera and exteroceptive sensory systems (e.g., vision, audition, olfaction, etc.) with abstract conceptual knowledge and past experiences to form emotional predictions (Kleckner et al., 2017). Studies of the laminar organization of the primate brain (Barbas, 2015), functional connectivity gradients within the human brain (Zhang et al., 2019; Katsumi et al., 2022, 2023), and growing understanding of the normative role of predictive processing in brain function (Adams et al., 2013; Clark, 2013; Schulkin & Sterling, 2019), suggest that this network architecture may be the means by which emotion concepts represented via language help construct emotion.

The flow of predictions from regions associated with abstract representation and semantics

Tract-tracing studies of the primate brain have indicated a consistent structure of information flow within the cortex that is based on the gradients of laminar development. Barbas (2015) developed a model of cortical information flow based on the observation that different areas of the cortex vary in their number of distinct layers in a systematic way, and that this variation in laminar development maps onto the patterns of neural connection between cortical areas. Feedforward neural signals originate in areas with more developed, or granular, laminar structure and terminate in areas with less developed (agranular or dysgranular) laminar structure.

Feedback signals follow the opposite pattern. With respect to emotion, neural projections have been found from limbic cortices involved in semantic representation (Hoffman et al., 2015; Patterson et al., 2007), such as the ventromedial prefrontal cortex, to subcortical and brainstem structures involved in visceromotor regulation. This may be one mechanism by which conceptual representations “seed” action preparation.

For instance, based on incoming sense data, the brain may predict an instance of “fear,” which in turn may generate activation of the autonomic nervous system and skeletomotor system preparing the body to flee. Simultaneously, limbic cortices such as the ventromedial prefrontal cortex also project to motor, interoceptive, and sensory cortices (Barbas, 2015; Kleckner, 2017). These projections may represent predicted motor sensations, visceral sensations, and visual, auditory, olfactory, etc. sensations that are expected in the next moment. Critically, if predictions are sufficiently incorrect, prediction error signals are sent back to limbic cortex from motor, interoceptive, and sensory cortices to update the next wave of predictions. In this way, conceptual predictions only guide emotional experiences and behaviors to the extent that they are well-tuned to context. Prediction errors serve as learning signals (Clark, 2018; Friston et al., 2016), which may be the mechanism by which concept knowledge about emotions is updated via experience over the lifespan. For instance, while out for a run, the brain might predict an instance of “fear” in response to a snake laying on the path ahead. However, if visual prediction errors update that prediction to suggest that the object is only a stick laying vertically in the path, then the next wave of predictions would update that visual experience. As anyone knows, in this experience, one still receives that first set of prediction errors from the body, resulting in a brief wave of heightened arousal before the conscious experience that it is not truly a snake. Following

such an experience, learning may occur such that one's model of "fear of snakes" may be fine-tuned to represent how frequently one actually encounters snakes on their run.

In humans, the laminar gradient of feedback prediction and feedforward prediction error has been replicated with studies of functional connectivity gradients in the cerebral cortex, cerebellum, and hippocampus (Katsumi et al., 2021). Intrinsic functional connectivity in the cortex is organized primarily into a *predictive model to error* gradient, which is anchored at one end by default mode network regions that initiate prediction signals and fronto-parietal network regions that generate estimates of the precision of those signals. At the other end of the connectivity gradient are sensory cortices that generate prediction error signals and salience network regions that are thought to weigh the value of prediction errors. These findings suggest a neural organization of the predictive brain whereby agranular and dysgranular limbic cortices in the default mode network initiate visceromotor prediction signals informed by prior experiences and concept knowledge that are represented in default mode network regions. These prediction signals are sent to subcortical and brainstem structures responsible for visceromotor control that then coordinate the body's response given those predictions. Simultaneously, the prediction signals travel along efferent pathways to primary motor, interoceptive, and sensory cortices, preparing for motor action and for expected changes in incoming internal and external sensations. Afferent interoceptive and exteroceptive signals from the body and the world are then compared to those expected sensations, and any differences are sent as prediction errors in feedforward pathways to the limbic cortical regions in the default mode network, updating the internal model of the body in the world and fine-tuning subsequent predictions (Katsumi et al., 2022; Kleckner et al., 2017).

Through the lens of predictive brain function, emotions arise out of the process of prediction. This framework provides a mechanistic explanation for how and why concept knowledge is integral to emotional experiences and perceptions. The regions that comprise the default mode network are well-known to be involved in representing sensory information “offline”—they are active during autobiographical memory (Andrews-Hanna et al., 2010; Buckner et al., 2008; Schacter et al., 2007), semantic knowledge (Binder et al., 2009; Binder & Desai, 2011), mind-wandering (Mason et al., 2007), and prediction (Bar, 2009). The neuroanatomy of regions that comprise the default mode network makes them well-suited for such “offline” representation of prior sensory representations. The regions within the default mode network have lower neuronal density and higher connection distances than regions within primary sensory cortex, such as V1 (Collins et al., 2010). The result is that regions within the default mode network may represent sensory information more abstractly and with fewer dimensions than primary sensory regions (see Satpute & Lindquist, 2019). Since regions of the default mode network (e.g., vmPFC) project to amygdala, ventral striatum, and brainstem nuclei involved in visceromotor regulation and to primary sensory cortices, it is well-positioned to use representations of prior experience to initiate visceromotor and external sensory predictions. Regions of the default mode network further receive projections from visual cortex, auditory cortex, and primary interceptive cortex, making them well-positioned to resolve prediction errors from the viscera and the world and update the internal model (see Barrett, 2017; Barrett & Simmons, 2015; Chanes & Barrett, 2016). Insofar as words such as the English language categories “anger,” “disgust,” “fear,” “joy,” etc. help to acquire, organize, and update the content of the internal model, language is a core part of emotion construction in the brain.

The implications of the relationship between language and prediction are widespread; many of them we see in the literature reviewed at the beginning of this chapter. Language and emotion develop together across childhood (Mitchell et al., 2021; Nencheva et al., 2023; Nook et al., 2019; Ogren & Sandhofer, 2022; see Nook & Somerville, 2019; Shablack & Lindquist, 2019; Widen, 2013 for reviews), access to emotion concept words alters the experience and perception of emotion (Brooks et al., 2017; Fugate et al., 2010; Lee et al., 2018; Lindquist & Barrett, 2008), individual differences in the way that emotion concepts are represented and used in everyday life are reflected in the neural representation of those emotions (Brooks et al., 2019; Hoemann et al., 2021; Lee et al., 2017), impairment of default mode network regions critical to the representation of emotion concepts is associated with impairment in emotional processes (Bertoux et al., 2020; Campanella et al., 2014; Grossi et al., 2014; Jastorff et al., 2016; Lindquist et al., 2014; see Satpute & Lindquist, 2021 for a review), and impairment in lateral prefrontal regions critical to the access of emotion concept knowledge is associated with impairment in emotional processes (Souter et al., 2021). Finally, the last two decades of neuroimaging research have converged on a representation of emotion in the brain that is made up of large-scale, domain-general functional networks that are also implicated in the predictive generation of emotion using concept knowledge (Barrett et al., 2016; Doyle et al. 2021; Kleckner et al., 2017; Kober et al., 2008; Touroutoglou et al., 2015; Huang et al., 2018).

Outstanding questions and future directions

In this chapter, we have argued for a role of language in emotion that represents a fundamental shift from prior models of emotion and its neural instantiation that saw emotions as innate natural kinds and only left room for language as a translator. Instead of being innate, emotions are constructed by a predictive brain striving to maintain allostasis, and concepts

acquired through language serve as seeds for predictions that are experienced as emotion. This has implications for cultural and individual variations in emotions which have only begun to be explored (see Lindquist et al., 2022, for a discussion of culture and emotion), as well as for our understanding of emotional development.

We close by suggesting some directions for future research that will enhance our understanding of the role of concept knowledge in emotion, and ultimately our understanding of emotion itself:

- What are the cross-cultural differences in the neural correlates of emotions? Where do these differences primarily occur? If they are linked to representations in the default mode network, this would be consistent with predictive processing.
- Do variations in the neural representation of emotions map onto variations in the structure of emotion concepts in different languages?
- How do emotional development and language development interact in the brain? What does this relationship look like in early development? The development of the default mode network over the first two years of life is influenced by the caregiver relationship, and this relationship may scaffold the development of conceptual knowledge (Atzil et al., 2018; Atzil & Gendron, 2017). How might the caregiver relationship influence emotional and language development together in the brain?
- How are individual differences in emotional granularity reflected in the brain? If these differences are reflected in the default mode network, this would be consistent with the proposed role of the default mode network in representing emotion concept knowledge, knowledge which then “seeds” the experience of discrete emotions (Satpute & Lindquist, 2019).

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