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Emotional Objectivity: Neural Representations of Emotions and Their Interaction with Cognition

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Abstract

Recent advances in our understanding of information states in the human brain have opened a new window into the brain's representation of emotion. While emotion was once thought to constitute a separate domain from cognition, current evidence suggests that all events are filtered through the lens of whether they are good or bad for us. Focusing on new methods of decoding information states from brain activation, we review growing evidence that emotion is represented at multiple levels of our sensory systems and infuses perception, attention, learning, and memory. We provide evidence that the primary function of emotional representations is to produce unified emotion, perception, and thought (e.g., "That is a good thing") rather than discrete and isolated psychological events (e.g., "That is a thing. I feel good"). The emergent view suggests ways in which emotion operates as a fundamental feature of cognition, by design ensuring that emotional outcomes are the central object of perception, thought, and action.

Contents

1. INTRODUCTION

Since Plato's dialogues, Western culture has opposed emotion against reason. We think of reason as the foundation of culture and science, the royal road from barbarism to civilization. Historically, Western culture prescribed that allowing oneself to be guided by emotion is bad—the domain of women and the colonized. Consistent with this distinction, since Darwin and James, emotion—when it has been considered a valid area of research at all—has constituted a research domain separate and independent from the study of cognition. Within this domain, across many diverse models and theories, there has been agreement that emotion serves an evolutionarily conserved and adaptive system. All emotion models posit that emotional systems recruit physiological and motor responses to aid survival by allowing an organism to rapidly identify relevant events and prioritize resources accordingly. Moreover, since Paul MacLean (1949) coined the term limbic system in the mid-twentieth century, there has been a concerted effort to locate these conserved systems within a discretely emotional brain. Affective neuroscience has sought to identify emotion systems that are distinct and often opposed to evolutionarily newer regions subserving so-called cooler forms of cognition. Yet due to recent innovations in brain research, this siloized view of emotion and cognition is changing. An emerging view in cognitive neuroscience is that, rather than constituting a distinct and opposing system, emotion is a fundamental, inseparable component of cognition and its neural underpinnings (Lewis 2005, Pessoa 2008, Pessoa & Adolphs 2010).

A rapidly accumulating body of evidence indicates that all events are filtered through the lens of whether they are good or bad for us. In this article, with a focus on recent methodological approaches that characterize emotions as information states in the human brain, we review growing evidence that representations of emotion engage the whole brain rather than being restricted to

conventionally defined emotional circuitry. Emotional representations are observed at multiple levels of the nervous system and are both abstract/amodal and concrete/sensory specific. Emotional information not only engages the whole brain during an emotional experience but also tunes what we see of the world and helps determine how and what we learn and remember. Thus, rather than opposing emotion to cognition, we provide evidence that the primary function of brain-state representations is to produce unified emotion, perception, and thought (e.g., "That is a good thing") rather than discrete and isolated psychological events (e.g., "That is a thing. I feel good"). This understanding offers insight into how emotion operates as a fundamental feature of cognition, ensuring that emotional outcomes are the driving principle of perception, thought, and action.

2. BEYOND DIMENSIONS AND BASIC EMOTIONS: A MULTIPLICITY OF EMOTIONAL REPRESENTATIONS IN THE HUMAN BRAIN

Historically, emotion researchers have mostly agreed that at least some components of emotional experience are instantiated in conserved biological systems. For decades, a debate has raged about whether the fundamental components of emotion are discrete basic emotions (anger, fear, happiness, etc.), subserved by modular neural systems, or whether emotional states are points in a two-dimensional space along an axis of valence (goodness/badness or approach/avoidance) and emotional arousal (from calm to excited/agitated).

With the advent of human brain imaging, researchers hoped that identifying the neural substrates of emotion would settle the issue. Initially, they aimed to identify brain regions dedicated to a specific emotion (e.g., the amygdala and fear) or dimension (e.g., the amygdala and negative valence). This attempt was unsuccessful, as regional activation patterns turned out to be complex and context dependent. More recently, the emphasis has shifted to a focus on networks or systems, an approach made more tractable by innovations in approaches to analyzing brain imaging data.

In order to understand how thinking about brain systems involved in emotion evolved, it is helpful to understand how they are operationalized in human neuroimaging research. Briefly, functional magnetic resonance imaging (fMRI) measures the blood-oxygen-level-dependent (BOLD) response. The BOLD response is an index of magnetic properties associated with the change in ratio of oxygenated to deoxygenated blood as it changes over a period of several seconds in response to a stimulus or cognitive event. The spatial unit of measurement in fMRI research is the voxel (or cubed pixel), created by imposing a three-dimensional grid pattern on the brain. A voxel encompasses activity in a region composed of gray matter, white matter, cerebrospinal fluid, or a combination of these, and may indirectly reflect the activity of ∼630,000 neurons.

In the univariate approaches to analyzing fMRI data that characterized the early years of fMRI research, separate regressions are run on BOLD activation in each of thousands of voxels separately or on activity averaged across the voxels in a prespecified brain region. This process produces the familiar blobs, or heat maps, depicting clusters of adjacent voxels showing statistical maps indicating voxels that reliably differentiate experimental conditions. While the univariate approach has been useful in basic brain mapping projects, such approaches are hampered by a number of limitations, including huge numbers of statistical comparisons (Poldrack & Farah 2015). They are also limited to simple contrastive comparisons of more or less activation between experimental conditions, which can be hard to interpret—especially considering the indirect nature of the BOLD response. This approach treats each voxel independently, which clearly does not reflect the structural or functional anatomy of the brain or characterize brain networks at any scale. With regard to research on emotion, attempts to localize the neural correlates of specific emotions by using these univariate methods have been inconsistent. For example, attempts to map activation

Valence: refers to a continuous scale of subjective feeling, from positive to negative, or the degree of approach versus avoidance that is elicited

Emotional arousal: the degree of physiological arousal or subjective feeling of agitation or excitement, which can be either positive or negative in valence

fMRI: functional magnetic resonance imaging

BOLD: blood-oxygen-level dependent

Voxel: a three-dimensional pixel; in fMRI, it refers to a cubed unit created by imposing a grid on the brain for measurement purposes

Univariate analysis of functional magnetic resonance imaging (fMRI) data: individual regressions are performed in each voxel or prespecified brain region to localize activation that differentiates between experimental conditions

of the amygdala to fear or negative emotion have been complicated by findings that the amygdala is sensitive to many forms of emotional and otherwise salient stimuli, including appetitive and surprising ones (Sergerie et al. 2008). With regard to debates about dimensional versus discrete emotions, studies reporting lists of multiple brain regions activated above a statistical threshold in support of either view have failed to provide conclusive evidence (for a review, see Kragel & LaBar 2016). As a way of addressing some of these limitations, human brain imaging research has been moving away from relying solely on univariate approaches and toward multivariate and network approaches to data analysis (Kragel et al. 2018).

Rather than measuring relative degrees of BOLD activation in a single voxel, multivariate approaches such as multivoxel pattern analysis (MVPA) focus on patterns of activation across distributed voxels. Cross-voxel patterns of activation that predict a category of stimulus or cognitive process elicited by a task are interpreted as neural representations or readouts of that stimulus or process. In some of these so-called mind-reading approaches, machine learning classifiers are trained on one data set to be able to predict the stimulus category or cognitive process elicited in any given trial versus another (e.g., on the basis of the activation pattern in a given trial, the classifier can predict to a certain level of accuracy whether the participant is looking at a face or a house). In a recent innovation, more computationally intensive convolutional neural nets have also been deployed (see, e.g., Kim et al. 2019).

Another MVPA approach, representational similarity analysis (RSA), uses correlation matrices to examine the degree of similarity or dissimilarity between voxel activation patterns that index a given cognitive process (Kriegeskorte & Kievit 2013). RSA emphasizes the relationships between stimuli and processes in an abstract and multidimensional representational space. For example, in regions of the ventral visual cortex that are sensitive to object categories, we may represent the face of an individual (e.g., the President of the United States) as more like the face of another individual (the friendly barista who makes your coffee every morning) than a given building (the White House). At the same time, regions of the brain sensitive to other semantic associations may represent the President as closer to the White House than the barista. So we can say that in the representational space of the ventral visual stream, faces are closer to other faces than they are to buildings, but in another region objects associated with the presidency are closer in representational space than those associated with your morning coffee routine. In yet another region, such as regions of the ventral prefrontal cortex that are sensitive to emotional associations, depending on your feelings about the President, his face may be represented as closer to or farther from the delightful coffee-producing barista versus a loathed sadistic dentist. By characterizing the representational geometry of regional activity patterns, representational mapping reveals not only where and what but also how information is represented.

With regard to the debate about whether the brain represents emotions as dimensional or discrete, more fine-grained multivariate approaches have suggested that the answer to the question of whether emotional representations reflect basic or dimensional emotions is "yes, and," rather than unequivocally supporting one view over another. Recent studies using MVPA have examined BOLD or electrophysiological responses to (*a*) emotionally or motivationally salient stimuli, such as emotionally arousing pictures or sounds (Baucom et al. 2012; McNamee et al. 2013; Chikazoe et al. 2014; Chang et al. 2015; Kim et al. 2015, 2019; Bush et al. 2018), (*b*) emotional states evoked by memories or film clips (Sitaram et al. 2011; Kassam et al. 2013; Kragel & LaBar 2015; Kragel et al. 2016; Saarimaki et al. 2016, 2018), and (*c*) emotionally expressive faces or bodies (Peelen et al. 2010). Such studies have found evidence of dimensional representations (Baucom et al. 2012, Bush et al. 2018, Kim et al. 2019), discrete emotions (Peelen et al. 2010; Sitaram et al. 2011; Saarimaki et al. 2016, 2018), or both (Kassam et al. 2013, Kragel & LaBar 2015, Grootswagers et al. 2017). What is found often depends on the type of paradigm used (e.g., responses to salient

Multivoxel pattern analysis (MVPA): multivariate analysis approach that examines patterns of fMRI activation across multiple voxels to predict a stimulus category or cognitive process

Representational similarity analysis (RSA): a form of MVPA that examines correlations between voxel patterns to detect similarity between representations of stimuli or cognitive processes

stimuli versus evocation of emotional state), the stimulus set used (for example, stimuli in the International Affective Picture System (IAPS) and the International Affective Digitized Sound System are selected to reflect dimensions of valence and arousal rather than discrete emotions), and what the classifiers are trained on. Overall, these studies tell us that measurable patterns of brain activity (i.e., brain states) are indeed correlated with things we subjectively experience and describe in language. Notably, however, many of these studies have observed predictive patterns in voxels well outside of traditional emotion areas of the brain (e.g., Sitaram et al. 2011; Vickery et al. 2011; Baucom et al. 2012; Kassam et al. 2013; Chang et al. 2015; Kragel & LaBar 2015; Saarimaki et al. 2016, 2018), suggesting the ubiquity of the influence of motivation and emotion on brain activation in areas traditionally associated with cognition. Below, we review in more detail findings of representations of emotional feelings or states; of responses to emotional meaning in sensory systems; and of emotionally modulated learning, attention, and memory.

3. MAPS OF EMOTIONAL FEELINGS

MVPA has established a consistent relationship between distributed voxel activation patterns and subjectively felt emotional states, which have been elicited in several ways. For example, in one study, method actors were asked to use scenarios to evoke nine prespecified emotions (Kassam et al. 2013). On the basis of patterns of brain activation—which extended beyond conventionally defined emotional circuitry—the researchers used a classifier to predict the subjectively experienced emotion within each subject. The classifier also did reasonably well in predicting one participant's emotional state when trained on the brain activity of other participants. The researchers then employed principal components analysis (PCA) to reduce the data. This analysis revealed one component that mapped well onto the continuum of valence and another that mapped (somewhat less well) onto arousal, suggesting that the activation patterns also reflected dimensional experience. As classifiers were able to successfully decode discrete emotions and, to an extent, dimensions of valence and arousal from brain activation, we can conclude that the brain represents all of these aspects of emotional experience. We can also conclude that such representations are extracted from activity in regions that extend well beyond limbic circuitry.

In other studies, participants watched films and listened to music designed to evoke specific emotions (Kragel & LaBar 2015, Saarimaki et al. 2016). On the basis of activation patterns from voxels distributed throughout the brain, classifiers predicted each emotional state at above-chance levels. They also predicted emotions evoked by music from those evoked by film, and vice versa, suggesting that the states were independent of stimulus modality. Using guided imagery to elicit emotion, one group of researchers added eight nonbasic emotions to previously studied basic emotions (Saarimaki et al. 2018). In this study, although the classification accuracy was better for basic emotions, it was above chance for most of the other emotions. Again, these findings indicate that a wide range of subjectively experienced emotional states can be decoded from patterns of BOLD activation across the whole brain.

Another study aimed to identify a neural signature of negative emotional response [picture-induced negative emotion signature (PINES)]. A total of 185 adults rated how intensely negative emotional scenes made them feel (Chang et al. 2015). Researchers used a classifier to successfully predict which of two images was experienced as more or less intensely negative. The PINES model mapped onto a distributed pattern of activations in the left amygdala, right anterior insula, posterior cingulate cortex, and high-level visual cortex, although many other clusters contributed as well. The signature was distinct and dissociable from a signature of somatic pain elicited in a separate study. Some regions (amygdala, insula, and anterior cingulate cortex) were common to maps of both negative affect and pain, but patterns were mostly uncorrelated. PINES predicted

increasing levels of negative affect in response to pictures but not increasing levels of somatic pain, and vice versa for the pain signature. Thus, PINES was specific to negative affect as elicited by pictures—at least relative to pain. In contrast, canonical resting-state networks could predict the stimulus modality (picture or pain) but not variations in experienced intensity.

The PINES network was also fractionated into subnetworks, including canonical limbic networks, and virtual lesions were created by removing one of these at a time. The model was able to perform effectively without any one of the subnetworks. This finding provides evidence against a structure or network-centric view of emotion that has been the focus of much research since MacLean, and it supports a view that the whole brain is the emotional brain. Additional studies using multivariate approaches to decoding responses to emotionally salient images have found representations of valence from voxel patterns across the whole brain (Baucom et al. 2012; Kim et al. 2015, 2019), supporting the claim that valenced information is widely distributed.

Another approach to examining emotional responses in the brain involves the use of classical conditioning and reinforcement learning paradigms, wherein neutral stimuli come to be associated with reward or punishment. Multivariate approaches to the reinforcing and punishing stimuli themselves have revealed that information related to motivational/emotional states extends well beyond conventionally defined reward circuitry. For example, in one study participants played either a rock–paper–scissors or a penny-matching game (choosing head or tails) against a computer (Vickery et al. 2011). In this study, more than 30% of the voxels across the whole brain were able to discriminate wins from losses. Both wins and losses were discriminable from widely distributed activations elicited in trials in which there were no wins or losses (i.e., ties), indicating that these large-scale effects were valence related. In contrast to this highly distributed response to reward, the pattern of activity predicting the actual choices made was much more localized, suggesting that the motivational response reflected the ubiquity of brain regions that are sensitive to emotional/motivational outcomes.

There is also evidence of whole-brain signatures of emotional states that spontaneously rise and fall when we are not occupied with a specific task or external event. Using emotion decoding algorithms developed previously (Kragel & LaBar 2015), researchers predicted emotional-state from resting-state activations (patterns of correlated BOLD activity between regions in the absence of external stimulus or task) of nearly 500 participants (Kragel et al. 2016). Correlated activations from voxels all over the brain suggested that the brain as a whole spontaneously fluctuates between emotional states over the course of minutes. Moreover, state and trait anxiety scores predicted more classifications of fear, and depression scores predicted more sadness and fewer contentment classifications. These findings confirmed that subjective states mapped onto brain states and suggested trait-level patterns in emotional fluctuations across the whole brain.

William James famously proposed that, when we unexpectedly meet a bear in the woods, we know we are afraid because we feel our racing hearts and sweating palms. Since then, somatic information has been considered to be a central feature of emotional feelings (see, e.g., Damasio 1996, Craig 2002). Moving away from brain-centric cognitive neuroscience, an increasing number of studies have incorporated indices of somatic processes to investigate brain–body interactions linked to emotion.

A recent study harnessed the statistical power of online investigations alongside a large brain imaging database to identify embodied "fingerprints" of emotional states, very broadly construed (Nummenmaa et al. 2018). These authors aimed to measure dimensions of subjective experience, including intensity of bodily sensations, saliency of mental experience, and valence across 100 subjectively experienced states. The states were indexed by 100 prechosen words, which the authors characterized as reflecting homeostatic (e.g., hunger) and emotional (e.g., pleasure) states as well

as such "cognitive" states as recall. They asked online participants to illustrate their assessment of the relative similarity of the 100 words in "feeling space" by moving them closer to or farther from one another on a screen. In a separate study, the authors asked online participants to color in the parts of a body icon to indicate where each state was felt. They also measured neural representations mapping onto as many of those words as they could find using a publicly available fMRI database, Neurosynth (see **http://neurosynth.org/**). They found that words mapped in feeling space clustered into five categories: positive emotion, negative emotion, cognition, illness, and homeostasis (homeostasis included "motivational" states such as hunger, thirst, and sexual desire). Each of the 100 individual states was associated with a distinct body map, which the authors describe as a fingerprint of that feeling state. The more similar two fingerprints were, the more similarly they were subjectively experienced in general. The authors then used RSA to look at representational similarity between features of subjective experience and patterns of brain activation. The activation patterns from the fMRI patterns were correlated with the rated bodily saliency of the words, the body map patterns, and to a lesser extent the semantic similarity of the words. The authors interpreted this finding as indication of neural signatures of subjectively experienced body states.

Other studies have linked patterns of emotion-related brain activation directly to somatic and visceral signals. Classifiers have been trained to predict dimensions of arousal and valence elicited by emotionally evocative sounds based on heart rate variability (Nardelli et al. 2015). Responses to heart rate have been observed in many regions across the brain, as well as in the primary somatosensory cortex (S1) (Kern et al. 2013). Finally, in a study directly linking somatic responses to decoded brain states (Bush et al. 2018), researchers used MVPA to predict brain activation patterns associated with valence and arousal from skin conductance responses. Skin conductance sensitivity to arousal was associated with activation in midline regions such as the dorsal cingulate cortex and precuneus (Bush et al. 2018). Thus, indices of physiological arousal have been decoded from patterns of brain activation distributed beyond regions directly implicated in visceral information and autonomic activity.

Focusing more specifically on a single emotional state (response to social threat), another study (Eisenbarth et al. 2016) delineated common and distinct relationships between activity in two different somatic systems (skin and heart) and brain-wide patterns of activation. To induce stress, researchers asked participants to prepare speeches on highly technical topics (e.g., tariffs) to give to a panel of experts while fMRI, heart rate, and skin conductance were measured. They trained a classifier on whole-brain patterns of activation, used it to predict heart rate and skin conductance responses, and then examined the brain maps reflecting the regions that contributed to each prediction. In this study, the pattern of activity associated with autonomic activity mapped reliably onto a canonical limbic network. Thus, unlike in many studies examining multiple emotions reviewed above, brain activation predicted by autonomic indices of the stress response mapped fairly well onto established emotional circuitry identified in nonhuman animal studies. This finding suggests that physiological/somatic aspects of some emotional responses can be tied to precise biological processes in evolutionarily conserved circuitry. Yet, as the evidence reviewed above indicates, subjective experience of emotion involves representations of emotion that extend beyond this limbic circuitry to engage other cortical and subcortical structures implicated in many aspects of cognition and action. Moreover, distinct patterns of emotional representation can be observed in subjectively experienced body states that extend beyond the brain. Indeed, in the rush to model emotion in the brain, it is important to recall that—by definition—emotional systems must engage the whole body to prepare the entire organism to respond to what is important to its survival and well-being.

4. REPRESENTATIONS OF AFFECTIVE AND MOTIVATIONAL VALUE ACROSS THE SENSES

Value: refers to the magnitude and probability of reward associated with a stimulus

OFC: orbitofrontal cortex

Dimensional views of emotion have assumed the existence of a universal, amodal hedonic system, one that allows you to evaluate your morning espresso, the smell of freshly cut grass, and a gentle caress as pleasurable, each in its own right. The relative pleasantness of these experiences can be rank ordered in a space that would, at the other extreme, be occupied by things you find distinctly unpleasant—the sound of a dentist's drill or the smell of rancid milk. To be able to compare such discrepant forms of stimulation and choose the appropriate courses of action, the brain has to convert a multiplicity of sensory experiences into a common currency. Numerous neuroimaging findings clearly suggest that diverse rewards activate a shared or common set of interacting brain regions responsible for maintaining amodal representations of pleasantness (Berridge & Kringelbach 2015).

While affective neuroscience has focused on dissociating neural signatures of valence from arousal, parallel research in value-based decision making has focused on dissociating the overlapping constructs of salience (motivational importance) and value (degree of reward). One influential study investigated the role of the orbitofrontal cortex (OFC) in coding the common modality-general value currency of stimuli that ranged from concrete primary rewards (food) to those that were more abstract (trinkets and money) (McNamee et al. 2013). On each trial, participants indicated how willing they were to pay for each type of reward. To test common currency (category-independent value), a classifier was trained to detect value in one category and tested in the other categories. To detect category-dependent value, the classifier was trained on one category and tested on its ability to predict value only from that category. Category-independent coding for trinkets and food was observed for two regions of medial OFC. Within the OFC, there were also indices of a ventral–dorsal gradient ranging from category specific to category independent. While this study found evidence of a common currency for value that was consistent with a role for OFC in dynamic appraisal of sensory information (Dixon et al. 2017), all stimuli in this study were visual and focused on reward. Thus, further questions concern the representation of valence in the presence of both rewarding and aversive stimuli, as well as the relation between common and sensory-specific information about valence.

5. MODALITY-SPECIFIC REPRESENTATIONS OF AFFECT

It is not clear whether an abstract, amodal representation of valence is the only form of internal currency, or whether it is computed (i.e., an eigenvector) from modality-specific instantiations of valence. A common hedonic valence code implies a reduction in the dimensionality of the information. Yet, a high-dimensional evaluation of stimulus features may be advantageous in ecological settings. Maintaining higher-granularity valence representations that are interleaved within specific sensory modalities could be important in the adaptive guidance of action, especially in situations of uncertainty. Action selection frequently occurs in the context of multiple stimulus attributes whose relative importance requires some degree of dynamic calibration. For instance, an animal foraging for food might need to emphasize a highly specific set of stimulus attributes within its environment (e.g., a food source that is high in protein and salt content), rather than simply searching for something pleasant in an overly abstract sense. In other instances, natural contents may offer competing affordances: It may be prudent to avoid a food dish that is visually repulsive, for example, no matter how pleasant its aroma might be.

In humans, there is evidence for modality-specific representations across all sensory systems (for a review, see Miskovic & Anderson 2018). Multivariate pattern analyses have been used to

recover both modality-general and modality-specific representations of valence, with evidence that modality-specific valence can be decoded solely on the basis of information from the primary sensory cortices. In the next two subsections, we focus on touch and taste as a representative proximal systems and vision as a representative distal system.

5.1. Pleasurable Touch and Pain: The Cutaneous System

S1 is modulated by centrally mediated expectations of pain and pleasure (Pleger et al. 2008, Gazzola et al. 2012). Yet beyond central modulation, recent findings indicate that the very structure of the wiring of the cutaneous system, from its interface with the world on the skin to the central nervous system, is emotionally valenced. Within the cutaneous system it is well established there are fast myelinated afferent fibers that facilitate sensory discrimination, conveying information about the timing and location of sensory stimulation. In addition, it has long been known that, within the pain system, nociceptors (pain receptors) convey information about affective aspects of pain through additional, slower, unmyelinated afferent pathways. More recently, evidence of a parallel system for pleasant touch has emerged, revealing mechanoreceptors (which are responsive to mechanical stimuli such as touch or sound) found only in hairy skin and not on the glabrous skin of the palms, where previous research had focused (McGlone & Reilly 2010, McGlone et al. 2014).

Studies using a technique called microneurography, a method of recording single peripheral nerve activity, in humans have shown that these C-tactile afferents respond more to pleasant soft brushes than to neutral stimulation, and they show the highest firing rates at stroking at speeds that are subjectively rated as most pleasant (Olausson et al. 2002, Loken et al. 2009). These findings have been interpreted as supporting the importance of affiliative social touch in mammals. Thus, in the cutaneous system there are dedicated channels where valence is coded from the sensory periphery and from the moment of contact, rather than evaluated centrally and then conveyed to sensory cortices via reentrant processing. These dedicated channels project to the insular cortex and OFC, which have been found to be sensitive to the valenced dimensions of pleasurable and painful touch (Olausson et al. 2002, Rolls et al. 2003).

Furthermore, discrimination between pleasant and unpleasant touch has been observed in the insula, but not in S1, of two-month-old infants (Jonsson et al. 2018). This finding suggests that the evolutionarily older unmyelinated pathways function earlier in infancy and rely less on learning than the slower-developing, fast-acting pathways for sensory discrimination (Jonsson et al. 2018). The existence of channels dedicated to pleasurable and aversive touch—distinct from discriminatory function—supports the position that affective valence is built into or easily imprinted onto sensory systems and, in this modality, begins to operate early in infancy.

5.2. Taste: The Gustatory System

Similarly, in the gustatory system, information is affectively valenced from the point of interaction with the world. Beginning at the tongue, taste receptors tuned toward sweet and bitter may serve as primary reinforcers and punishers, providing clear evidence that valence is integral to the most fundamental characterization of taste (Barretto et al. 2015, Peng et al. 2015). Functional neuroimaging in humans indicates that the affective quality of taste is encoded in response patterns within the anteroventral insula and posterior OFC, the putative primary and secondary regions of the human gustatory cortex (Small et al. 2003). Using high-resolution fMRI with MVPA, a recent study identified regions of the insula and overlying operculum sensitive to the subjective quality of sensation (e.g., sweetness, saltiness) in the gustatory cortex (Chikazoe et al.
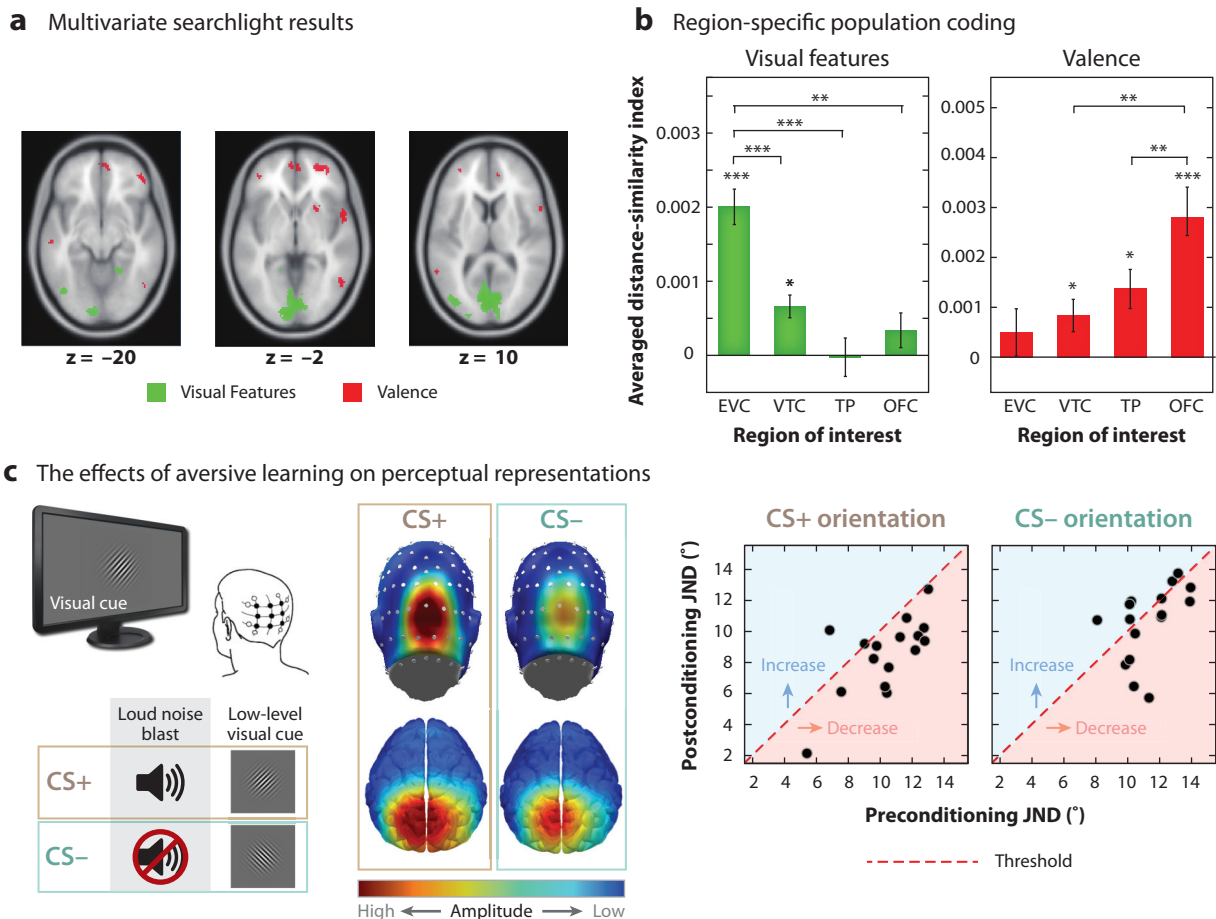
2019). Having expectations about the pleasant or aversive quality of taste also modulates responses in more posterior regions of the human insula, which are arguably more sensory in function (Nitschke et al. 2006). Together, these findings imply that at the level of the sensory cortices, sensitivity to the hedonic impact of taste is not clearly separable from the basic analysis of stimulus input. This conclusion is also suggested by the results of a representational similarity analysis of the gustatory-specific cortex demonstrating that similarity or dissimilarity in taste-evoked subjective affect corresponded to population-level activity across stimuli (Chikazoe et al. 2014). The representational geometry of activity patterns in the gustatory cortex indicated that extreme positive and negative valence were the furthest apart.

5.3. Vision

Humans are exceptionally visual creatures. Our ability to rapidly increase activation in the visual system in response to emotional events, so that we see what is relevant more selectively and vividly, is particularly adaptive. A recent fMRI study aimed explicitly to decode patterns discriminating modality-general from modality-specific dimensions of emotional valence (Chikazoe et al. 2014). Participants viewed a variety of complex natural scenes from the IAPS ranging in valence from unpleasant to pleasant. In a separate experiment, the same participants were exposed to a range of pleasant to unpleasant tastes. Analyses of common currency focused on the OFC. Here, voxel activity was organized by valence independently of sensory origin—that is, the OFC again showed a common neural code. In this experiment, the common code integrated information from two modalities, useful for equating the aversiveness of the sight of a carcass with a nasty smell or a rotten taste. By contrast, multivoxel patterns of activity in object-sensitive regions of the ventral visual cortex were diagnostic of valence specific to the visual modality, not shared with gustatory experience. Thus, a dissociation was observed wherein the OFC coded a common currency representing stimulus valence across sensory modalities, while regions of high-level visual cortex coded affective information that was specific to visual information. This last finding suggests that the relative pleasantness of objects in the world may be coded as a feature of their processing that distinguishes more from less salient items at the level of high-order visual cortex. Critically, these brain responses were distinct from those representing low-level physical or even high-level object properties (e.g., animacy) of the images (**Figure 1a,b**). The implication is that the body and brain are constructed such that the emotional valence of events can be instantiated distally where our senses meet the environment. Encoded as objective features of the world, the specific appetitive-to-aversive qualities of stimuli are then integrated into a common code that can guide further sensory processing, tune attention, and prioritize learning and memory for what is most important.

6. HOW DOES EMOTION INFLUENCE COGNITION?

The multitude of studies finding that emotional and motivational information can be read out from activation across the brain is indicative of the influence of emotion and motivation on cognition. Emotional arousal signals events that are important to attend and remember in the interest of survival. As a result, we typically remember emotionally arousing events better than mundane ones (LaBar & Cabeza 2006), reliving the birth of a child or a teenage humiliation with a high degree of vividness decades later. We also pay heightened attention to emotionally relevant aspects of our environment that signal potential punishment and reward (Pourtois et al. 2013, Markovic et al. 2014). Indeed, emotion influences a host of cognitive processes, including attention, working memory, learning, episodic memory, cognitive control processes, decision making,

a Multivariate searchlight results

b Region-specific population coding

c The effects of aversive learning on perceptual representations

Figure 1

Region-specific population coding of visual and affective content of visual stimuli. (*a*) Multivariate searchlight analysis (an MVPA technique that searches the whole brain for regions where affective/visual information can be decoded) revealed distinct areas representing coding of visual (*green*) and affective (*red*) features of emotional scenes. (*b*) Averaged distance-similarity index, a measure of correspondence between neural representations and measures of subjective valence and visual features in the regions of interest. The transverse section level is indicated by the *z* coordinates in Montreal Neurological Institute (MNI) space. The error bars represent the standard error of the mean. ***$p < 0.001$, **$p < 0.01$, and *$p < 0.05$ Bonferroni corrected (data from Chikazoe et al. 2014). (*c*) In aversive conditioning experiments with steady-state visual evoked potentials, a simple, low-level visual cue such as a sinusoidal grating with a specific angle of orientation is rhythmically modulated and entrains populations of neurons in human visual cortex. A specific orientation (e.g., at 45° clockwise) is consistently paired with an unpleasant loud noise blast (CS+ cue), while a distinct orientation (e.g., at 45° counterclockwise) signals respite from the aversive sound (CS− cue). Subsequently, the CS+ cue amplifies responses over occipital electrodes relative to the CS− cue (more red indicates higher amplitude), an effect that can be source-localized to early visual cortex (data from Miskovic & Keil 2014). Psychophysical methods demonstrate that aversive conditioning can also enhance visual discrimination acuity, leading to lower thresholds for the detection of changes in the orientation of conditioned gratings (data from Rhodes et al. 2018). Abbreviations: CS, conditioned stimulus; EVC, early visual cortex; JND, just noticeable difference; MVPA, multivoxel pattern analysis; OFC, orbitofrontal cortex; TP, temporal pole; VTC, ventral temporal cortex.

and spontaneous thought (for a review, see Okon-Singer et al. 2015). In the following subsections, rather than attempting to be exhaustive, we focus on cognitive neuroscience research that probes current questions about emotional modulation of associative learning, attention, and memory.

6.1. Learning

Above, we have stressed the sensitivity of primary sensory cortices to valenced information. There is also evidence that primary sensory cortices can be rapidly shaped by emotional learning, such that the resultant learning is not restricted to central modulation of the senses by the amygdala, hippocampus, and other multimodal structures. Rather, primary cortices can show plasticity in responses to emotional salience: Both aversive and appetitive conditioning studies in nonhuman animals have provided evidence that rapidly learned associations with aversive or rewarding outcomes tune activity to conditioned stimuli in the early auditory and visual cortices (for a review, see McGann 2015). Aversive conditioning elicits stronger (higher-amplitude) responses within a given population of neurons (Gdalyahu et al. 2012). Moreover, with training, theta oscillations of rat V1 neurons evolve from responding to visual features of stimuli to the timing and rate of associated reward—that is, to coding learned affective motivational meaning (Zold & Hussain Shuler 2015). In the primary auditory cortex, conditioning can rapidly increase metabolic activity and shift tuning of individual neurons toward the conditioned auditory frequency, reshaping tonotopic maps (Weinberger 2004). In the olfactory system, aversive conditioning modulates activity in olfactory sensory neurons, indicating that this system can respond to affective salience at its earliest point of contact (Kass et al. 2013). We suggest that the magnitude of representations of conditioned stimuli primary in sensory cortices reflects the magnitude of its affective relevance within an organism's behavioral economy (Rutkowski & Weinberger 2005).

Basic representations of valence may also be embedded in distributed modality-specific population codes (representations emerging from joint activities of large populations of neurons) between and across regions that include higher-order sensory cortices (Chikazoe et al. 2014). In humans, population-level neuronal processes underlying rapid visual cortex plasticity have been observed with aversive conditioning (**Figure 1**) (Miskovic & Keil 2013a,b; 2014). Using steady-state visual evoked potentials (ssVEPs, or electroencephalogram activity elicited by measuring power evoked by flickering stimuli at a fixed frequency), Miskovic & Keil (2013b) demonstrated that selective amplification of visual cortex activity for a conditioned stimulus (CS+) occurred only when the aversive outcome immediately followed the CS+. Such changes also exhibited associative specificity when presented in compound arrays (Miskovic & Keil 2013a). These authors interpreted their results as reflecting the importance of Hebbian-like associations between cell assemblies within the visual cortex rather than by prefrontally mediated processes. In a later study directly examining neural functions associated with short-term plasticity, ssVEPs were used to examine effects of conditioning on orientation tuning (sensitivity to the orientation of the lines of a grating) in the visual cortex (McTeague et al. 2015). In this study, enhancement of activity for the conditioned orientation was accompanied by the greatest suppression of activity for orientations that were most similar to the conditioned one, suggesting a tightening of tuning to features associated with affective meaning. Thus, although the data are still preliminary and controversial, there is some evidence that visual cortex sensitivity to affective–motivational salience increases gain in neurons that are preferentially tuned to relevant features and increases the specificity of neuronal representations. Converging psychophysical evidence suggests that these learning-dependent changes translate into improved sensory discrimination for conditioned cues (see, e.g., Li et al. 2008, Rhodes et al. 2018).

Emotional or motivational salience: refers to the magnitude and probability of both reward and punishment associated with a stimulus

ssVEPs: steady-state visual evoked potentials

6.2. Attention

Learning about the affective qualities of the world also tunes attention to them, such that we prioritize features of emotionally relevant information before we ever encounter it. A large body of research has investigated the phenomenon we have called affect-biased attention, defined as attentional guidance by objects or events associated with emotional arousal (Todd et al. 2012a). While emotional salience influences attention in multiple sensory domains, in this section we focus on visual selective attention. Visual selective attention involves prioritizing information for awareness and action by enhancing visual cortex activation to relevant stimulus features and locations while suppressing activation to competing ones. Building on canonical models that emphasize voluntary attention to what is currently task relevant (task-based attention) and reflexive attention to low-level visual features of a stimulus (feature-based attention), recent models have emphasized a third category of mostly implicit guidance of attention shaped by personal history (Awh et al. 2012, Chelazzi et al. 2013, Todd & Manaligod 2018). The diverse processes subsumed under the category of history, or selection history, include statistical learning, semantic relatedness, and history of association with reward and punishment. Which sources of attentional guidance take precedence at any moment are thought to depend on the goals that are prioritized in that context (Todd & Manaligod 2018).

As we review below, although there is overlap between the psychological constructs and underlying brain systems, research on affect-biased attention has focused on modulation of the visual cortex by networks centered on the amygdala (or amygdalae, as this structure consists of two clusters of distinct subnuclei), while that on reward-biased attention has focused on modulation by midbrain reward circuitry. Competing influences of these modulatory systems are thought to be resolved when or before attention is ultimately prioritized at the level of cortical topographical priority maps of the visual field, where patterns of neuronal firing predict the location of subsequent eye movements (Bisley & Goldberg 2010, Awh et al. 2012).

Recent theoretical frameworks have emphasized the dynamic nature of priority landscapes, emphasizing constant shifts in topography that accompany changes in what is currently relevant (Todd & Manaligod 2018). These, in turn, are informed by memory—by neurocognitive patterns developed through experience, which are activated in a manner specific to a given context (Anderson 2015). For example, the aspects of the same winter landscape that capture attention for their threatening and rewarding qualities will be different when we are driving on slippery roads versus when we are skiing.

6.2.1. Affect-biased attention.

Almost two decades of research have revealed that association with emotional arousal, both positive and negative, prioritizes attention when spatial and temporal resources are limited (for reviews, see Mather & Sutherland 2011, Todd et al. 2012a, Markovic et al. 2014, Vuilleumier 2015). Whereas much laboratory research has focused on processes occurring over minutes, hours, or days, attentional tuning to affective salience can also result from experience on much longer timescales. A study using magnetoencephalography observed prioritization of combat-related stimuli for soldiers returned from duty in Afghanistan (Todd et al. 2015b). This effect was heightened in the presence of posttraumatic stress disorder (PTSD). In soldiers with PTSD, reduced activation in cingulate regions associated with fear regulation was accompanied by increased activation in the visual cortex for combat-related stimuli relative to healthy soldiers with the same level of combat experience. Similarly, compared with control participants, airplane passengers who experienced a near crash in the middle of the Atlantic showed attentional prioritization of stimuli associated with the event a full decade after the event (Lee et al. 2013). Together, these findings suggest that long-term life history plays a crucial role in emotional tuning of attention.

Affect-biased attention: guidance of attention by stimuli associated with emotional arousal linked to history of pleasure or pain

Reward-biased attention: guidance of attention by stimuli associated with the probability of gaining or losing reward

6.2.2. Reward-biased attention. Recently, a growing body of attention research has focused on the influence of reward on attentional prioritization (for a review, see Chelazzi et al. 2013). These studies have shown that attention is guided by the features of stimuli as well as the spatial locations that have been associated with reward (Anderson et al. 2011, Chelazzi et al. 2014). Learning to associate locations in the visual field with reward can alter visual priority maps (Chelazzi et al. 2014), and reward-associated stimuli are prioritized under conditions where attentional resources are constrained in time as well as space (Raymond & O'Brien 2009). More specifically, attention has been found to be prioritized for stimuli associated with gaining reward over those associated with preventing loss (Hu et al. 2018). Moreover, recent research suggests that reward-biased attention is context specific, such that attentional capture depends on whether a stimulus feature has previously been rewarded within the current situation (Anderson 2015). These findings provide evidence not only that reward influences attentional tuning to currently rewarded aspects of the environment but also that such tuning to the environment is shaped by a longer-term history of association with reward in a context-dependent fashion.

6.2.3. The role of the amygdala and locus coeruleus in biasing visual cortex response to reward and punishment. Electrophysiological studies in nonhuman primates have indicated an important role for the amygdalae in biasing visual attention to both reward and punishment (Peck & Salzman 2014). A number of human lesion and imaging studies have also implicated the amygdalae in prioritization of affectively salient stimuli. An influential line of research has examined the role of the amygdalae in prioritizing awareness of affectively salient stimuli when there is temporal competition for resources (Anderson 2005). Early evidence of a key role in such affectively biased attention came from a study of S.P., a patient with extensive amygdala damage. Compared with healthy controls, S.P. showed a deficit in attentional prioritization of emotionally arousing relative to neutral words (Anderson & Phelps 2001). These results indicated that the amygdalae directly and selectively influence perceptual awareness so as to enhance sensitivity to the emotionally significant, consistent with anatomical findings that this region projects directly to all regions of the ventral visual stream (Amaral et al. 2003, Catani et al. 2003). A subsequent fMRI study examined affect-biased attention using aversive Pavlovian conditioning to endow a subset of house images with emotional salience (Lim et al. 2009). This study found that houses that had been paired with shock elicited coactivation between the amygdala and place-sensitive regions of the visual cortex, suggesting that emotional learning via the amygdala plays a role in prioritized attention to stimuli associated with emotional arousal. On the basis of the above findings, models of affectively biased attention have emphasized a role for amygdala projections to the visual cortex (Pourtois et al. 2013, Markovic et al. 2014).

6.2.4. The locus coeruleus/norepinephrine system and individual differences in affect-biased attention. The locus coeruleus (LC), a nucleus in the brain stem that produces norepinephrine (NE), is an important hub of circuitry underlying direction of cognitive resources to salient aspects of the world (Sara 2009; for reviews of the effects of the LC/NE system on emotional modulation attention and memory, see Markovic et al. 2014, Todd & Manaligod 2018). The LC projects to many regions of the cortex, including the visual cortex, and is reciprocally connected with the amygdalae, which are dense in NE receptors (Sara 2009). A variant of the *ADRA2b* gene, which codes for the α2B NE receptor, is thought to be associated with greater NE availability and has been observed in ~50% of North American Caucasian populations. Carrying this deletion variant has been associated with higher levels of affect-biased attention (Todd et al. 2013a) and with enhanced amygdala activation (Schumann & Sommer 2018), as well as with enhanced effects of emotional arousal on memory (de Quervain et al. 2007, Todd et al. 2013b; but see

Schumann et al. 2018). The deletion variant has also been associated with emotionally enhanced perceptual vividness (Todd et al. 2015a) and biases in judgments of facial emotion (Ehlers & Todd 2018). In healthy populations, this genetic variation has consistently been associated with greater expression of typically observed effects of emotion on cognition, particularly attention and memory (Xie et al. 2018). These findings indicate that the LC/NE system plays a key role in effects of emotion on attention and memory in general, as well as on underlying trait differences.

6.2.5. Basal ganglia and biased attention to reward.   Whereas the amygdalae have been shown to play a role in biasing visual attention to reward, most human studies have emphasized the role of basal ganglia regions that are hubs of reward circuitry. A recent study used MVPA to examine patterns related to reward-related attentional capture (Hickey & Peelen 2015). The results showed enhanced visual cortex encoding of targets that were associated with reward. Importantly, effects of reward on visual cortex activation were associated with the degree to which a rewarding distractor elicited greater activity in the basal ganglia and connected regions. Thus, there is a relationship between activity in nodes of reward circuitry and visual cortex modulation associated with reward-biased attention. Consistent with this finding, individual differences in dopamine release in the striatum have been found to be associated with the extent to which attention is captured by task-irrelevant stimuli associated with reward (Anderson et al. 2016). Such patterns of value-driven attentional capture are also associated with addiction (Anderson 2016) and have been observed to be more extreme in participants in treatment for substance abuse (Anderson et al. 2013).

In summary, both emotional salience and reward guide attention via multiple routes and neuro-modulator systems, and they reflect the imprint of memory operating on a number of timescales. But the relationship between attention and memory is not a one-way street. Enhanced attention to emotional stimuli combines with other factors to modulate subsequent memory for emotionally relevant events.

7. MEMORY

Typically, emotional arousal enhances memory for past events, increasing subjective vividness if not accuracy (LaBar & Cabeza 2006). This phenomenon is known as emotional enhancement of memory (EEM). In healthy adults, fMRI data from more than 500 participants have confirmed that EEM involves interactions between the amygdalae, which play a role in tagging emotional salience of objects and events, and the hippocampus, which is crucial for contextual information that underlies episodic memory (explicit memory for events) (Fastenrath et al. 2014). Yet emotion does not only globally enhance memory: Effects are selective and subject to multiple boundary conditions, as many factors contribute to EEM. Such factors include the delay between encoding and retrieval, the timing of emotional arousal relative to the remembered event, the type of memory tested, whether memory is for a specific item or for the context in which that item was encountered, and emotional valence (for reviews, see Talmi 2013, Yonelinas & Ritchey 2015, Bisby & Burgess 2017, Bowen et al. 2018). Several lines of research have begun to investigate how emotional arousal facilitates specific mechanisms of memory encoding and consolidation, including reinstatement of patterns of sensory memory traces and pattern separation for memories of sensory information. The latter process is facilitated by specific subfields of the hippocampus (Hunsaker & Kesner 2013). In this arena, recent human brain imaging research has led to new insights into the role of valenced emotion on distinct memory processes and putative mechanisms, as well as the relationship between arousal and timing at various memory stages, ranging from encoding (initial laying down of memories) to consolidation into longer-term memories to retrieval of the memories later on.

7.1. Emotional Arousal, Subjective Perception, and Attention at Encoding

Building on our findings that emotion enhances perceptual vividness, reviewed above, we have also investigated whether enhanced sensory processing of emotionally salient events contributes to enhanced memory vividness. We found that emotional enhancement of perceptual vividness at encoding predicts a proportion of the variance in subsequent memory vividness indexed by both recognition memory, where participants indicate whether they have seen a scene before, and cued recall, a process that requires more detailed recollection (Todd et al. 2012b). Perceived vividness at both encoding and memory were found to be associated with activation of overlapping amygdala and visual cortex regions at the time of encoding (Todd et al. 2013b). In contrast, hippocampal activation at encoding predicted subsequent memory vividness but did not reflect emotional enhancement of perceptual vividness (Todd et al. 2013b). This dissociation is consistent with other findings showing that, although hippocampal activation can be modulated by signals related to salience from the amygdalae, it can discriminate more detailed mnemonic information (Leal et al. 2014a).

Moreover, the vividness effect we observed was not due to enhanced frontoparietally mediated task-based attention but rather to affect-biased modulation by amygdala circuitry (Todd et al. 2012b). Yet emotionally salient events also evoke enhanced executive attention, which also reliably facilitates memory (Talmi et al. 2007, 2008). One way of avoiding confounds from enhanced executive attention at encoding is to examine effects of emotional arousal either before or after encoding of neutral events. This strategy has led to greater understanding of effects of emotion on memory consolidation processes.

7.2. Effects of Emotional Arousal on Consolidation: The Importance of Timing

We can intuitively suppose that it is advantageous to remember seemingly innocuous events that precede emotionally important ones in order to better predict the future. An enduring question regarding emotional memory processes concerns how we distinguish the significant from the mundane on the basis of events that occur somewhat later. Emotional arousal can modulate memory for neutral events that happen immediately beforehand, suggesting that arousal plays a role in postencoding consolidation processes (Anderson et al. 2006, Knight & Mather 2009). Nonhuman animal research has established a key role for NE-mediated basolateral amygdala activity in these consolidation processes (Roozendaal et al. 2009, McGaugh 2018); however, whether NE enhances or suppresses memory varies depending on a number of factors (Knight & Mather 2009). For example, one influential theoretical framework proposes that postencoding emotional arousal enhances memory for goal-relevant items, while suppressing it for goal-irrelevant events, and does so via glutamatergic amplification of noradrenergic activity (Mather et al. 2016).

Further probing the specificity of postencoding arousal effects, the synaptic tag-and-capture model proposes that initially weak memories for neutral information are strengthened if subsequent related information, mediated by the same category-selective region of perceptual cortex, is associated with emotional arousal. In a study testing this hypothesis, participants initially categorized pictures as objects or tools (Dunsmoor et al. 2015). Then new examples of objects in one of the categories were paired with shock, while examples of the other category were not. Following conditioning, participants encountered a third set of examples of stimuli in each category, again with no shock. Recognition memory for stimuli from the preconditioning, conditioning, and postconditioning phases was tested immediately, after 6 h, and after 24 h to allow comparison of different periods of consolidation, including sleep. After 24 h, examples of the conditioned category that were encountered before, during, and after conditioning were better remembered than those from the nonconditioned category. After 6 h, there was only a memory enhancement for

categorically related items encountered before and during conditioning. Finally, with immediate testing, there was a memory benefit only for the items that were actually paired with shock, and none for categorically related items encountered before or afterward, suggesting that pre- and postencoding arousal effects arise after longer-term consolidation processes. Moreover, effects of preencoding arousal may require sleep. This hypothesis is consistent with findings that sleep is required for arousal-related sharpening of some forms of mnemonic representation of high-level sensory information—effects mediated via amygdala interactions with category-specific regions of the ventral visual stream (Sterpenich et al. 2014).

Other studies have used RSA as an elegant tool to measure reinstatement of patterns of voxel activity initially observed at encoding. In such studies, if voxel patterns observed after encoding are more similar to those at encoding, they are thought to index better reinstatement of representations that strengthen memory. For example, RSA has been used to examine timing effects of preencoding arousal on reinstatement of patterns of brain activation linked to specific forms of recognition memory: recollection (the ability to remember details of encoding event) versus familiarity (the ability to indicate that an item is familiar without remembering context) (Tambini et al. 2017). Participants viewed blocks that were series of emotionally arousing and neutral scenes, counterbalanced in order between participants. Recognition memory was tested 6 h later. Neutral images were better recollected when they followed emotional blocks but not when they preceded them, indicating sustained effects of preencoding arousal influence recollection but not familiarity. The results indicated that hippocampally mediated reinstatement of brain activation patterns underlies memory for details. Finally, patterns of connectivity between the amygdala and other brain regions were more marked for neutral blocks that followed emotional blocks, a finding that was interpreted as reinstatement of emotion-related brain states that facilitate better recollection.

RSA has also been used to examine reinstatement patterns of category-specific sensory information associated with consolidation of conditioned memory. Studies in rodents have found that, during sleep, rats show greater amygdala–hippocampal reactivation patterns for a running direction associated with an aversive event than for a safer direction (Girardeau et al. 2017). A recent study in humans used the strategy of conditioning stimulus categories (animals versus fruits and vegetables) that evoke category selectivity in the ventral visual cortex, and used RSA to examine patterns of activity in these regions during rest periods following conditioning (de Voogd et al. 2016a). This study found that spontaneous off-line reactivation of visual cortex activity was stronger for the conditioned category. Moreover, hippocampal coactivation with category-specific patterns of activity predicted fear memory, indexed by pupillometry measures of arousal, 24 h later for the conditioned category only. Amygdala–hippocampal coactivation also increased during rest in general. The authors interpret the hippocampal–visual cortex coupling as indicating systems-level consolidation processes associated with emotional arousal tested as long as 24 h after learning. Importantly, the hippocampal role in reinstatement of visual cortex information extended beyond the explicit recollection process to pupil responses to acquired stimulus salience.

Older studies have suggested that emotional arousal mediated by amygdala activation enhances memory for gist at the expense of detail (Adolphs et al. 2001). Building on these studies, one line of inquiry has focused on effects of hippocampally mediated pattern separation processes as a biologically grounded means of operationalizing the concepts of gist and detail (Segal et al. 2012; Leal et al. 2014a, 2017; Leal & Yassa 2014; Cunningham et al. 2018). A wealth of neurobiological evidence indicates that the cells in the dentate gyrus of the hippocampus specialize in separating out representations of similar events such that they can be recollected individually (Hunsaker & Kesner 2013). An outstanding question has been whether arousal/information from the amygdalae impairs pattern separation, resulting in a strong but "gisty" memory. Results of multiple studies

indicate that reduction versus increase of pattern separation with emotional arousal depends on the timing of the memory test, and that patterns of reduction/increase can differ in older relative to younger adults (Leal et al. 2014a,b; Leal & Yassa 2014). In young adults, postencoding arousal created by a stressful event increases pattern separation 24 h later (Cunningham et al. 2018). Building on evidence that the dentate gyrus receives NE modulation both directly and via the basolateral amygdala, another study found that individual differences in salivary α-amylase, as an index of LC activity, were related to better pattern separation performance 15 min after encoding (Segal et al. 2012). Overall, a picture emerges in which earlier claims of general effects of arousal on gist versus detail have given way to a more nuanced picture in which effects of amygdala-modulated arousal or NE activity on pattern separation depend on a host of timing factors. These include amount of consolidation time, timing of arousal in relation to encoding, and life-span stage. Moreover, these studies have consistently used negatively valenced stimuli or arousal inductions, leaving open valence-related differences in arousal effects.

Effects of amygdala activation and NE modulation of memory have also begun to be disambiguated. A study measuring recognition memory 24 h after aversive conditioning to a specific category of stimulus (vegetables versus animals) found that EEM was more related to amygdala activation than to indices of NE activity at encoding (de Voogd et al. 2016b). Finally, acute stress also modulates subsequent memory. As with EEM in general, effects of acute stress on episodic memory are subject to numerous boundary conditions, including whether the stressor occurs before, during, or after encoding; the amount of time that elapses between stressor and encoded event; and gonadal hormone status (Shields et al. 2017).

7.3. Effects of Valence

Notably, most of the studies reviewed above have focused on effects of negative emotion. However, valence-related differences in memory effects have also been observed. Negative stimuli elicit greater visual cortex activation reinstatement and amygdala–visual cortex activity relative to positive stimuli (Kark & Kensinger 2015). Moreover, whereas negative valence increases memory for specific items at the expense of memory for associations between stimuli, an effect mediated by greater amygdala versus hippocampal activation at encoding (Bisby et al. 2016), positive valence enhances associative memory, an effect potentially linked to attentional broadening by positive affect (Madan et al. 2019).

8. EMOTIONALLY BIASED COGNITION AND PSYCHOPATHOLOGY

While much remains to be learned about the myriad ways in which emotional information modulates cognition, the rapid retuning of sensory cortex plasticity, enhancement of sensory encoding, and reinstatement of key sensory features are notable features of emotional cognition. Given the central role of emotion in cognition in healthy populations, it is no wonder that many forms of psychopathology involve distortions of affective cognition.

Whereas affective modulation of attention, learning, and memory serve an overall adaptive function, distinct patterns of affective bias are symptomatic of psychopathology: Extreme attentional biases to threat characterize anxiety disorders, and biases in attention to trauma-related cues and altered biases in attention to reward-related cues are linked to depression and addictive behaviors. Importantly, they often involve distortions in the representation of emotional features of the world. A number of forms of psychopathology are also associated with altered emotional learning and memory. Anhedonia in depression is associated with an inability to acquire associations with reward (Vrieze et al. 2013), and anxiety and depression are characterized by biases

toward remembering negative events (Lemoult & Joormann 2012). PTSD is in part defined by the presence of involuntary, intrusive, and vivid memories of traumatic events, in part via memory processes modulated by stress hormones in interaction with gonadal hormones and the endocannabinoid system (for recent reviews, see Wolf et al. 2016, de Quervain et al. 2017). In all of these cases, an otherwise adaptive affective coloring becomes maladaptive when it is extreme or rigid or inappropriate to the context. Yet the fact that so many forms of psychopathology are characterized by altered influences of emotion on cognition highlights the fundamental role emotion plays in cognitive processes once thought to be solely within the domain of higher cognition.

9. CONCLUSIONS

Historically, the overlapping fields of psychology and cognitive neuroscience, deeply embedded in Western dichotomies between emotion and reason, have relegated the study of cognition and emotion to discrete domains. In this article, we have reviewed studies exploiting recent advances in brain imaging to find that emotional information is represented across the whole brain and distributed throughout the body, is instantiated in the most distal sensory receptors, is centrally translated into an amodal common currency, and rapidly shapes the sensitivity of primary sensory cortices. Together, these findings suggest emotional information constitutes a feature that is built into our representations of the external world in a manner similar to such "objective" features as shape and color, and that primary sensory representations are rapidly modulated by emotional learning. Such sensory-specific representations are then integrated into more integrated and abstract representations of valence and salience in regions of the association cortex. However, such a proposal remains controversial, and an important program of future research will be to test emergent hypotheses about perception and learning rigorously and explicitly.

We have also reviewed the degree to which emotional and motivational information guide attention and modulate processes involved in encoding, consolidation, and retrieval of memory via multiple routes and on many nested timescales. Importantly, such emotional influences on attention and memory involve selecting for and reinstating representations of those very same emotionally laden sensory features of the world. Finally, we briefly described evidence that it is precisely such modulation of cognition by emotion that is altered in many forms of psychopathology. Convergently, these data suggest that at each moment before, during, and after our senses meet the world, what we experience is fully filtered by our emotional appraisals of what is good and bad for us. This in turn shapes what we experience in the future. We propose that, rather than providing a separate channel of information, emotion is a fully integrated feature of cognition. Like other mammals, we are enmeshed in the world such that emotional outcomes are the central organizing feature of perception, attention, learning and memory, guiding awareness, and informing action.

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