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Mapping the interconnected neural systems underlying motivation and emotion: A key step toward understanding the human affectome

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ABSTRACT

As a part of a larger Affectome Project (http://neuroqualia.org/background.php) with an overarching goal of mapping and redefining biological substrates of feelings and emotions, we explored the neural underpinnings for the functions of motivation and emotion. Historically emotion and motivation have been placed into distinct neural circuits and examined separately. We propose a novel view of significant neural convergence of emotion and motivation, in contrast to conventional neural-based frameworks emphasizing segregation. Evidence from diverse research areas in emotion and motivation was reviewed, pinpointing key neural regions of overlap. The findings support important neural sharing between emotion and motivation, suggesting that these two functions are tightly intertwined with one another in the brain. Neural overlap does not necessarily imply continuous functional overlap. Even if identical brain regions/systems are activated for motivation and emotion, this activation may involve distinct and unique patterns of connection and information flow as the network shifts functionality. This review highlights the crucial importance of further research to explicate the patterns and modes of responding of these overlapping systems.

1. Section I. introduction, theoretical background, and approach

Mapping the affectome requires linking feeling states to neural circuits and physiological processes. There is a global interdisciplinary working group collaborating on a project to unite diverse research areas and comprehensively map functional neural models for emotions and related feelings. The project has been labeled 'The Human Affectome Project' (see http://neuroqualia.org/index.php) and the diverse task-force includes researchers in psychology, neuropsychiatry, neuroscience, economics, and computer science. This overarching goal of mapping the human affectome is being accomplished by having a number of research teams review and synthesize more specific affective neuroscience topics pertinent to the overall objectives. This task would be incomplete without a team that carefully examines the affective neuroscience literature to uncover potential relationships between brain networks underpinning emotion and motivation, which is the team authoring this article.

The goal of the present review, therefore, is to carefully describe the neural systems subserving motivation and emotion in the brain, based on relevant animal research, human research on brain bases of motivation and emotion, and human research on the development of these neural systems. From these findings, we present a novel view that emphasizes integration of emotion and motivation, to the point that they merge into a single process and involve overlapping brain substrates. Neural research on the interface of these networks with neurological correlates of related cognitive and cultural processes is explored. In general, this model contributes to the literature by highlighting the interconnectedness of the neural systems underlying motivation and emotion, and proposing possible loci and neurotransmitters that forge the interconnections between them. We then

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suggest important directions for future research to test and refine the model.

As a guide to the review, we ask some key questions: What are motivation and emotion and how do they relate to one another? What neural structures and systems are associated with motivation and emotion? How do systems associated with motivation differ from or overlap with those associated with emotional states? Are there unique neural regions, pathways or networks involved in social motivation and emotion? What are important developmental processes and sensitive periods in the development of brain systems subserving emotions, motivation and their integration and regulation? What neural systems serve cognitive functions that play a role in motivating goal-directed behavior? What role does culture play in socializing distinct ways of integrating emotion and motivation and what neural systems "embrain" culture? How can mapping these neural systems help scientists and clinicians in understanding or predicting normal and pathological states related to emotion and motivation and using this information in an ethical and effective way? We will now begin by providing the conceptual definitions of motivation and emotion used in this review.

1.1. Emotion and motivation: definitions, overlap and divergence

At the linguistic core, motivation and emotion share the Latin root, '*motus*', which means 'to move'. Despite their shared linguistic root and many interrelated processes, motivation and emotion are usually considered significantly different in elemental ways. Following an abundance of empirical work on emotion and motivation, there is still little consensus in psychology and neuroscience on defining the *concepts* of motivation and emotion and their relationship—as evident in a recent special issue in the journal *Emotion Review* (Hommel et al., 2017). Nevertheless, motivation and emotion can merge or operate in synchrony to coordinate movement at all levels and create feelings that function across both brief and lengthy spans of time (Morewedge and Buechel, 2013).

Motivation can be defined as the process that determines the direction (i.e. defining which goals an organism seeks to approach or to avoid) and energization (i.e. the mobilization of resources to carry out an action) of behavior (Elliot, 2006). That is, motivation is a psychological process integrating diverse inputs used to form behavioral responses aimed at satisfying needs as well as determine outcome valuation or desired end states of action. This process refers to the pursuit of both conscious (e.g., Locke and Latham, 1990) and unconscious goals (e.g., Dijksterhuis, 2010; Schröder and Thagard, 2013). Movement in motivation science means the initiation, maintenance, and termination of action. This involves instrumental behavior to obtain reward or avoid negative outcomes (Berridge, 2004; Deckers, 2005; Toates, 1986), but also to execute actions for their own purpose—often termed intrinsic motivation (Herrnstein, 1977; Kruglanski et al., 2018). A functional nesting occurs naturally in motivational processes. For example, sensorimotor states become conditionally activated based on alterations in motivational states (Berridge and Cromwell, 1990; Cromwell and Atchley, 2015). Contemporary views forge motivation with other psychological processes, synthesizing a comprehensive, integrated representation of experience that can be used to monitor and compare diverse needs and subsequently guide action strategies more effectively during development (Dweck, 2017a,b).

A key process often contributing to motivation is emotion. Emotions can be defined as organized affective and behavior-promoting reactions to significant internal and external events. Emotions are about how such events are relevant to the individual and the individual's goals, needs, or concerns (e.g., Barrett, 2013; Frijda, 1986). As such, affective states can influence specific, goal-oriented responses to contextual challenges that threaten the individual's wellbeing (e.g., fear → security; anger→ damage). They can also help direct behavior aimed at satisfying personal goals rather than addressing external threats to the individual's wellbeing. These latter motivated actions are often viewed as intrinsically motivated behaviors (interest → exploration). Importantly, emotions typically induce bodily reactions related to resource mobilization (Frijda, 1986). However, emotions do more than mobilize behavior. They also often involve the experience of emotional feelings (affect). Emotional feelings may amplify motivation by bringing attention to unsatisfied needs or desires, creating increased urgency and amplifying behavior inclinations (e.g., Tomkins, 1984), and emotional movements include not only behaviors directed at individuals' goals and desired end states, but also at important functions, including social communication functions (e.g., Buck, 1984; Barrett and Campos, 1987). As a result, facial expressions, gestures, postures and reflexive movements, which may be conditioned to neutral stimuli, all may be responses to emotion (Izard, 1971; Ekman, 2003). To better clarify words used to describe emotion and motivation, the Affectome Mapping Project included a detailed linguistic analysis as a unique starting point in the review process.

1.2. Language and motivation/emotion semantic analysis of attraction/repulsion words

Understanding the words used to describe affective and homeostatic feelings will aid in the developmental of clearer definitions and a better understanding for how emotion and motivation overlap. Our team explored intersections between English words denoting affect, and how they relate to words used to describe motivational states. For the current review, this focuses on affect and motives. Emotion and motivation can both easily be represented by feeling states and possibly similar words are used to represent these affective and motivational feelings. It is worthwhile to explore the themes in the list of emotion-motivation words identified by the linguistic team of the Affectome Mapping Project. The linguistic analysis was a multi-step process using machine learning methods to search a large database followed by manual annotation and semantic analysis. The linguistic analysis team extracted potential words related to feelings from a Google n-gram corpus that includes approximately 8 million books (see Younes and Reips, 2019 for details on the n-gram corpus) using pointwise mutual information with morphological variants of the word 'feel'. A subset of the human affectome project team (> 100 researchers) worked to classify each of the words obtained into distinct categories based upon affective properties of valence and intensity. The manual annotation led to 9 categories of feelings and a dataset with 3664 words related to diverse feeling states (see Siddharthan et al., 2018 for more details).

Our team reviewed the meanings associated with 114 words for feelings linked to attraction or repulsion out of the larger dataset. This set included 44 words denoting negative valence (e.g. repulsion) and 70 words positive valence (e.g., attraction), drawing on techniques of semantic analysis (Lakoff, 1987). One basic distinction concerned words about actions (N = 24, such as *capture, charm, invite, repel*), versus non-actions (N = 90). Themes identified included the intensity of valuation (medium vs. strong), and words connoting psychological manipulation to gain the alliance of others.

For this article on motivation, the feelings associated with action are highly relevant, given the prevailing definition of motivation as the potential for movement. Among the action words, interestingly, people were the prototypical target for most of the words, although some words could also refer to objects. The most common theme among the action words, occurring in 18 out of 24 words, was using psychological manipulation to bring a desired person closer (e.g., *enchant, tempt, fascinate*). Most of the words referenced attracting a target using one's personal charisma, such as *charm, captivate*. A smaller set of words included meanings that connote using trickery, such as *beguile, bewitch and lure*. Only three of 24 words were about repulsion. Two of three referred to psychological techniques (*scorn* and *repulse*). One of the words, *repel*, could refer to either human or inanimate objects. The remaining three words among the 24 action words referenced the expectation of attaining the goal (*capture, catch* and *clinch*), obviously

relevant to the importance of goal expectancy in the literature.

A striking aspect of these action words was the positivity bias. Most words were positive; only three words concerned repulsion. This is noteworthy because of the negativity bias that pervades human information processing. The negativity bias is the finding that even when positive and negative situations are of equal magnitude, the negative events will be given more weight or will capture more attention (Ito et al., 1998). The main explanation for this is relevant to this article's theme of appraising the cost of action: neglecting or misjudging a negative event can be more costly than missing a positive event.

One explanation for the positivity bias found in the action words is that language evolved during an era of human history when social interactions and building alliances were increasingly necessary for achieving high status in social groups. During this time, trust and cooperation became more successful strategies than backstabbing and subterfuge (Tomasello, 2009). Consistent with this, it has been recently observed that English words demonstrate a positivity bias (Kloumann, Danforth, Harris, Bliss, & Dodds, 2012). However, the positivity bias was absent among the larger set of 90 non-action words, where attraction and repulsion words were relatively equally common (46 % vs. 54 % respectively). The non-action words included appraisals of a situation/person which were either attributes of objects (e.g., *precious, rotten*) or states of mind about people or objects (*want, detect*). Non-actions also referred to attitudes (*romantic, lousy*), ongoing moods (*languish*), or reactions to a thing or event (*horror, welcome*).

One theme among these non-action words was valuation. Almost half of the words (42 of 90) had extreme connotations. Words like *devote, worship, yearn* focused on high levels of positive attraction to a target person/object, while words like *repugnance, ignominy, detest* indicated strong repulsion. Words that connoted a medium level of strength comprised roughly half of the non-action words (43/90). Positive examples included *appeal, admire, like, desire*; negative examples included *cold, unconcerned, distaste*. Only 5 of this set of non-action words connoted low strength of interest in the target, and all of these were words about a low level of attraction: *inclination, tendency, disposition, predilection, preference* (i.e., there were no words referring to a low level of repulsion). One note of interest here is the many of the words with medium-levels of valuation can be understood as basic-level meanings (such as *like, desire, cold, distaste*). The lack of either positivity or negativity bias in these words is consistent with the intuition that it is a basic human need to convey both negatively and positively valenced appraisals regarding moods and states of mind.

The emotion-motivation words analyzed here were all identified *a priori* as words describing both a motivation and an emotion. Therefore, the list cannot be used to quantify the overlap between motivation words and emotion words. As an exploratory measure, we scrutinized online lists of motivation words (e.g., https://thegoalchaser.com/motivational-words-list/). These lists reflected the commonsense meaning of motivation as attaining goals. The majority of these words did not overlap with emotion words on our list, but referenced states, attitudes and goals, such as *ambition, commitment, courage,* and *glory*. While not emotion words *per se*, such words are clearly emotion-laden (a term used to refer to words having affective connotations).

Examining interrelationships between emotion-motivation words is relevant to themes identified in the current review because many of the words concern complex emotional psychological states (e.g., *tempt, bewitch*) that naturally link to motivated actions. Also common were words that reflected evaluation, which is important since a key function of emotion, as noted in this review, is to guide organisms in switching from an action that has low expectation of reward to one with greater probability of reward. When the emotion and motivation merge linguistically, a value for an outcome or event is clearly communicated. The English language contains many words with meaning that links and refers to both motivation and emotion. Neural systems could also overlap, and understanding how these functions merge linguistically and biologically can aid researchers in creating working definitions for these processes that guide future empirical studies.

2. Section II. What neural structures and systems are associated with motivation and emotion? Neuroscience as a guide to understanding emotion, motivation, and their intersection

2.1. Neuroscience-based theories of emotion

An effective strategy for better understanding the relation between motivation and emotion is to utilize neuroscientific evidence to define and understand these psychological processes. Multiple perspectives have emphasized an emotional *or* a motivational brain without making an attempt to integrate the two processes together. The search for the circuit of emotion has a long history, including work by Paul Broca, emphasizing the medial ring of the central nervous system as the emotional center (Broca, 1878). An important step forward in mapping the emotional brain occurred when James Papez published his seminal article detailing a circuit of emotion (Papez, 1937). He focused on patient cases in which he observed severe debilitating emotional disturbances and then found damage to key regions such as the cingulate gyrus and subareas of the thalamus and hypothalamus.

The emotional brain was further elaborated by the extensive work of Paul MacLean (1949) as he developed his concept of the triune brain. For him, the neural apparatus could be divided into three parts, based in phylogeny, with the lowest part fulfilling the most basic functions and having reptilian origins, the medial part originating with early mammals, and the highest part being more truly human. The emotional or visceral brain was localized in the medial ring and contained a focal point within the hypothalamus. MacLean is attributed with coining the term 'limbic system,' as his emotional brain acted as an interface between the neocortical higher order cognitive regions and the lower reptilian brain involved in action sequences and reflexes (MacLean, 1952). When examining the types of behaviors under scrutiny, it appears that these early proposals for limbic system emotional functions could be linked equally to motivational processing. Yet the majority of these theorists, as well as modern day affective neuroscientists, have proposed neural locations or circuits for emotion and either neglected or downplayed the essential process of motivation in this same circuit.

Following the pioneering work of Philip Bard (1928) and Walter Cannon (1931) the neural hotspot for emotion in many of these early models was the diencephalon including thalamus and hypothalamus, a brain region that also has been thought to be key in motivational processing involved in primary systems of hunger, thirst, reproduction and sleep (Stellar, 1954; Miller, 1963; Teitelbaum and Epstein, 1962). Traditional accounts frequently discussed the functions of motivation and emotion separately, yet seemed to map them onto brain areas and discrete subregions that significantly overlapped. Although key brain regions involved have not significantly changed since early circuitry renditions, and continue to include cingulate, amygdala, mesolimbic and mesocortical regions of interest (Fig. 1), more recent models of emotion circuits have emphasized the role of the amygdala more than the hypothalamus. Moreover, although the circuit has not changed dramatically, the list of functions has grown significantly with some specific functions primarily being emotional processes and others being primarily motivational ones (Fig. 1). Each brain region can be parsed into demarcated emotional and motivational subregions, and a select neural interface could act at a single location to combine and synthesize these processes.

2.2. Neuroscience-based theories of emotion-motivation integration

Some theoretical accounts from affective neuroscience have attempted to compare and functionally assimilate motivation and emotion. One example is Gray's (1987; Gray & McNaughton, 2003) influential theory of motivation and emotion that attributes motivational directions and related emotional experiences to neural circuits–A

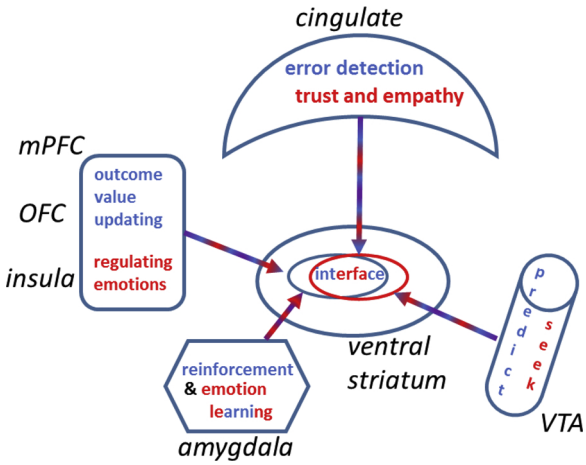

Fig. 1. Some of the major regions of the brain involved in motivation and emotional processing. An example function is placed within each brain region for either motivation (blue) or emotion (red). Cingulate cortex has been shown to be involved in detecting errors and in social emotions. Prefrontal cortical regions have been shown to contain neural activity linked to reward valuation and express plasticity in activations when value changes. In addition the same regions have been shown to be key in regulating and mainly inhibiting emotions. The amygdala has been shown to be a key node in connecting emotions with novel stimuli and developing reinforcement strength over time. The ventral striatum and tegmentum regions are the foundation of motivational processing with the forebrain striatal regions as a key interface area that combines input from diverse other brain regions. Ventral tegmental area has been proposed to be involved in initiating prediction error signals as well as primary affective consciousness of seeking.

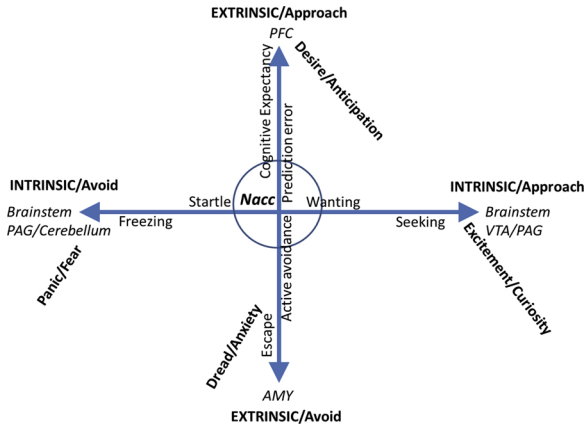

Fig. 2. Two pathways each spanning the intrinsic-extrinsic dichotomy. On one end of the spectrum there is approach and on the other, its opponent state, avoidance. Emotional/motivational operating systems are listed along the dimensions for each intrinsic/extrinsic path. On the intrinsic spectrum are basic motivational responses with neural substrates proposed to contain ancient, conserved architecture for response production. For the extrinsic spectrum there are cortical and subcortical limbic regions in the forebrain that integrate cognition with emotion-motivation and produce more complex behavioral strategies. In the middle is the motivational hotspot, the nucleus accumbens (NAcc) that acts as an interface for the intrinsic-extrinsic divide as well as provides a bridge for approach-avoidance action selection. Other neural regions listed: periaqueductal gray (PAG); ventral tegmental area (VTA); amygdala (AMY) and prefrontal cortex (PFC).

Behavioral Activation System (BAS), which engages approach-anger and a Behavioral Inhibition System (BIS), which is associated with inhibition-anxiety. A key neural locus is the septohippocampal system as it interacts with brainstem serotonin signals. The BIS is highly sensitized and reactive to approach/avoidance conflict, leading to anxiety and inhibition of behavior. The BAS is reliant on brain dopamine levels. Higher levels of BAS activity are related to impulsivity and addictive-like behavior. This work is such a fine example of emotion-motivation integration not only because the work clearly represents emotional-motivation merging but also connects both processes to personality theory and clinical work. Thus, the applications of this theory have broadly influenced fields of psychiatry, neuroscience, developmental science, and biomedical research.

Another example of functional integration is Buck's (1985) "prime theory" that essentially links motivation as the driving force (e.g., voltage) and emotion as the readout (e.g., current) and posits that the two work so closely that normal behavior continuously incorporates the conjoined processes. These ideas fit Panksepp's (1998) framework of affective neuroscience, which includes a system of emotional operating systems that could be easily relabeled motivational operating systems. Such theories suggest that there should be a great degree of overlap in the neural networks underpinning motivation and emotion (e.g., Pessoa, 2009). One current focus in affective neuroscience is localizing discrete brain substrates for individual emotions. There is an abundance of work delineating specific locales for basic, but less often complex affective states (e.g., a recent human affective neuroscience example focusing on parsed neural networks for individual emotions, Saarimäki et al., 2018).

Individual motivational processes do connect with diverse emotional states in certain states and conditions. For example, both anger and joy are associated with approach motivation (Carver and Harmon-Jones, 2009) but involve different discrete hotspots (e.g., for anger vs. joy) with overlapping neural networks (e.g., approach, see Gainotti, 2019). Moreover, the degree of emotion-motivation merging of pathways would depend upon whether the emotion process involves threat, punishment, or reward and, if reward, whether the reward is intrinsic to the activity versus extrinsic (the action is instrumental for attaining a desired consequence) (Fig. 2).

Although Gray's, Buck's, and Panksepp's theories postulate a close interconnection between emotion and motivation, most neuroscientific work has drawn distinctions between "motivational" (i.e. behavior producing) and "experiential" (i.e. affective) processes triggering or maintaining behavior and has attributed different neural circuits to each process. Accordingly, motivation and related affective experiences have been considered to be functionally independent from one another, though they can and do interact. Examples are the updated version of the LeDoux (2012) theory of fear and Berridge's model of distinct neural circuits involved in wanting (i.e. motivation) and liking (i.e. experience) (Berridge and Robinson, 2016; Castro and Berridge, 2014). However, of course, if motivation is defined in a way that requires behavior and "affect" is defined in a way that precludes behavior, they will necessarily be functionally distinct. Neuroscience-guided approaches can remove tautological explanations and definitions and allow for emotion and motivation to be grounded in objective neural states and connectivity within a circuit (Panksepp, 1998). New possibilities could arise in predicting emotional as well as motivational states based upon neural activation (Kassam et al., 2013).

2.3. Approach

This review paper, thus, takes on the task of comparing and critiquing work on the interface between emotion and motivation creating a novel outlook for the field that redefines the borders of these psychological processes. The information was gathered by the set of authors, with different authors focusing on different sections based on their own areas of expertise. A section focused on non-human animal models and other sections focused on human neuroscience research, with one focused on motivation and emotion in adults, one on social motivation and social emotion in adults, one on the development of brain systems underlying motivation and emotion, one on the interface of relevant cognitive processes, and one on culture-brain interfaces in motivation and emotion. Authors have their individual perspectives and expertise

on the topics they reviewed. The reviews were not exhaustive, but focused on delineating core regions of the brain involved in motivation or emotion for the section in question, and then exploring how closely related these brain regions and circuits are to one another. Then, the results of these focused searches were compared and contrasted with one another to ascertain overarching patterns of similarities and differences in brain systems involved. This approach is novel in reviewing and integrating numerous disparate literatures: animal models of motivation and emotion, human research on overall motivation, social motivation, emotion, motivational development, emotional development, and so on, to better understand, how these two distinct processes could rely on the similar/overlapping, or disparate neural substrates. Deliberating on this issue could initiate new approaches to think about plasticity of function in brain regions involved in both emotion and motivation as well as how functional impairments are connected with one another.

We begin with a discussion of animal behavioral and neural science research on motivation and emotion interactions that in some ways provides a distinct view from work on human motivation. Neuroimaging studies of humans recently have added new substantial ways of thinking about the neuroscience of motivation and these are discussed along with specific findings on social motivation and brain function. Next, we examine how the neural underpinnings of motivation and emotion, including both structures and interconnections, develop from infancy onward. Finally, we extend the discussion by exploring the links of motivation and emotion brain systems to those serving related cognitive and cultural functions. We end with conclusions regarding what we know and what we need to know about the brain bases of motivation and emotions.

3. Section III. Animal models of motivation, emotion, and their interrelations

3.1. Animal models of motivation

Non-human animal work has been crucial to the progress made in behavioral and brain research in motivation. Jaak Panksepp was one of the most prolific researchers in the recent past who advocated for animal studies on the brain basis of motivation and emotion (Cromwell, 2018). His seven emotional operating systems arise from ancient, conserved brain circuits that are built on the foundation of natural selection (Panksepp and Biven, 2012). He proposed that focusing on these well conserved circuits provided the best options in the search for new treatments for mental illness (Cromwell and Panksepp, 2011).

The operating systems arising from these conserved brain circuits can be intrinsically motivated. Intrinsic motivation is distinguished from other types of motivation based on the locus of reinforcement, namely that emitting the behavior or engaging in the activity *is its own reinforcement*; no external reinforcement is present or needed. Herrnstein (1977) captured the power of intrinsic-innate motivation eloquently by writing:

> "When a predator stalks its prey, the reinforcer seems to involve stalking and capturing. The mouse as food reinforcer precipitates out at some later point in its encounter with the cat. You may want to account for predatory behavior by postulating secondary reinforcers converging down to food as primary, but I am skeptical. And until someone makes a stalking, pouncing predator out of a cow or a mouse and extinguishes those responses in a cat, skepticism seems tenable" (Herrnstein, 1977, p. 600)

Another example of behavioral as reward is inherent behavioral switching or spontaneous alternation of outcome choices that animals emit within a self-paced, free operant/choice environment despite the fact that roaming and switching activity reduces optimal food intake levels (Ricker et al., 2016).

An interesting system reflecting intrinsic motivation in animals is the system devoted to play behavior. Animals will work to engage in play and spend significant time playing using reciprocal bouts of contacts, pins and crawl over movements (Panksepp et al., 1984). Animals' (including humans') inclination to engage in play, an activity that has no extrinsic reward but seems highly motivated, was an important basis for Robert White's (1959) proposed "effectance motivation" (see section V). Many highly motivated behaviors can be engaged in as play, including birdsong. Riters et al. (2017) proposes that song practice in starlings is a form of play because it requires neither direct external triggers nor specific goals (Burghardt, 2005).

Similarly, the seeking system is a powerful system that produces invigorated search and exploration. Panksepp postulated that the primal system, seeking, is originally and principally an action system independent of external triggers, cues or incentives. The most conserved core of the seeking system could be thought to activate intrinsic urges that compel an organism to move and forage in an environment with the goal of exploration *per se* replacing external outcomes. This intrinsic system is dynamic as urges wax and wane. Yet, in keeping with most types of motivation, it rapidly becomes directed at achieving a desired end, and, as such, does not remain solely intrinsically motivated. It may become focused on a particular need, such as hunger, when that need is strong. Fatigue and satiety potently reduce or terminate exploration for food and activate rest within the behavioral satiety sequence (Halford et al., 1998; Finger et al., 2011). It is usually expressed in flexible searching strategies that depend upon environmental pressures and evolutionary history of the organism (O'Brien et al., 1990; Lorenz, 1981).

Dopamine is at the forefront of these basic emotional-motivational operating systems. Seeking, as a system, has been linked with dopamine using a diverse array of methods (Fig. 3; Ikemoto and Panksepp, 1999). Deep brain stimulation of the midbrain regions and the nucleus accumbens (NAcc) consistently activates exploration and sniffing. Recent work has extended the key dopamine neuronal activity from the ventral tegmental area (VTA) to other dopaminergic regions in the lateral midbrain including the substantia nigra (Fig. 3; Ikemoto et al., 2015; Morales and Margolis, 2017).

Endogenous opioid systems normally work hand-in-hand with catecholamines in invigorating action strategies. These signals are linked to affective responses and can induce direct consummatory behavior

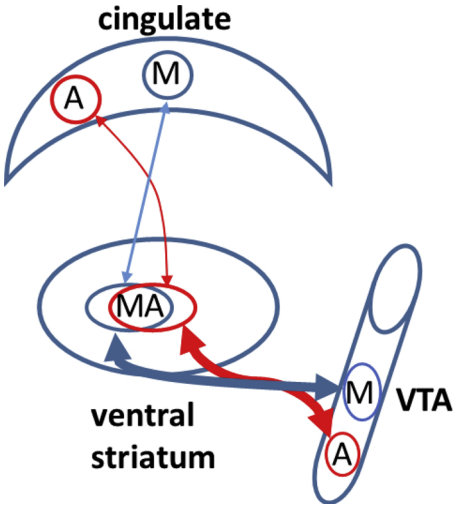

Fig. 3. The SEEKING circuit includes bottom-up signals from brainstem regions including the ventral tegmental area (VTA). Interface area within the ventral striatum operates the SEEKING system without initial external triggers. Behavior can be reinforcing per se and action strategies are controlled from inherent command systems. Different organisms can produce diverse strategies that include mobile searching, sendentary 'wait and attack' or a combination of moving and waiting described as 'saltatory predation' (O'Brien et al., 1990).

(Castro and Berridge, 2014; Smith and Berridge, 2007). These same neuropeptides and chemicals converge in the avian brain to produce reward and motivation to sing (Pawlisch and Riters, 2010; Riters, 2010). This avian work transitions into recent work on animal reward, social motivation and social affect. In particular, numerous studies on diverse species show that animals' reactions to affective situations evoke empathy from conspecifics, leading to altruistic motivation (Panksepp and Panksepp, 2013; Watanabe, 2011, Perez-Manrique and Gomila, 2017). Moreover, rats, dogs and primates all display inequity aversion, responding in predictable ways to social settings in which a conspecific obtains a higher value reward (Oberliessen et al., 2016; Brosnan, 2006; Range et al., 2009). These reactions may not always include detailed social representations and experience but be better explained as a relative reward effect that alters the value of an outcome based on a natural function that integrates motivation with a socially-induced contrast effect (Douglas et al., 2018). These socially-induced relative effects could involve key regions of the brain including the striatum during social-reward behavioral tests (Baez-Mendoza et al., 2016, 2013). These animal studies have clear implications for human intrinsic motivation as a spontaneous tendency without immediate rewarding outcomes (e.g., Deci and Ryan, 1985; Di Domenico and Ryan, 2017).

Seeking systems and related feeling states disappear after extended locomotion/ exploration or outcome acquisition. Outcome values shift from more to less rewarding and even paradoxically from rewarding to 'repulsive'. Cabanac (1971) labeled this 'alliesthesia', and the effect is observed pervasively in animals, including humans. Understanding and predicting dynamic properties of outcomes and motivation, such as when approach changes to avoidance, is a key ingredient that makes motivation highly interesting and powerful but also difficult to study and track over time. One way of understanding how outcomes change from valued to repugnant is by postulating a change in the emotional state they induce. Therefore, the study of valuation can be seen as at the nexus of motivation and emotion. Before elaborating on animal studies parametrically manipulating valuation, we will therefore consider animal models of emotion.

3.2. Emotions in non-human animal models

Examining motivation in animal models has been well-established and accepted since early work in psychology (Thorndike, 1898; Watson, 1913). Labeling, examining and uncovering the neural basis for affective states has been much more contentious. Only recently has the newly coined 'Affective Neuroscience' field allowed work on emotions in animals to enter mainstream research (Panksepp, 1998). The arguments against inferring emotional states and feelings in animals include the beliefs that animals do not experience emotions either at all or in a similar way to humans (e.g., LeDoux, 1996). Non-human animals have been proposed to have 'meaningless' emotions that lack an interpretive label based on a situation (Barrett, 2017; Averill, 1980). Animal researchers who study fear responses in animals have distanced themselves from questions of affective 'neuroqualia' (localization of subjective feelings in the brain), stating that labeling emotions and feelings is not scientifically justified and these reactions by animals should be termed 'threat detection and defense responses' (LeDoux, 2014).

On the other side of the argument, the inference that animals have emotions has been made in a convincing manner both historically (Darwin, 1859) and by contemporary researchers studying rodent models (Berridge, 2019; Panksepp, 2011) as well as other non-human animal models, including avian (Papini et al., 2019), primate (de Waal, 2019), and other non-traditional models (e.g., lizards, Cabanac, 1999, and fish, Cerqueira et al., 2017).

The rationale for ascribing emotion and even feelings to non-human animals is multifold. First, one can argue that it is more parsimonious to assume that the same process underlies the same context-behavioral response pairing in animals and humans if the inferential basis for that process is no better in one species than in the other (Panksepp and Biven, 2012). Scientists of emotion have argued that it is just as difficult to appreciate and measure emotions in humans as it is in non-human animals, and since similar difficulty in measuring this introspective state exists across all animals (Nisbett and Wilson, 1977; SchoolerMauss, 2010), then the inferences in non-human animals are justified. This argument is sustained by evidence suggesting that affective reactions can occur unconsciously (Zajonc, 1980; Damasio, 2004, Berridge and Kringelbach, 2015) in all organisms. This basic idea undermines the validity of reifying verbal reports as the *sine qua non* for emotion (Greenwald and Banaji, 2017). Researchers who study preverbal infants have long argued, in fact, that emotions may be more accurately measured in infants, before socialization/social desirability affects voluntary expression and verbal report (e.g., Izard, 1971). A similar argument could be given for studying emotional behaviors in non-humans.

Contentiousness aside, the study of emotions using rodents is expanding from basic states to complex emotions, including empathy (Panksepp and Panksepp, 2013) and social distress (Kim et al., 2010). The psychological process labeled liking has been explored in depth as a sensory affective state providing insight into the core neural basis of pleasure (Berridge, 2019). Hedonic hotspots have been mapped using diverse techniques with specific locations within the nucleus accumbens, ventral pallidum and amygdala (Berridge, 2018a,b). Liking appears quite fragile, with small lesions of the ventral pallidum disrupting the ability to experience sensory hedonic states (Cromwell and Berridge, 1993).

A major boost in examining animal emotions arrived when researchers uncovered the complexity of high frequency ultrasounds emitted by rodents in emotionally charged situations (Knutson et al., 2002; Cromwell and Atchley, 2015; Cromwell and Ricker, 2018). These ultrasonic vocalizations (USVs) provided a possible window in the emotional lives of rats and mice (Burgdorf et al., 2000; Panksepp, 2000; Wohr et al., 2016). Jaak Panksepp was a key player in advocating the study of these USVs and was not shy about his thoughts in terms of the calls demonstrating intensity of emotions. Labeling 50 KHz rat USVs as rat 'laughter' and examining these laughs during a rodent tickle paradigm led to a burgeoning field of rodent affective neuroscience (Panksepp, 1998). There is growing evidence that these USVs indicate emotional arousal, with support arriving from research on both positive and negative affective states (Panksepp, 2005). Whether these are tickle-induced 50 kHz USVs in rats (i.e., induced by heterospecific play) or shock-induced 22 kHz calls, the evidence strongly supports these calls as being important indicators of the intensity of emotional states, that are generated and regulated by processes in the brain that also indicate their valence (Panksepp and Burgdorf, 2000; Burgdorf, Knutson, & Panksepp, 2000; Brudzynski, 2007, 2013; Portfors, 2007). Focal points, similar to the hedonic hotspots for pleasure, include regions of the NAcc and mesolimbic pathways connecting the midbrain and forebrain reward centers. Negative valenced USVs have been mapped to regions of the anterior cingulate cortex (ACC) and brainstem regions of the periaqueductal gray (PAG) (Panksepp, 2003).

Complex emotional states such as empathy and inequity aversion have recently been examined in greater detail using rodent models (Langford et al., 2006; Meyza et al., 2017; Douglas et al., 2018). Subregions of the amygdala (e.g. the basal nucleus) and PAG (e.g. the ventrolateral portion) have been pinpointed as being involved in social-related emotional states (Kiyokawa et al., 2007; Mikosz et al., 2015). The current debates on usefulness of neuroscience methods in revealing emotional experiences continues (Adolphs, 2017). What might matter most is the impact that examining these states in non-human animals has had in the development of new ways to understand human emotion (Panksepp and Bivens, 2012). Panksepp, for example, took the perspective that examining the core, basic elements of affective feelings with non-human animal models provided the most effective route both to understanding emotions impaired in mental illness and to

development of new ways to reduce and treat these impairments (Panksepp, 2011). These fundamental ideas are the foundation justifying work in psychopharmacology and biomedical research on neuropathology of mental illness.

3.3. The interface between motivation and emotion: motivation, incentives and reward valuation

Using animal models, motivational science in psychology has parametrically examined determinants of preference, choice, response effort and incentive contrast, to name a few key emotion-motivational processes. The gold standard technique used to examine motivation-emotion interactions is the conditioned place preference (CPP) task (Tzschentke, 1998). This task examines the preference of an animal for a previous location associated with a reward. Animals demonstrate clear place preference for external rewards like food, drugs and even play partners (Lahvis et al., 2015). Moreover, as mentioned earlier, animals will also work to engage in play, which is typically viewed as an intrinsic reward (Panksepp et al., 1984).

One paradigm in motivation science used to explore reward comparison is called “incentive contrast” (Flaherty, 1996). Earlier work recording from single units within the striatum in animal models found activation of these units linked to reward quality and quantity (Hassani et al., 2001; Cromwell and Schultz, 2003). Later work observed these activations to be dynamic rather than static, and to show variability depending upon the possible alternative outcomes (Cromwell et al., 2005). The paradigm of incentive contrast focuses on elucidating the direction and intensity of motivation and emotion based on relative reward shifts. Upshifts in reward value lead to positive contrast and downshifts to negative (Crespi, 1942). Recent behavioral work has found that these effects can occur for instrumental and anticipatory actions during reward acquisition (Webber et al., 2015). Most interestingly, monitoring striatal reward activity has shown that when the value shifts, striatal activity linked to approach behavior also changes. These are relatively small shifts in value (2 vs. 4 sugar pellets) but they can lead to a significant change in neural activity (Webber et al., 2016). Using ultrasonic vocalizations to index affective state reveals that affective shifts can accompany changes in motivation when reward value goes up or down (Binkley et al., 2014; Cromwell and Ricker, 2018).

Animal work on incentives, cues and expectancies has been successful in delineating neural circuits involved in learning and behavioral plasticity. A crucial element that motivation depends upon is that of valuation, the process of linking value to an outcome or external event. Value hierarchies are set and constantly re-evaluated as outcomes shift up or down depending on a host of factors. Work on reward processing and choice examines variables such as outcome magnitude, probability, and effort or delay related to the outcome. Rodent models are exceptionally useful in examining these processes, as these animals produce heterogeneous chains of instrumental action depending on various factors. One current example under investigation is the sign-and goal-tracking responses of animals following Pavlovian-instrumental learning. After conditioning that uses a lever as a food-predictive cue, some animals will compulsively search in the area of the food while others will stick to the lever as a sign (Kaveri and Nakahara, 2014). Opioid activation in forebrain regions such as the central amygdala amplify the sign tracking of the animals, making the incentive-induced motivation more intense and consistent over time (Castro and Berridge, 2017; DiFeliceantonio and Berridge, 2012; Tom et al., 2018).

Other regions, such as the prefrontal cortex (PFC) in rats and other animal models, play crucial roles in incentive learning and the influence of expectancies on goal-directed behavior (de Wit et al., 2009). The NAcc is involved heavily in the production of both positive and negative affective strategies involved in approach and avoidance (Faure et al., 2010). Combinations and interactions among glutamate, dopamine and gamma amino butyric acid (GABA) generate motivational-emotional interactions that can span desire to dread (Richard & Berridge, 2011). These interactions intimately depend upon the PFC to moderate intensity and link the motivational processing to planning and expectancy systems (Richard et al., 2013). Recent work has shown that the ventral striatal regions may produce more fine-grained reward comparisons (Webber et al., 2016).

3.4. Conclusions

Non-human animal work clearly highlights key overlapping neural substrates for motivation and emotion. These functions seem to exist as dynamic, interactive events in the brain that influence experience and behavior. The regions comprising the mesolimbic reward pathway are activated to integrate information triggering exploration and evaluating reward outcomes. Later, the same pathway, utilizing different molecules and signaling devices, plays a key role in the affective experience following/accompanying the reward experience. A similar merging and interposition of emotion and motivation occurs prior to the outcome, as reward expectancy co-mingled with anticipation.

These tight links between emotion and motivation are not consistently expressed (Binkley et al., 2014) and the degree of functional and neural overlap depends upon the predictability of the outcome and the level of experience the animal has with the behavioral-outcome associations. On one side of the equation, primary affective-motivational systems tap into substrates rooted in innate neural networks, which can transition into habits disconnected from emotional processing (Alcaro and Panksepp, 2011; Blakemore et al., 2017). On the other side exists higher order calculations of value that essentially require experience and a vast network of distributed memorial representations that must be combined in order to produce an accurate updated reward value (Blanchard and Hayden, 2014; Beer et al., 2006; Chiew and Braver, 2014). Work in non-human animal models has enabled development of frameworks for human neuroscience, to explore motivation and emotion while keeping in mind their roots of adaptive action in the context of risk (Kacelink and Bateson, 1996). Recent research in human neuroscience using neuroimaging tools has extended the work, implementing complex/culture-dependent motives and outcomes such as monetary incentives and social reward.

4. Section IV. Human neuroimaging of motivation and emotion

4.1. Methods of studying human brain functions and their development

Our current understanding of the brain basis of human motivation and emotion has largely been derived from functional magnetic resonance imaging (fMRI) studies using the blood-oxygen level dependent (BOLD) response. Structural MRI (sMRI), used in parallel with fMRI, is key in learning about neuroanatomical organization at a single time point. It also provides a template to use in localizing activity in fMRIs. However, sMRI has a limited spatial resolution and therefore does not necessarily detect small change in different structures over time (see Graham, Pfeifer, Fisher, Lin, Gao, & Fair, 2015). Importantly, sMRI does not provide data on the functional capacity of the neural regions visualized. For this reason, fMRI methods are needed. Using fMRI, typically the human participant responds to an emotion or motivation-inducing task, and activation patterns are inferred from BOLD signals. In addition to task-related fMRI, resting state functional connectivity MRI (rs-fcMRI) is used. In rs-fcMRI, the trajectory of changes in brain activity (BOLD signals) for a particular ROI during a scan lasting five or more minutes is correlated with that of another ROI or with all other voxels in the brain. The strength of the correlations is used as an indicator of the connectedness of those structures, and the direction of the correlation is considered an indicator of whether the relation is excitatory or inhibitory. In addition, this approach can be used to map entire functional networks. Finally, it can be used to understand interactions within and between such networks.

4.2. Human fMRI studies of motivation: the neuro-circuitry of distinct phases of motivation in humans

Similar to non-human animal studies, human motivation has been defined to include the drive towards both extrinsic rewards, such as money or substances of addiction, and intrinsic reward arising from the execution of the behavior itself. A useful model to guide human neuroimaging work is presented by Kim (2013) in which motivation is operationalized into three phases: (1) *generation*, which includes the anticipation of a reward; (2) *maintenance*, which involves value-based decision making; and (3) *modulation*, which requires cognitive regulatory control.

Both animal model and human studies find that the striatum, including the NAcc, is sensitive to potential rewards, anticipation of which generates motivation (Bjork et al., 2004). Moreover, the degree of activation of the NAcc correlates with participants' self-rated degree of excitement. The magnitude of the potential reward is also believed to be significantly influential, with anticipation of greater reward associated with greater NAcc activation (Peterson, 2005).

The maintenance phase of motivation involves distinct roles within the striatum. "Grit", that is, long-term perseverance to achieve a goal, is associated with ventral striatal functional connectivity to a medial prefrontal network, while a "growth mindset", the belief that one can improve talents, is associated with both ventral and dorsal striatal functional connectivity with regions important for error-monitoring (Myers et al., 2016). Moreover, the mPFC has been associated with the receipt of or enjoyment of a reward (Haber and Knutson, 2010), and its activity is positively correlated with the perceived probability of gain (Knutson et al., 2005). The orbitofrontal cortex (OFC) is also crucial in value-judgement (Kim, 2013). Taken together, these findings suggest that the striatum, prefrontal and frontal cortical regions are important in driving the maintenance of motivation.

The attentional state is considered important in the modulation of motivation and task persistence, and attentional networks are in turn influenced by one's motivational state (Paschke et al., 2015; Bourgeois et al., 2016). Aspects of the PFC, anterior cingulate cortex (ACC) and ventral striatum appear to be crucial hubs for regulation of motivation (Botvinick and Braver, 2015) and are linked to psychological aspects of cognitive and behavioral control (Kim, 2013).

4.3. Emotion-motivation interaction using fMRI in humans

As outlined in the previous section and in Fig. 1, the neurocircuitry used in motivation heavily overlaps with that for emotion in their cortico-basal ganglia-cortical loops; however, differences in functional neuroanatomy have also been demonstrated. In emotional processing, for example, the hypothalamus is also demonstrated as important for the "top-down" regulation of emotions via endocrine and autonomic mechanisms (Pessoa, 2017). Moreover, the nuclei of the solitary tract in the medulla, have been implicated in the "bottom-up" feedback of bodily functions associated with affective states to the medial OFC, cingulate gyrus, and the insula (Craig, 2002). Such fMRI studies commonly report on emotion and motivation as distinct processes. However, relatively few attempts have been made to specifically disentangle the emotional components of motivation.

One approach to compare neural networks between emotional and motivational stimuli has been to use facial affective displays and a monetary incentive tasks as representative stimuli, respectively (Park et al., 2018). Shared valence effects have been demonstrated, with increased activity in the ventromedial PFC for positive valence effects (happiness and monetary gain) and increased activity in left inferior frontal gyrus (associated with the dorsolateral PFC) for negative valence effects. In addition to this, social approach-avoidance tasks have also been utilized. Affect-congruent tasks (approach-happy face stimuli; avoid-angry face stimuli) appear to have less activity in the left lateral OFC compared to affect-incongruent responses (Roelofs et al., 2009). Moreover, although this research demonstrated differences based on negative versus positive valence of emotion, there is also evidence of differences based on which *specific* negative emotions are elicited. When angry faces are used to elicit emotion, they typically elicit avoidance in the perceiver, since they are perceived as threatening/fear-provoking. However, when anger is elicited in the participant, it tends to be associated with approach motivation and a different neural response (Carver and Harmon-Jones, 2009). Taken together, there is preliminary human fMRI-based evidence that there are distinct neural networks associated with distinct emotional components of motivation.

4.4. Intrinsic vs. extrinsic motivation in humans

In the human neuroimaging literature, motivation is commonly divided into extrinsic and intrinsic determinants. Extrinsic motivation includes rewards that are external to the subject, such as financial incentives and substances of addiction. Intrinsic motivation refers to one's inherent tendency to seek experiences that generate feelings of interest and enjoyment through task novelty, challenges and mastery (Ryan and Deci, 2000a,b).

Extrinsic motivation studies in humans commonly use monetary incentive delay-tasks (MIDT), such as those developed at the Symbiotic Project of Affective Neuroscience Laboratory at Stanford University (see Peterson (2005) for an overview). In this type of task, individuals are asked to react to a target stimulus, presented after an incentive cue, to win or avoid losing an indicated reward. Recently published meta-analyses of fMRI findings using MIDTto examine the anticipation component of reward have demonstrated activation of the striatum, thalamus, and the insular and anterior cingulate cortices, in anticipation of both loss and gain (Oldham et al., 2018; Wilson et al., 2018). These studies concur that these aspects of the neural networks are activated regardless of the valence (that is, positive or negative). By contrast, the orbitofrontal and ventromedial PFC appear to be more specifically activated in the reward outcome phase of motivation, and it is hypothesized that these regions are involved in processing and strengthening the relationship between stimulus and outcome (Oldham et al., 2018)

The findings with the MIDT have some overlap with findings from disorders of addiction, as another significant area of research for extrinsic reward-driven behavior. Addiction involves aspects of impaired decision making and learning, and poorly regulated motivation. For example, alcohol-related cues result in greater activation in the ventral striatum in individuals with an alcohol use disorder (Wrase et al., 2007), emphasizing the importance of the striatum in the anticipation of perceived extrinsic rewards. Moreover, reduced ventral striatal recruitment during the anticipation phase of monetary-related cues was associated with higher level of impulsivity in those with an alcohol use disorder (Beck et al., 2009). Ventral striatal dysfunction may therefore represent the neural substrate for the "impulsivity hypothesis" -that is, those with substance use disorders are more sensitive to reward stimulation and have a reduced capacity for inhibitory control. Hommer et al. (2011) provides a more complete review of neuroimaging studies in addiction.

There are relatively fewer fMRI studies examining intrinsic motivation. As with extrinsic motivation, striatal activation has been repeatedly observed in participants with intrinsic motivation (Gruber et al., 2014; Murayama et al., 2010). The anterior insular cortex has been more explicitly linked to intrinsic motivation, and its activity correlated with participants' self-reported sense of satisfaction (Lee and Reeve, 2013). This has been replicated, with additional evidence for the interaction between the anterior insular cortex and striatum in the pursuit of intrinsic rewards (Lee and Reeve, 2017). A recent review of intrinsic motivation supports the dopaminergic models of intrinsic motivation, with neuroimaging evidence that it involves switching between networks for salience detection, attention and self-referential cognition (Di Domenico and Ryan, 2017)

A number of fMRI studies have examined the interaction between intrinsic and extrinsic motivation, albeit with somewhat conflicting results. For example, Murayama et al. (2010) showed that performance-based monetary rewards undermined intrinsic drive, which was associated with reduced activity in the ventral striatum and prefrontal cortex. However, Albrecht et al. (2014) could not support the "crowding-out" effect due to the monetary reward. Thus, further research is required to disentangle the complex interplay between intrinsic and extrinsic determinants of motivation.

4.5. The disordered brain – apathy as the inverse of motivation

Finally, it is worth commenting on apathy, a disorder of motivation, as an alternative lens through which one can highlight the human neurocircuitry of motivation. Apathy can be defined as a lack of interest and motivation, and is associated with adverse outcomes such as poor function and reduced treatment response in various conditions (van Reekum et al., 2005). It is considered to be a core feature of depression and a negative syndrome associated with schizophrenia, and is common in cortical and subcortical dementias. It also increases with age, particularly in males (Brodaty et al., 2010).

Apathy in schizophrenia has commonly been associated with dysfunctional signals for an expected value of a reward, in the context of learning (Waltz and Gold, 2016). Monetary incentive delay paradigms have shown that people with schizophrenia have a deficit in action valuation, associated with reduced activity in the ACC (Walter et al., 2010). Moreover, in subcortical regions, altered fMRI activity has been shown in the ventral striatum during anticipation, but not actual receiving, of rewards (see Kos et al., 2016, for a review). This suggests that motivational deficits in schizophrenia may be associated with abnormal anticipation and processing of rewards in the striatal and cingulate regions, which are typically associated with motivation. Similar relationships have been observed in major depression (see Eshel and Roiser, 2010; Pizzagalli, 2014, for reviews).

Parkinson's disease (PD) is another disorder for understanding amotivation, and it provides an exemplary model for the role of dopamine. The pathophysiological model includes a deficiency of dopamine in the substantia nigra of the basal ganglia, and treatment with dopamine-replacing or enhancing agents can result in disorders of impulse control and addiction (Dagher and Robbins, 2009). Apathy is a common and disabling feature of PD, affecting up to approximately 70% of those with PD (Kostic and Filippi, 2011). Interestingly, there have been few fMRI studies of apathy in PD to date. Of note, people with PD showed reduced functional connectivity, primarily among limbic striatal and frontal cortical regions, compared to healthy controls and people with PD who lack apathy (Baggio et al., 2015). Moreover, in an analysis of resting state fMRI in people with PD, greater apathy was associated with increased fractional amplitude of low frequency fluctuations in the right OFC and bilateral subgenual cingulate cortex (Skidmore et al., 2013). Thus, fMRI studies of apathy add weight to the importance of the frontostriatal circuits in normal and pathological aspects of motivation.

4.6. Conclusions

Human fMRI studies have investigated the underlying neural circuitry of motivation and its phases, including the generation, maintenance and regulation of motivation. Although there is significant variability in how motivation is operationalized across studies, many have considered motivation in terms of extrinsic compared to intrinsic drives. Regardless of the paradigm, similarly to the results of animal studies, human motivation commonly involves the mesolimbic and mesocortical dopaminergic pathways, with different regions within the frontal cortex and the striatum modulating different aspects of motivational behavior. Further research is required to satisfactorily disentangle complex relationships between emotion and the cognitive and behavioral components of motivation.

5. Section V. Social neuroscience and motivation-emotion interaction

Over the past few decades, social neuroscience has begun to identify neural systems that are critical to human social behavior. Social context is important for generation of emotions and motivation, as well as the important social communication functions of emotional expressions, and therefore is particularly important to study in relation to human motivation and emotion. Insights regarding the role of the motivational neural systems are important guides for identifying the underlying components of a variety of behaviors in a social context. Certain social emotions are also especially important in guiding, amplifying and reinforcing social behaviors. This section reviews our current understanding of the role of brain mechanisms associated with motivation-emotion interaction that facilitate or regulate social behaviors. Specifically, we focus on the neural correlates of social motivation, which is mainly characterized by the pursuit of social reward and the avoidance of social punishment. We then focus on the neural correlates of social orienting and social maintenance that are also relevant to social motivation. Next, we focus on social facilitation, where an individual's performance can be enhanced when working in the presence of others. We also focus on the influence of motivation on social emotion, particularly from the neuroscience perspective.

5.1. Neural bases of social motivation

Social motivation can be described as a set of psychological dispositions and biological mechanisms biasing the individual to preferentially orient toward the social world (i.e., social orienting), to seek and take pleasure in social interactions (i.e., social reward), and to work to foster and maintain social bonds (i.e., social maintaining)(Chevallier et al., 2012). Among these three components, the neural correlates of the pursuit of social reward, such as approval from others, and those of a highly related process, the avoidance of social punishment such as disapproval from others, have been well established. Similarly to material rewards and punishments, the processing of social rewards and punishments can be subdivided into two successive processes: anticipation of the desired outcome and appraisal of the experienced outcome, with the former anticipatory phase being critical in motivational processes. The possibility of obtaining social reward typically facilitates approach behavior, whereas the possibility of social punishment typically triggers avoidance behavior.

As outlined in Sections II and III, signals associated with the anticipation of material rewards have been identified in dopaminergic neurons in the ventral tegmental area (VTA) and substantia nigra and in other dopaminergically innervated structures, including the dorsal striatum, ventral striatum/nucleus accumbens, and orbitofrontal cortex (O'Doherty, 2004; Ruff and Fehr, 2014). An important question is how the neural bases of anticipation of material reward overlap with those of social reward. Several neuroimaging studies have directly addressed this question (e.g., Dichter et al., 2012; Izuma et al., 2010; Kohls et al., 2012, 2013; Rademacher et al., 2010; Radke et al., 2016; Spreckelmeyer et al., 2009), and the current consensus points to a significant overlap between the neural mechanisms of anticipation of social rewards and anticipation of material rewards. For example, Spreckelmeyer et al. (2009) modified the monetary incentive delay task (MIDT; Knutson et al., 2001a,b), which is a suitable paradigm for determining the anticipatory neural responses to monetary gain or loss, to study the processing of positive social feedback, and found that the anticipation of both social and monetary rewards elicited activation of the dopaminergic reward circuitry, including the nucleus accumbens (NAcc). More recent studies have replicated these findings (Dichter et al., 2012; Kohls et al., 2012, 2013; Rademacher et al., 2010), supporting the idea of a "common neural currency" of rewarding information (Montague and Berns, 2002).

Another theoretically notable idea in this field is that the neural correlates of the avoidance of social punishment overlap with those of

the pursuit of social reward, as is the case of material rewards and punishments (e.g., Carter et al., 2009). Kohls et al. (2013) used the delay incentive paradigm combined with dynamic video stimuli to examine participants' motivation for social reward acquisition and social punishment avoidance. The researchers found that both the anticipation of social reward acquisition and the anticipation of avoidable social punishment reliably recruited the activation of the NAcc. Furthermore, stronger NAcc activity was accompanied by faster reactions from the participants to obtain the desired outcomes. Similar to the findings of the MIDT described in Section III, the bivalent activation in the NAcc, along with the reaction time data, suggest that this region plays a key role in forming both approach motivation and avoidance motivation for social engagement.

In addition to the neuroimaging evidence, patient studies also provide insight into the role of the neural systems associated with social motivation. For example, autism spectrum disorders (ASD) can be regarded as a case of reduced social motivation (Chevallier et al., 2012). A recent meta-analysis of fMRI data demonstrates that individuals with ASD show atypical neural processing of social and nonsocial rewards (Clements et al., 2018). This result indicates that general atypical reward processing in ASD encompasses both social reward and nonsocial reward, a finding that echoes the notion of common neural currency. To extend Section III "Disorders of motivation-apathy," deficits in social reward processing are also observed in psychiatric disorders, including mood disorders and schizophrenia. Sharma et al. (2016) reported that greater depression severity significantly correlated with reduced bilateral ventral striatum activation to social reward in the bipolar depressed group. In addition, decreased left orbitofrontal cortical activation was correlated with more severe symptoms in bipolar depression. Lee et al. (2019) reported that patients with schizophrenia showed reduced neural sensitivity to social rewards in regions including the ventral striatum, ventromedial prefrontal cortex (i.e., medial orbitofrontal cortex), and anterior cingulate cortex. A notable finding in this study is that these effects were specific to social as opposed to nonsocial reward processing, raising the possibility that the neural overlap between social and nonsocial reward depends on the context.

Prior neurocognitive studies have also attempted to clarify the neural mechanisms associated with social orienting and social maintenance. Social orienting is characterized by the fact that objects with social relevance, such as eyes and faces, are prioritized for attention. Accumulated neuroimaging evidence suggests that the amygdala plays a key role in directing attention to biologically relevant social information conveyed by eyes, faces, or biological motion (Adolphs and Spezio, 2006) and in calculating and updating social orienting values (Klein et al., 2009). Furthermore, individual differences in social orienting are reported to be related to functional differences in the orbitofrontal–striatum–amygdala network. Schirmer et al. (2008) reported that stronger social orienting is associated with enhanced amygdala and orbitofrontal activity in response to emotionally relevant stimuli. The neural correlates of social maintenance, an individual's desire to engage with others over sustained periods of time, have also been gradually delineated. For example, Quirin et al. (2013) reported that the affiliation motive, which refers to a tendency toward establishing, maintaining, and restoring positive relationships with other individuals (Atkinson et al., 1954), is associated with activity in the right subcortical basal ganglia; whereas, the power motive, which refers to a tendency toward influencing others or obtaining control over them (Veroff, 1957), is associated with activity in the left prefrontal cortex. Taken together, these findings indicate that social motivation is represented not only by typical reward-related brain regions supported by the dopaminergic system, but also by additional neural networks.

5.2. Neural bases of social facilitation

Social facilitation can be defined as an improvement in performance produced by the presence of others. The study of the social facilitation of individual behavior has attracted much attention since Zajonc (1965) revived interest in it in the mid-1960s (Geen, 1991). A number of behavioral studies have reported social facilitation effects, not only in humans but also in other species (Baumeister, 1984; Bond & Titus, 1989; Fragaszy and Visalberghi, 1990; Miramontes and Desouza, 1996; Strauss, 2002; Visalberghi and Addessi, 2001; Zajonc and Herman, 1969; Douglas et al., 2018). From a neuroscientific perspective, recent neuroimaging studies have begun to clarify the neural mechanisms underlying social facilitation effects. These studies have shown that the presence of an audience influences charitable donation (Izuma et al., 2010), unskilled physical exertion (Yoshie et al., 2016), effort mobilization (Gendolla and Richter, 2006) and cognitive performance (Dumontheil et al., 2016; Muller-Pinzler et al., 2015), and have shown that when subjects were observed by others, they exhibited increased brain activity in regions responsible for mentalizing (e.g., medial prefrontal cortex) and increased sympathetic activation.

While these studies clarified some basic neural processes related to audience observation, it is less clear how the neural processes related to motivated performance are influenced by the presence of an audience. In this sense, a recent study reported by Chib et al. (2018) is noteworthy. They used fMRI to record brain activity while participants engaged in a skilled-task during conditions in which they were paid based on their performance and observed or not observed by an audience. The results revealed that during social facilitation, social signals represented in the dorsomedial prefrontal cortex enhanced reward value computations in the ventromedial prefrontal cortex. Further analysis showed that functional connectivity between the dorsomedial prefrontal cortex and ventral striatum was increased during social facilitation, indicative of a means by which social signals serve to modulate brain regions associated with the regulation of behavioral motivation. These findings represent an important step toward understanding how neural processing of the presence of others gives rise to the enhanced motivational state that results in social facilitation of incentive-based performance.

5.3. Motivational influence on social emotion

It is also assumed that motivational processes are closely linked to the neural processing of social emotions, which are defined as affective states that depend on the social context and arise when people interact with each other (Lamm and Singer, 2010). While basic emotions such as fear or anger are elicited often by non-social stimuli, social emotions, such as embarrassment, guilt, shame, or admiration typically involve a real, internalized, or imagined other person. These rather complex emotions can consist of multiple stages, each with various types of motivation triggered by different internal or external cues.

Social emotions, such as compassion and empathy-induced personal distress, inherently include motivation that drives people to approach or avoid engagement with others' emotions. Notably, some past neuroimaging studies have demonstrated that brain regions relevant to basic motivation are parts of the neural correlates of various kinds of social emotions Singer et al. (2006); Takahashi et al. (2009). For example, Singer et al. (2006) reported that male participants showed increased brain activity in the ventral striatum and orbitofrontal cortex while observing an unfair economic game player receiving painful stimulation. Further analysis revealed that individual differences in an expressed desire for "revenge" covaried with brain activity in the ventral striatum. These results are in line with a neuropsychological study with patients with Parkinson's disease suggesting a role for dopamine in altruistic punishment decisions (Djamshidian et al., 2011). In another example, Takahashi et al. (2009) reported that stronger schadenfreude, a rewarding feeling derived from another's misfortune, is associated with stronger ventral striatal activation when misfortunes happened to envied persons. Paralleling these neuroimaging findings, a series of neuropsychological studies with patients with Huntington's disease (HD) has demonstrated that patients with HD show lower

schadenfreude, and this reduction was associated with atrophy in the ventral striatum and the mentalizing-related cortical network (Baez et al., 2016, 2018).

However, one major noteworthy point is that these neural correlates, which apparently overlap with motivational neural systems, are likely to be organized in terms of appraised valence rather than motivational orientation. To address this issue, researchers need to devise experimental paradigms that attempt to isolate the motivational components from emotional processing based on well-established theoretical accounts. In this respect, a "motivated" account of empathy (Zaki, 2014), which is regarded as other-oriented social emotion (Decety and Lamm, 2006), deserves attention. This account assumes that at least three phenomena—suffering, material costs, and interference with competition—motivate people to avoid empathy, and at least three other phenomena—positive affect, affiliation, and social desirability—motivate them to approach empathy. In a similar vein, another notable theory on empathy and compassion proposed by Singer and Klimecki (2014) presents some empirical evidence in terms of motivation-emotion interaction. These researchers proposed a distinction between empathic distress and compassion. Empathic distress (also called "personal distress"; see Batson et al., 1987) refers to a strong aversive and a self-oriented response to the suffering of others, accompanied by the desire to withdraw from a situation to protect oneself from excessive negative feelings. There is now ample evidence for the existence of "shared neuronal networks" underlying empathic experiences in the domain of pain, including the anterior insula and anterior cingulate cortex (Fig. 4). Compassion, on the other hand, is conceived as a feeling of concern for another person's suffering and is accompanied by the motivation to help. Compassion is therefore associated with approach and prosocial motivation. Interestingly, the compassion-related neural network includes the VTA, the dorsal and ventral striatum, and the orbitofrontal cortex, which are regions that highly overlap with the dopaminergic innervated brain regions (Klimecki et al., 2013). Although it is difficult to precisely disentangle the underlying motivational components of empathy at the neural level, these observations provide a novel framework for better understanding the relationship between motivational processes and empathy in terms of approach and avoidance motivation.

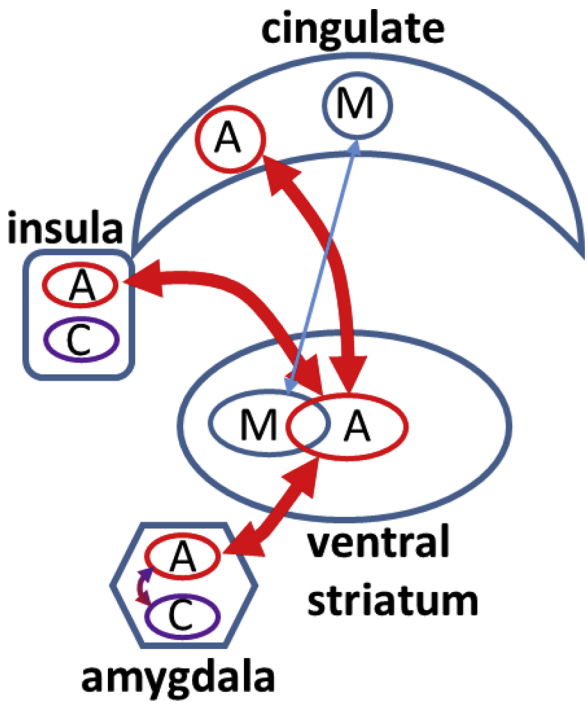

Fig. 4. Social motivation-emotion driven by social feelings and affect. Empathy circuitry involving potential diverse sites that incorporate social emotion (feelings of sadness) with motivational processes that lead to care-giving and altruism.

5.4. Conclusions

In humans, as in non-human animals, motivation and emotion seem to utilize networks of similar brain areas, including dopamine-rich pathways involving the striatum/ NAcc and VTA, and limbic structures, such as the amygdala, the cingulate cortex and frontal cortex. Social reward and non-social reward involve similar circuits, and social pain and physical pain do as well. For human neuroscience, social influences are natural and powerful variables to study, but difficult to manipulate and control. Human neuroimaging results suggest a neural circuitry related to social loss and social gain. Centered in the dorsal anterior cingulate cortex and anterior insula, this region is an example of overlap of function. It encodes social information and can interact with positive or BAS and negative or BIS subsystems. This example of overlap suggests new directions to determine how these brain regions can incorporate opponent (inclusion and exclusion) emotional-motivational state information (Fig. 4). These directions can be facilitated by incorporating work from non-human animal models of social reward and loss (Panksepp, 1998). Evidence supports the existence of similar neural systems involved across a wide range of species (Panksepp and Panksepp, 2013). Although social influences are often difficult to manipulate and control, future studies need to expand this line of research to further address questions concerning a neural link between motivational processes and various kinds of social emotions.

Now that we have reviewed research showing highly interconnected motivation-emotion pathways in the brains of non-human and human adults, the review moves to address crucial questions related to how these interconnections and pathways develop from infancy through maturity.

6. Section VI. Motivational development and its relation to emotion and brain development

6.1. Processes of brain development, and their relevance to motivation and emotion

The preceding sections primarily described neural systems empirically associated with motivational and emotional processes in mature animals and humans. However, in order to fully understand the neural underpinnings of motivation, emotion, and their interface, one must address the *development* of these neural systems. Development is not simply maturation or even construction of brain *structures*; to a much greater extent, it involves forming *connections* among the brain systems subserving particular sensory, cognitive, emotional, motivational, social and other behavioral processes. Moreover, even though the brain does continue to form synapses throughout the lifespan, and myelination improves connective efficiency throughout childhood and at least early adulthood, there seem to be sensitive periods during which particular parts of the brain undergo rapid change and are more susceptible to the environment. Further, in the absence of relevant experiences and behaviors, children become increasingly less able to develop the pertinent neural pathways, and in the presence of maladaptive experiences and behaviors, they may develop atypical pathways and behaviors (e.g., Kolb & Gibb, 2011).

The most relevant influences on this developing "connectome" can be conceptualized using mnemonics of "fire together wire together", "use it or lose it", "experience-expectant development", and "experience-dependent development". Briefly, "fire together wire together," describes the finding that the presynaptic-postsynaptic connection is strengthened and/or made more efficient with repeated use (Löwel & Singer, 1992). Empirical evidence has supported both of these processes, especially strengthening (Cohen, Quarta, Bravi, Granato, & Minciacchi, 2017).

"Use it or lose it" (activity-dependent synapse formation/elimination) summarizes the fact that the person's behavioral and sensory responses to the environment impact which connections are "pruned". Dendrite formation begins prenatally and the number of synapses peaks by the end of the second year of life, after which synaptic pruning is a more common developmental process (Tierney & Nelson, 2009). To the extent that a person never engages in a behavior, the neural connections supporting that behavior are pruned/lost. This is very relevant to motivated versus unmotivated behavior. To the extent that one is unmotivated to engage in approach behavior in a given context, and/or such behavior is associated with emotions that foster avoidance or withdrawal, the approach pathway will become weaker or will be pruned, and the avoidance pathway will become stronger. In contrast, to the extent that approach behavior is highly motivated and/or associated with positive, rewarding emotion, the behavior will be repeated and the approach pathway will be strengthened. Importantly, although synaptic connections continue to be made throughout life, typically, they are easier to construct and/or function better if constructed earlier in development. The important role of early experience in shaping these connections and brain development, more generally, is manifested in terms of two different types of experience-based neural development: "experience-expectant" and "experience-dependent/adaptive".

"Experience expectant" development occurs when certain environmental inputs are *expectable and needed* to promote normative developmental change (e.g., Rutter et al., 2004). This is typical of early synaptogenesis of basic connections within functional systems. Almost all infants are exposed to these minimal environmental conditions, and absence of such exposure leads to highly atypical development. For example, experience-*expectant* processes lead to the development of infant-caregiver attachment and basic connections among brain structures associated with attachment such as the locus coeruleus and the anterior cingulate (Opendak et al., 2017). Caregivers' mere presence buffers stress-related hormonal production such that infants do not associate their parent with stress-related threat (fear conditioning to the caregiver is disrupted), and infants become attached even to abusive caregivers (see Gunnar, Hostinar, Sanchez, Tottenham, & Sullivan, 2015).

In contrast, "experience-dependent" development occurs when the specific trajectory of development is shaped by the *nature* of environmental inputs. For example, the amygdala-hippocampus-PFC system, critical for threat-related learning and for appropriately regulating many emotions, is disrupted by repeated caregiver-associated threat, such as abuse, resulting in increased risk for behavioral disorders involving emotion dysregulation (Opendak et al., 2017). Given that important changes take place in the brain during infancy and childhood via these processes, it is important to examine the brain bases for motivation and emotion in infants and children, to better understand how the systems associated with motivation and emotion become interconnected during these earlier periods, and how they are similar and different from those associated with motivation and emotion in mature humans. A majority of research with infants and young children has utilized EEG-based methods, given difficulties in studying infants/young children using MRI methods. We will present the EEG-based results first. However, recently, MRI-based data have been obtained in infants and young children, and these will be reported as well.

6.2. Frontal lobe lateralization and approach versus inhibition motivation

Gray and McNaughton's (2000) BIS, alluded to earlier, is conceptualized as a regulatory system that is responsive to goal/motivational conflict. At high levels, the BIS is associated with anxiety and inhibition. However, more generally, the BIS serves to regulate the individual's emotions and behavior, inhibiting impulsive approach responses (Gray and McNaughton, 2000). Gray and McNaughton (2000) view the septo-hippocampal system, including the connection of these structures to the prefrontal lobes and the cingulate gyrus, as central to the BIS. Despite this, frontal lobe asymmetry has been the focus of most inquiry into relevant approach and avoidance motivation in early development. Although Gray and McNaughton's theory was rarely explicitly discussed in connection with this lateralization research, recently the connection between their BIS and the concept of temperamental behavioral inhibition (e.g., Fox et al., 1995; Kagan et al., 1984), which has been linked to frontal lobe asymmetry, has been discussed clearly (Barker et al., 2019).

The original line of developmental research on approach and avoidance motivation that has, in keeping with Gray and McNaughton's (2000) approach, focused on brain, temperamental, and physiological processes associated with approach and inhibition, has been very successful in predicting concurrent emotions, as well as the development of psychopathology longitudinally (e.g., Fox, 1991; Fox et al., 2005; Henderson et al., 2015; White et al., 2017). Early work of Davidson and Fox (1982) demonstrated that, beginning in infancy, there are systematic, asymmetrical, frontal EEG responses in the infant alpha frequency band to positive versus negative affective stimuli. Much research followed, suggesting that relative left activity was not only associated with positive emotional responses, but also with anger. Davidson (1994, 1998) initially hypothesized that relative frontal lateralization of alpha activity is best understood as relating to approach versus withdrawal behavior. More specifically, left frontal brain activity seemed to be connected to an appetitive/reward system associated with approach behavior, and right frontal activity was instead linked to a withdrawal/avoidance system.

Fox and colleagues have been studying infants' and children's brain and physiological responses reflective of approach and inhibition for decades (e.g., Fox, 1991; Fox et al., 2005; Henderson et al., 2015). Their groundbreaking research showed that beginning in infancy, children showed relative left frontal asymmetry when experiencing an inclination to approach and relative right frontal asymmetry when demonstrating wariness/ behavioral inhibition. In a longitudinal study, four-month-old infants' emotional and motor reactivity to visual and auditory stimuli was assessed (Hane et al., 2008). They classified infants into groups with: a) above average positive emotion, below average negative emotion, and above average motor activity (Positive Reactivity, PR (or temperamental exuberance); b) above average negative emotion, below average positive emotion, and above average motor activity (Negative Reactivity, NR (or temperamental inhibition); or c) the remaining infants (average reactivity). The concept of temperamental inhibition was first proposed by Jerome Kagan (Kagan et al., 1984). Kagan and colleagues had found temperamental inhibition to be quite stable and predictive of social avoidance. However, they did not examine whether specific brain differences distinguished these children from uninhibited children.

Fox and colleagues followed the children labeled as inhibited longitudinally to observe whether similar behavioral outcomes obtained in their inhibited sample, and to ascertain whether these patterns, if found, were associated with differences in frontal lateralization. When these infants returned at 9 months, the positive reactivity (PR) group showed more positive emotion, more approach, and less avoidance than the average reactivity group. Importantly, the temperamentally inhibited group showed higher relative right frontal asymmetry, the PR showed high relative left frontal asymmetry, and the average reactivity group showed relatively symmetrical EEG frontal activation. Thus, the approach/ exuberance versus avoidance/inhibition tendencies were relatively stable, beginning in early infancy, and found to be associated with relatively stable frontal EEG patterns and relatively stable emotional patterns across the first 9 months of life.

These approach tendencies are not only stable as responses to novel nonsocial stimuli; they also are evidenced in infants' interactions with their mothers. Infants' degree of involvement in an interaction with their mothers at 7 months was moderately and significantly related to their degree of involvement in an interaction with their mothers at four years of age. Moreover, their relative right frontal asymmetry at 14

months was strongly and significantly negatively correlated with involvement in interaction with their mothers at age four (Likata, Paulus, Kuhn-Popp, Meinhardt, & Sodian, 2015). More recently, Fox, his colleagues, and other researchers have found that temperamental inhibition (relative right frontal activation and negative/inhibited behavioral responses to novelty), predisposes children to a higher risk of internalizing disorders such as anxiety disorders (especially social anxiety) and depression (e.g., White et al., 2017). In contrast, strong approach tendencies and the temperamental style of exuberance, place children at risk for developing externalizing difficulties such as ADHD and conduct disorders (e.g., Rydell et al., 2003). Interestingly, children manifesting temperamental *inhibition* in early childhood show higher striatal activation to rewards as adolescents (Guyer et al., 2006).

Barker et al. (2019) have proposed that the temperamental characteristic, behavioral inhibition, involves heightened sensitivity to both approach and avoidance motivation in the context of novelty, particularly in novel social contexts, leading to prolonged BIS responses to approach/avoidance conflict. The authors proposed that, in addition to right lateralization in the PFC, behaviorally inhibited children have heightened activation of the avoidance motivational system, including the amygdala and the bed nucleus of the stria terminalis (BNST), as well as heightened activation of the approach motivational system, including the dopaminergic pathways originating in the striatum.

In addition to findings regarding striatal activation and temperamental inhibition, researchers from a different lab found that children of depressed mothers, even though never diagnosed with depression themselves, showed a developmental trajectory of *decreasing relative left* frontal activation from age 3 years to age 6 years. In contrast, children of non-depressed mothers showed a pattern of relatively symmetrical frontal activation that was stable from 3 to 6 years of age (Goldstein, Shankman, Kujawa, Torpey-Newman, Olino, & Klein, 2016). This research demonstrates the value of examining the developmental course of EEG asymmetry, especially in relation to disorders such as depression, that are associated with dysfunctional patterns of approach or avoidance motivation (in this case, diminished approach motivation). It also shows that it can be useful to compare trajectories of approach and avoidance tendencies, rather than simply focusing on approach or avoidance. However, it is important to examine the development of subcortical structures and connectivity in order to truly understand the brain systems underlying motivation and emotion. We will start with the development of the amygdala and its connectivity with the prefrontal cortex.

6.3. Amygdala connectivity to the prefrontal cortex

The amygdala is particularly relevant to the interface between motivation and emotion, because it has been strongly associated with both fear/avoidance learning/responses and with quick emotional responses to relevant positive and negative affective stimuli, including other people's emotional facial expressions. The amygdala is highly mature by the eighth prenatal month (Ulfig, Setzer, & Bohl, 2003). Moreover, it forms connections to many parts of the brain, including systems believed to underpin avoidance and reward learning, and salience responses needed for decision-making and memory. Probably the most widely discussed amygdalar connections are to two regions of the PFC – the medial PFC (especially ventromedial (VM), and sometimes including the Anterior Cingulate Cortex (ACC)) and the orbitofrontal PFC.

Both the medial PFC and the orbital PFC show connectivity to the amygdala beginning in infancy. There is rapid development of this connectivity in the first year of life; however, there is further important development of amygdala-PFC connectivity, including myelination, increased interhemispheric connectivity, and increased synaptic density throughout childhood and adolescence (Happaney, Zelazo, & Stuss, 2004; Gee, Humphreys, et al., 2013). Both the VM PFC and the amygdala show early and continued growth of connectivity to the anterior insula, forming a network now widely construed as a *salience network* (Anderson, Bechara, Damasio, Tranell, & Damasio, 1999; Bechara, 2004; Graham et al., 2015).

Damasio and his colleagues observed that individuals who had damage to the VM PFC prior to 16 months had devastating long-term outcomes. Even though individuals with VM PFC damage were able to report a logical cognitive understanding of a situation and its consequences for them, they were unable to make reasonable choices based on this information. They seemed insensitive to negative and positive consequences of their behavior that should motivate particular future choices (e.g., Anderson et al., 1999). The salience system, including the VM PFC, the amygdala, the somatosensory/insular cortices, and the peripheral nervous system seems to be responsible for these effects. These researchers have hypothesized that people who have such damage are unable to effectively process the somatic cues of emotion and use them to motivate appropriate choices for future behavior (e.g., Bechara, Damasio, & Damasio, 2000).

The connectivity among the amygdala, the insula, and the medial PFC is already apparent in neonates, although it continues to develop throughout childhood and adolescence. Moreover, individual differences in this connectivity in neonates are associated with risk for stronger fearfulness, but also higher cognitive development at age 6 months (Graham et al., 2015). By 3–7 months of age, sad vocalizations activate the insula and orbitofrontal cortex more than do neutral vocalizations (Blasi et al., 2011). Moreover, in further support of the importance of this system for emotion and motivation, clustering coefficients for connectivity between the right inferior frontal gyrus and the right insula were significantly associated with externalizing behavior problems in 48-month-olds, and anxiety in 7 − 9 year olds was associated with significantly greater connectivity of the left amygdala to the salience system (anterior insula, VM PFC) and the ventral striatum (Wee et al., 2017; Qin et al., 2014).

The function of the connection between the amygdala and the PFC is typically conceptualized as a top-down (PFC to amygdala) process of emotion regulation in the service of more adaptive, planful behavior, however. In support of this inference in adults, rs-fcMRI shows an inverse correlation between the amygdala and the PFC (e.g., Gee, Humphreys, et al., 2013). Interestingly, however, this apparent cortical inhibitory influence on the amygdala typically begins to be evident around puberty; prior to that, the connection between the amygdala and the PFC more typically is excitatory (Gee et al., 2013; but see Rogers et al., 2017).

Tottenham and Gabard-Durnam (2017) argue that the amygdala "instructs the cortex" about what is salient and important. Thus, the positive relationship between the amygdala and the PFC in early development is a manifestation of this process. The findings regarding the importance of a bidirectional relationships among the VM PFC, the amygdala, the insula, and the peripheral nervous system in guiding "reasoned" behavior support this hypothesis. In addition, findings from children exposed to early separation from their caregiver and raised in orphanages further support this hypothesis (Gunnar et al., 2015).

6.4. Ventral striatal-nucleus accumbens motivation/reward system

As discussed earlier, the NAcc is strongly associated with reward-seeking, but also with avoidance learning, making it a key structure for motivated behavior (Faure et al., 2010). It shows strong connectivity to the amygdala and anterior insula beginning in the neonatal period and to the PFC by the end of the first year of life (Graham et al., 2015; Happeney et al., 2004). The connectivity of the ventral striatum to the ACC and hippocampus shows age-related change from early childhood through adulthood. Specifically, coupling between the ventral striatum and several parts of the ACC declines with age throughout this period; whereas connectivity to the anterior hippocampus increases with age, with little connectivity until adulthood (Fareri et al., 2015). In addition, adolescents, relative to children and adults, show increased reactivity in

the ventral striatum to larger versus smaller rewards (Fareri et al., 2015). Connectivity between the ventral striatum and the PFC continues to develop until at least early adulthood, and age-related change is still evident in the striatum from age 10 to age 25 (Fareri et al., 2015; Larsen & Luna, 2015). Interestingly, the developmental trend for the ventral striatum is an increase in dopamine function and responsivity to reward during adolescence, with myelination of cortico-striatal connections continuing until at least early adulthood (Larsen & Luna, 2015). This supports behavioral data suggesting that adolescents are more prone to sensation-seeking and risk-taking in comparison to children and adults (e.g., Larsen & Luna, 2015).

Not only is there normative change in the ventral striatum and its connections with other structures that are pertinent to motivation and emotion; individual differences in volume and connectivity of the ventral striatum are related to individual differences in motivational style ("grit"). In a recent study by Nemmi and colleagues, grit, long-term perseverance in the face of high challenge, was assessed by teacher report, and MRI was used to examine striatal shape and cortical thickness prior to an 8-week working memory (WM) training program. Both training gain on the WM training task and transfer gain to another WM task were assessed. Grit was significantly associated with both training and transfer gains, as well as with gray matter density in the NAcc. Moreover, six-year-old children with larger NAcc volume also showed greater gains from the WM training program. Finally, the brain region associated with grit showed strong connections to the orbitofrontal cortex. Grit was not, however, associated with cortical thickness of the frontal cortex (Nemmi, Nymberg, Helander, & Klingberg, 2016).

The study by Nemmi et al. (2016) was notable in relating brain measures to measures of “grit”, mastery, or achievement-related motivation. This domain of motivation is an active area of developmental research rooted in a seminal paper by Robert White (1959). White (1959) drew attention to the fact that although then current views of motivation emphasized achieving homeostasis via satisfaction of biological needs, such views were unable to explain a key intrinsic motive that seemed to drive human behavior, which White named “effectance motivation”. White noted that people often strive to *increase* stimulation and arousal, rather than to reduce it to a homeostasis-based calm level. Moreover, such strivings seemed essential to human adaptation—moving people to try to overcome challenges and to learn new ways of effectively interacting with the environment. This has obvious relevance to the development of the striatal system. In addition, it is very pertinent to the various networks associated with the amygdala. Many emotions are elicited in mastery situations, and some of those emotions motivate children to approach the task and keep trying, and others may promote giving up and withdrawing (e.g., Barrett and Morgan, 2018).

Developmental research also has been conducted based on functionalist perspectives that highlight the crucial role of specific types of emotions in directing and regulating behavior (e.g., Barrett and Campos, 1987). According to such approaches, not only does approach versus avoidance motivation affect which emotions one feels; the emotions one experiences affect whether one approaches or avoids or gives up on one’s goal-directed strivings (e.g., see Barrett and Morgan, 2018). The amount and type of emotion children show while trying to master a challenging task do predict children’s success in school (Berhenke et al., 2011; Józsa and Barrett, 2018). The importance of emotions for this type of motivation and its relation to success in school and life highlights the need for more research regarding the brain bases of mastery motivation.

6.5. Conclusions

In summary, most important motivational/emotional neural systems develop connectivity beginning prenatally and often continuing until at least early adulthood. The BIS is evident in infancy, and individual differences in this system are predictive of internalizing difficulties and striatal activation to rewards in adolescence. Noteworthy systems with particularly rapid development of connectivity in the first year of life include the amygdala's connectivity with the prefrontal cortex and the anterior insula and the connection of the NAcc to these same structures. The former connections may both "instruct the cortex" about which stimuli are important and enable top-down regulation of emotion. The latter connections seem to support reward-seeking and avoidance learning. Moreover, the volume of the NAcc is associated with individual differences in inclination to persevere in the face of challenge, a type of motivation linked to mastery of challenging tasks. It is important to track the development of these connections in order to better understand the nature of motivation and emotion at different points in development, as well as influences on the development of these connections. Finally, a type of motivation that is related not only to emotion but to social and academic/cognitive success is mastery motivation, on which almost no developmental neuroscience has been conducted. It deserves further research, given its relevance not only to emotional development, but also to the relation between motivation, learning, and cognition. It is this relation to which we turn now.

7. Section VII. Motivation, learning and controlled cognition: prediction, regulation and monitoring functions

7.1. Merging or non-merging of cognition with emotion/motivation

Cognition, learning and expectancies are central to understanding the intersection between motivation and emotions. In Kim’s (2013) account, motivation is a sequence of interacting and temporally overlapping dynamic processes that leads to behavior. When the levels of interaction are diverse and the temporal overlap is short among dynamic processes (e.g. early learning of behavior), then the motivational and cognitive processes merge in order to process a greater information load over time. Recent views emphasize integration and cognitive-emotion merging at functional and neural levels (Pessoa, 2013).

Similar to affective-cognitive relations, cognitive processes can be divorced from motivation when actions arewell learned or ‘habitual’ and when an intense level of responding is required (Panksepp, 1998; Cromwell and Panksepp, 2011). In these former cases, emotion could supplant cognitive functions in maintaining motivated action. Influential views of emotion-driven somatic markers emphasize the essential role emotion plays in decision-making and choice behavior (Damasio, 1996). This view twists cognitive dominance 180° by having emotion guide and control future cognitive influences. The view was built on historical models (James, 1884) which seemed paradoxical but recently are supported by neuroscience-based evidence highlighting the primary and controlling aspect of emotional feelings (Damasio, 1994). So far, our review has emphasized that motivational and emotional functions merge as an integrated process with a closely interconnected network of neurophysiological activity. Similarly, evidence supports an idea that motivation and cognition often merge during goal-directed action, depending upon the information being processed and the external and internal forces involved (Baars, 1998).

In goal-directed behavior, the outcomes are continuously being ‘revalued’. This function could span from near automatic forms of relative reward valuations possibly linked to emotion (Cromwell and Ricker, 2018; Webber et al., 2015, 2016) to more complex appraisals based upon long-term memory retrieval of choice context (Hayden, 2016) and multi-level value comparisons (Toates, 1986). Brain regions for these types of goal assessments during motivation arise from basal ganglia regions such as striatum (Cromwell et al., 2005; Webber et al., 2016), and prefrontal cortex (Cromwell et al., 2018). Neural activity in both regions encodes reward quality and quantity and tracks value shifts in a dynamic manner (Cromwell and Schultz, 2003; Hassani et al., 2001). The sensitivity of these systems to different types of rewards and incentives provides a neural basis for increases in motivation when

incentives change or in the context of variety (Myers et al., 2016; Leszczuk and Flaherty, 2000). When examining human motivation, changing incentives can increase task performance (Kurzban, Duckworth, Keble & Myers, 2013).

However, external rewards are limited in their ability to influence motivation for many of the mental tasks necessary for modern life. For tasks that were unanticipated during our species' evolutionary history, external incentives appear to increase motivation only for a short time. Examples come from the vigilance literature (discussed by Kurzban et al., 2013), as in the case where a soldier's awareness that he is monitoring for enemy warplanes does not prevent tedium and lapses of attention. Anticipation and predictability are key components to decision-making in risky environments (Schultz, 2010, 2015). Dopamine cell activity is sensitive to the level of prediction or surprise between reward outcomes and associated cues (Schultz, 2015). Possibly, dopamine cells provide the best example of the potential merging of cognition and motivation, as dopamine arriving to ventral striatal regions could produce the motivational signal of incentive salience and wanting while dopamine arriving to prefrontal locations (Tsutsui et al., 2016) brings information on associative strength in the form of a prediction error signal (Schultz, 2015).

7.2. Cognitive influences of outcome valuation

As just described, merging motivation-cognition and emotional processes play key roles in maintaining goal-directed action. Consider the paradox of motivation that occurs when humans pursue challenging intellectual activities. It is a common experience that initial excitement about a project can be supplanted by reluctance and apathy; then selection of action requires cognitive mechanisms. Why do mental tasks that are not inherently aversive, such as reading, studying, and writing, frequently grow tedious? This occurs even when the successful achievement is highly desired, such as graduating from college, becoming a doctor or learning a foreign language. In motivational theory, “delay discounting” leads to demotivation for mental labor when rewards are in the distant future. Animals' choices about actions are heavily influenced by proximate rewards (Vanderveldt et al., 2016; Ainslie, 2001). Temporally closer rewards, such as doing well on an exam or feeling good about one's effort, are usually small; moreover, even these are not immediate rewards. In Kim’s (2013) model, lack of rewards, and reward prediction error, engages cognitive control mechanisms. "The enemies for motivation regulation are the immediate impulse, the low executive processing capacity, and the lack of specific goals and plans" (Kim, 2013, p. 9).

Frontostriatal circuits, along with dopamine input, are critically involved in delay discounting and in monitoring the relative value, given a particular wait time until reward is received (Fig. 5). Optimal choice allows the organism to wait when the reward value is appropriate for the delay and respond early when it is not (Yu et al., 2014; Hayden and Platt, 2007). Cognitive functions allow diverse strategies to overcome maladaptive impulsive behavior, including making the long-term goal more salient via memory retrieval, monitoring current effort and progress, altering the plan and developing a new strategy, or alternative goal (Tang et al., 2018; Verdejo-Garcia et al., 2018).

Evaluating effort is another cognitive function linked to motivation. The greater the regulation of behavior required, the more the goal is associated with high level of effort (see review in Botvinick and Braver, 2015). Effortful control involves reasoning and integrating long-term memory with working memory, and it is primarily recruited for novel problem solving. Some theorists have argued that hominids evolved an amodal workspace where different sensory systems could share their outputs to facilitate trouble shooting (Baars, 1998). If this system were not routinely needed in animals’ lives, it could be recruited infrequently and save resources. It is plausible that animals, and perhaps humans in premodern societies, could depend on automated action plans that were richly interconnected with feedback loops from the environment

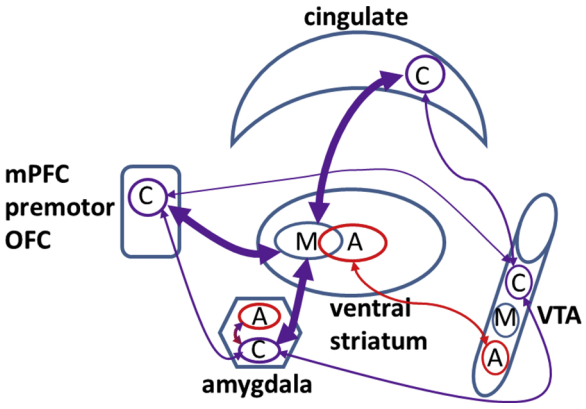

Fig. 5. Cognitive processes share similar sites and drive motivational functions with top-down information. This concerns outcome value as well as behavioral experience. Error detection preceded by error recognition or expectation allows for optimal motivation and emotion integration.

(Gigerenzer, 2008). The frequent experience of mental fatigue from cognitive tasks that humans report in many work situations may be a consequence of overuse of top-down cognitive control processes. Brain regions that encode the amount of effort required to complete a task and perform error monitoring continuously as feedback for behavior would necessarily connect motivation with cognition.

Pertinent to our current topic of emotion-motivation merging is that the brain basis for these functions overlaps dramatically with emotional systems involved in both intrinsic (e.g., seeking) and extrinsic (e.g., outcome valuation) functions (Salamone et al., 2018a,b).

Recently, theorists have drawn on classic models of reinforcement learning to produce computational models of reward maximization that include comprehensive, sensitive value monitoring. Shenhav et al. (2017) developed the concept of the expected value of control (EVC). EVC is the total reward expected when control is directed towards a specific activity, with a particular intensity, less the expected cost of this exertion of control. The cortical structures involved in the monitoring of error during motivated action include the dACC, anterior insula, lateral prefrontal cortex, and lateral parietal cortex (Fig. 5; Shenhav et al., 2017). A compact theory, EVC has considerable heuristic value. The parameters of the model allow theorists to specify variability in domain-specific processing capacity or cognitive skills. Different settings could explain individual differences in effort expenditure and preference for immediate vs. delayed rewards (see Botvinick and Braver, 2015). Control costs could also reflect the organisms' own history of prior control decisions. This resonates with Ainslie’s (2001) argument that will-power can be built up when individuals practice "inter-temporal bargaining" with their future self about preferring later-larger rewards to sooner-smaller rewards.

7.3. Conclusions

There are considerable clinical and policy implications of understanding limits on motivation and cognitive control. Self-control is necessary for individuals to experience optimal health, safety and financial outcomes. Given bounded rationality, and the load placed on executive functions by the complexities of modern life, it may, however, be optimal to tolerate some self-control failures. When possible, control could be off-loaded to the environment or to non-cognitive motivational processing states, so that good decisions are automatically suggested or shaped by ecological structures (Gigerenzer, 2008). These types of dissociations between psychological processes (cognition and motivation) may tap into similar brain regions (e.g. mesolimbic reward circuitry) but not utilize the integrated pathway involved in cognitive appraisals or complex cognitive judgements.

8. Section VIII. Cultural neuroscience and the emotion-motivation connection

Exposure to cultural influences can set and regulate the way approach and avoidance systems are balanced within the individual, and how either approach or avoidance is expressed as behavioral strategies observed in diverse situations (Kitayama and Park, 2014). Culture can also impact the development and expression of intrinsic and extrinsic motivation, as we review below. These diverse interactions highlight how the brain and underlying circuits that merge motivation with emotion become 'enculturated'. The process of neural enculturation occurs at several biological levels, from the gene to brain circuit activity (Kim and Sasaki, 2014). Cultural scripts shape humans' daily activities, decisions and behavior scripts (Kitayama and Tompson, 2010). Repeatedly enacting these scripts changes brain structure and processing, with the result that "culture gets embrained" (Mu et al., 2015).

8.1. An embrained culture: motivation and emotion processing

One view of the culture-brain relationship emphasizes the broad role of the cerebral cortex, given that social learning increases as a function of encephalization in primates, with chimpanzees, orangutans and capuchins showing the highest rates of social learning (Whiten and van de Waal, 2017). A second view focuses on the mirror neuron system as a key to cultural learning, given the importance of imitation and modeling others' behavior (Whiten and van de Waal, 2017). A third broad perspective is that gene-culture coevolution began when hominids' play period was extended into adulthood. The result was increased plasticity in the adult brain, and increasing integration of neural pathways between the brain's cerebellum and cerebral cortex. This integration allowed the cerebellum to expand its ability to adapt to the unexpected by predicting and anticipating future circumstances. This facilitated both trial and error learning and cooperating with others, and provided structure conducive for humans to develop cumulative cultures. These three accounts share the theme of merging motivation and emotional processing together as an interactive function dependent upon culture. Several of the specific brain networks and neurotransmitters overlap with the previous regions discussed, suggesting that core circuits of motivation/emotion involved in basic functions can mediate cultural differences.

8.2. An enculturated brain: motivation and emotion processing

A prominent strand of research has investigated the brain mechanisms that underlie how strongly cultures value individualism vs. collectivism (or interdependence; Markus, 2016). Note that there is widespread agreement that no culture is completely individualistic or collectivistic. However, the contrast between cultures varying in degree of individualism and collectivism still provides useful insights. In more individualist cultures, people view themselves as primarily separate from others, and consider first their own needs and goals. In more interdependent cultures, people feel rewarded when they can contribute to the success of close others or to group goals. Individualist cultures are the ones that psychologists have most frequently studied, but they are atypical, as anthropologists have long noted (e.g., Henrich et al., 2010).

Variation in individualist vs. interdependent self-construal has been linked to the volume of the orbitofrontal cortex (OFC), a region responsible for value-based decision making. In a recent study, Japanese young adults' OFC volume was related to their report of their extent of independent self-construal (Kitayama et al., 2017). Research participants were also required to form vivid images of external objects (object imagery). The highest level of interdependent self-construal was reported by those who were relatively low in the OFC volume but also high in object imagery. Kitayama et al. (2017) explain this as a consequence of how the cultural value of interdependence focuses people on duty towards others and heightened awareness of the environment around them.

Cross-cultural differences in making decisions based on other people's needs (sometimes called other-orientation) plausibly reflect or contribute to differences in the relative strength of humans' multiple motivation systems (Markus, 2016). Persons with individualistic values, and/or those living in individualist countries (such as the U.S.) typically attribute their choices as due to their personal wants, needs and values. In many scenarios, they will appear to be more intrinsically motivated. Persons who value interdependence, and/or those living in collectivist cultures (such as Asia) explain their behavior as responding to the influences of people around them. They may appear to be more extrinsically motivated (or motivated to help their group). Markus (2016) notes that this other-regulation is not superficial compliance, and should not be regarded as indicating mindless conformity or a weak will. Instead, other-regulation emerges from feelings of achievement that one has met the expectation of important persons; and of feelings of satisfaction that one is acting in accord with the norms for a specific situation.

Cross-cultural comparisons have challenged the common-sense assumption that individuals' own choice to complete a task increases their task motivation. In a seminal study, Iyengar and Lepper (1999) compared Anglo- and Asian-American children's performance on solving word–puzzles that belonged to different categories. Anglo-American children solved more anagrams, and spent longer exploring them during a free play period, when they had made these choices themselves. In contrast, Asian-American children showed these same signs of "intrinsic" motivation when they were informed that the category and marker colors had been selected by their mother (or, in a second study, a classmate). The authors propose that having choices made by relevant in-group members is rewarding to the Asian-American children because it "provides a greater opportunity to promote harmony and to fulfill the goal of belonging to the group" and helps "fulfill expected social obligations to family and friends" (Iyengar and Lepper, 1999, p. 363).

What are the neural correlates of self-centric vs other-centered motivation? Using event-related potentials and a flanker task, Kitayama and Park (2014) investigated whether European Americans and Asians would be more motivated to win rewards points for themselves or a friend. The measure of interest was an event-related potential sensitive to error responses, the error-related negativity (ERN). ERN occurs within 100 ms after the commission of an error and is thought to represent a learning signal arising from dopamine cells projecting to limbic regions such as anterior cingulate (Bromberg-Martin et al., 2010; Schultz, 2007). The greater the ERN, the better the signal that could be used to maximize performance. For European Americans, ERNs were greater in the self-condition than in the friend condition. Post-error slowing, an index of cognitive control to reduce errors, was observed in the self-condition but not in the friend-condition. This is consistent with Americans' being motivated to serve their own needs. Neither of these self-centric effects was observed among Asians, consistent with other-oriented values. It was noteworthy that interdependent self-construal mediated the effect of culture on the ERN self-centric effect.

Another key finding in cross-cultural comparisons is that more individualist cultures use declarations of emotional feelings and emotional displays to establish connections with others, and also use appraisal mechanisms to determine how to respond emotionally (Matsumoto et al., 2008). In contrast, persons who have more interdependent self-construals practice emotional restraint to protect group harmony and to de-emphasize the self when in groups; and also use suppression as an emotion-regulation mechanism more than appraisal. Brain systems that could mediate this type of cultural variation were studied by Immordino-Yang, Yang and Damasio (2014). They focused on activity in the dorsal and ventral sectors of the anterior insula (AI), brain regions long known to mediate motivation (see prior sections on fMRI studies; Mutschler et al., 2009). Videos were selected that would induce either admiration or compassion. Complex, social motivational

states were selected because it was likely they would be influenced by mechanisms that are shaped by culture, such as appraisal and expressiveness (Matsumoto et al., 2008). Cardiac arousal, fMRI and subjective feeling report were measured in Chinese participants (representing a collectivist culture) and Americans (individualistic culture).

In the Chinese group, reports of feeling strength tracked with ventral AI activity magnitude, but not dorsal AI. The ventral AI is involved with autonomic modulation. This pattern is consistent with the tendency of persons from China to use suppression strategies to respond to emotional stimuli (Matsumoto et al., 2008). The Chinese cultural values of self-regulation and calmness may result in conscious feelings becoming associated with the activity of the ventral AI because of its modulatory role.

In the American group, reports of feeling strength were more strongly correlated with activity fluctuations in the dorsal AI. The dorsal AI mediates awareness of one's physiological state, cognitive reactions and decision making (Mutschler et al., 2009). Individualistic cultures promote emotional expression, a part of individual assertion and relationship management (Matsumoto et al., 2008). Individuals from expressive cultures like American culture may learn that they can attend to somatosensory states when deciding how strongly they feel about a stimulus. The result is that report of feeling strength tracks the dorsal AI, given its sensitivity to somatosensory information. Different training appears to occur for cultural groups that practice emotion regulation and value calm states, such as the Chinese. For these individuals, judging how they feel may come to reflect the activity of the ventral AI because of its modulatory role (Immordino-Yang et al., 2014).

8.3. Conclusions

The enculturated brain (or embrained culture) presents interesting avenues to pursue in the study of functional interactions between emotion and motivation. The opportunities exist to study how complex emotions that influence motivational systems arise from cultural experience. Also important is how brain systems direct particular emotional-motivational combinations, thus enhancing or dampening how culture mediates important endpoints like affect regulation or goal valuation. The nesting of the psychological functions within cultural contexts must consider the information presented thus far in this review, such as basic animal models and human brain circuits of emotion-motivation interactions. Emerging fields like cultural neuroscience can better identify how brain circuits interact with societal pressures and cultural norms by drawing on motivational and affective neuroscience (Kim and Sasaki, 2014).

9. Section IX. General conclusions

Examining emotions and their role in behavior must integrate affective states, motivation and cognition in a multi-directional manner. This complex endeavor is a daunting process and thus it is not surprising that the majority of research focuses on a single psychological process or a unidirectional flow of influence. The current review examined multiple psychological processes and included overviews of developmental trajectories and cultural influences. It is appreciably easier to focus on a snapshot of a single psychological process, especially when each process is not well-defined. Certainly, the lack of clear definitions using language is not surprising given the top-down emphasis language has in constraining the way we communicate about psychological functions and Brain/Mind interfaces (Cromwell and Panksepp, 2011).

The key questions of how to define motivation and emotion and what brain structures and connections serve each (and both) have been explored in this review, and more questions were uncovered while putative answers proposed. Definitions for emotion and motivation continue to be a work in progress with the two processes being closely linked functionally, behaviorally, and neurophysiologically, and yet also being conceptually distinct. A review such as this, which assesses and integrates converging evidence across different research areas, helps move the field by uncovering the areas of overlap in brain systems underlying motivation and emotion as well as the many things we do not know about these interconnected systems. Are there different specific nuclei, neurotransmitter or synaptic pathways or other subtle differences between the brain systems serving emotion and motivation? And do pathways differ for different specific emotion/motivation combinations? Are there different specific neural connections between emotion and intrinsic motivational processes such as mastery motivation, grit, or autonomous striving versus extrinsically motivated behaviors? Does acculturation in different cultures impact these connections?

Our understanding of the neural bases for motivation and emotion is making progress and will continue to evolve as technological advances are made. We are optimistic that such progress will provide a better understanding of both motivation and emotion, as well as how they relate to one another. Our review strongly suggests that the answer to the question of whether emotion and motivation interact is a resounding yes, and more and more evidence from multiple levels suggest that these processes are so tightly woven together that they are inseparable. Our review suggests that the functions of motivation and emotion are underpinned mainly by overlapping, similar locations and networks in the brain, but may differ in specific connections and neurotransmitters that are most central, and, that these functions normally interact with one another, together moving behavior. The close connection can be undone and evidence from both animal and human work show that the functional ties can be removed in normal as well as pathological states. However, much more research is needed to better assess conditions under which motivation and emotion operate separately, how types of emotions impact these connections, and how differences in genetics, experiences, and their interconnection impact individual difference in emotions, motivation, and their interconnections.

Neuroscience can inform our understanding and research on motivation and emotion; in turn, neuroscience research must be informed by behavioral research. Much further neuroscience research is needed to investigate the many behavioral findings on motivation and emotion for which no brain pathways are known. It is rare for non-human, adult human, and developmental human studies on the brain and behavior to be brought together to inform understanding of any research area. Although much is still unclear, we believe this review fills a gap by bringing together research based in many different research areas and highlighting the remarkable similarity in findings.

9.1. Limitations in studying motivation and emotion

Examining motivation and emotion can be difficult in several ways. To fully understand the neural processes and mechanisms underlying motivation, first one must be able to manipulate and control the motivational process. To increase and decrease motivation through experimental methods might seem easy but it rapidly becomes quite complicated. The non-human animal work on reward deprives the subjects of calories or certain foods to motivate. Human work utilizes incentives such as money and social experience (e.g., Abe and Greene, 2014). Such approaches, however, cannot fully address the important domain of intrinsic motivation, in which the reward originates within the organism, rather than from external rewards or punishments. The onus is to find what motivates the organism, limit and control availability and measure the degree to which the subject pursues the outcome. The study of neural underpinnings of emotion can be even more complicated. As stated previously, a subset of researchers claims that non-human animal emotion cannot be studied either because the subjects cannot have emotion or because it is impossible to infer (Averill, 1980). It is very difficult to isolate and manipulate individual emotions, and most fMRI studies of emotions either require cognition (to respond

to the task) or require the assumption that stereotypical, static facial expressions elicit "real emotion" in the perceiver. Affective neuroscience is an important and growing research area, but many challenges still need to be addressed.

The neuroscience methods used to examine non-human animal models include lesion, optogenetic and pharmacogenetic approaches. At the neural level, these are standard and the most difficult element is the manipulation and control of motivational and emotional states. Work manipulating neural substrates in animals has many limitations, including difficulty in reliability and replicability. Methods to track or manipulate neural activity include optogenetic, in vivo neurophysiology and experimental lesions. These techniques typically have very high spatial and temporal resolution and current methods track individual cell types and discrete circuits and pathways. For example, several groups have developed ways to selectively turn on or off the direct versus indirect pathways of the basal ganglia using virally-infected genome transfer and pharmacology (Hikida et al., 2013). Current work delineated reward learning as a major function of the 'direct pathway' while aversion responding and learning depended more on the indirect pathway. These sorts of approaches that breakdown the cell ensembles into different groups and examine networks from one cell group subtype to another will deliver the most information on neural integration. Yet, most of this work is very crude in terms of behavioral paradigms and analysis (Krakauer et al., 2017). The tasks lack generalizability and constrain responding or merely test a few instances, missing the importance of the variability in the responding.

Human affective neuroscience has similar problems with validity and inferring states and processes from responses. These can be compounded in human studies due to the artificial and stressful nature of the neuroscience techniques. The neuroimaging methods such as fMRI come with significant limitations. These include 1) inabilities to obtain high resolution information about the functioning of key subcortical parts of the brain and their connectedness to cortical regions. A single voxel is estimated to contain over 5 million neurons, and that activation of a single voxel can represent a complex synthesis of diverse neuronal populations (Logothetis, 2008). Many of the most important subcortical regions such as ventral striatum or regions of the brainstem are typically not examined because they are unable to be imaged properly, 2) Constraints on movement during neuroimaging make it difficult to evaluate emotion and motivation accurately. As was detailed in the introduction, emotion and motivation share roots in movement and expression. Where animal models can provide so much rich behavior, human work typically offers sparse coding of behavioral endpoints, and 3) Network analysis concerning the development of connectivity has basic issues in that it requires inferences about the functions served by the network, typically based on knowledge of those functions in adult individuals. In addition, it makes inferences about connections based on co-activity.

Moreover, motivation is a complex concept with emotional, cognitive and behavioral components that are not easy to disentangle, which leads to variability in the definitions employed across studies (Kim, 2013). Studies are frequently exploratory, with multiple statistical comparisons between several regions of interest, and sample sizes are typically small, posing risk of a type I error. Moreover, the reward-based approach to studies of motivation has the assumption of salience of the object, with potentially significant inter-individual differences in what one derives pleasure and value from (Botvinick and Braver, 2015). Nevertheless, fMRI is a widely accepted methodology to provide a window into the overlapping and divergent networks involved in emotion and motivation.

These limitations are compounded with developmental affective and motivational neuroscience methods. Movement artifact difficulties are amplified in infants, primarily because of the impossibility of avoiding movement artifacts in alert infants. Event-related fMRI, thus, present stimuli (typically auditory) to infants *while they sleep*, to reduce head movement artifact, and research has demonstrated that infants' brains do react to stimuli in interpretable ways while they are sleeping. Since there are so many problems with fMRI, many studies of brain responses to stimuli in infants involved the cortex, using EEG or Event-Related Potentials (ERPs). Although these approaches are useful, a major limitation of EEG or ERP is they lack the ability to assess the functional activity of subcortical structures and the conjoint/interconnected activity of systems involving subcortical and cortical structures.

9.2. Future directions

Future work could more accurately isolate and manipulate emotions and intrinsic as well as extrinsic motivation in subjects at different levels (e.g., macro, meso and micro-levels). Even more interesting would be research that closely monitors motivation while emotion is being examined and vice versa to explore how these systems overlap. As stated previously, emotion and motivation are typically treated separately—one is under investigation and the other ignored. The different literatures reviewed in this article need to be further used to inform work at many levels of the organism –future work must go beyond a study of brain-behavior connections at a single time point to examine how genetic propensities interact with learning and culture in the development on the processes studied using the 'snapshot' approach. Plasticity of connectivity among brain sites in human imaging could be key as a marker for how brain regions shift functionality as emotion is manipulated separately from motivation, or whether emotion and motivation are inextricably intertwined. Do motivational systems arise at different time points relative to emotion, or do the change patterns vary for emotion and motivation? The answer to these questions remain unanswered.

9.3. Motivational and emotional events intertwined

Given the substantial overlap in neural systems underlying motivation and emotion, an important direction for future research is explicating whether or not these truly are distinct functions, and, if so, what distinguishes them neurologically. As indicated earlier, some theorists have proposed that emotions and other feelings are the only true motivators of behavior (Tomkins, 1991). Others have suggested that, even if not the only motivators, emotions are, at their core, important motivators of social communication and behavior (e.g., Barrett and Campos, 1987; Frijda, 1986). Our novel view proposes that the brain substrates for these processes might merge and dissociate given (1) the amount of experience; (2) the type of goal to be obtained; (3) the context, especially when embedded in social interactions, and the (4) cognitive input, including top-down self-control and memory. The merging systems could interact and overlap in many ways. Current evidence supports some independence with substantial convergence between emotion and motivation. The independent systems view emphasizes parallel processing and points of functional intersection; whereas, an alternative interpretation is that of overlapping or even isomorphic pathways that differ in terms of temporal or spatial processing (see Fig. 6). These two options could lead to distinctly different outcomes in terms of temporal and spatial interactions between psychological functions.

Parallel circuits might be more easily disentangled and allow for a greater level of independence in functional outputs. Merging neural ensembles would require some state shifts in order to have non-overlap (Fig. 6). For example, a hotspot for motivation and emotion would be comprised of a cellular group that receives a diverse set of inputs. One set of inputs would lead to an emotional output while a distinct set of inputs would lead to a motivational function. Then, another set of overlapping inputs would merge the two together (Fig. 6) leading to a unique combination that operates as an adaptive capacity in specific situations. Revealing details of functional neuroplasticity in the future will require thinking beyond a simple dichotomy of independent vs.

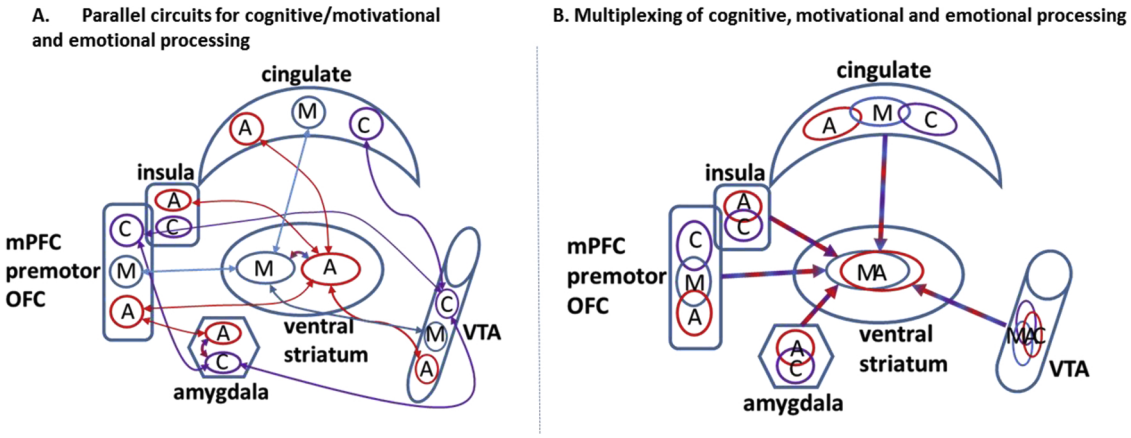

Fig. 6. Models of cognitive (C), motivational (M) and affective (A) integration within key brain regions including medial prefrontal cortex (mPFC), premotor cortex, orbitofrontal cortex (OFC), insula, cingulate, amygdala, ventral striatum and ventral tegmental area (VTA). A. A depiction of parallel pathways for cognitive, motivational and emotional processing. Heterogeneous cell groups are primarily involved leading to an independence of functioning within forebrain cell groups and a local intrinsic integration within specific subcortical sites (e.g., ventral striatum and amygdala). B. A depiction of overlapping cell groups involved in diverse functions. Cell ensembles at one point in time are mainly involved in cognitive-motivational processing while at another point in time emotional amplification of neural activity.

merged views of motivation and emotion, and instead will entail novel tactics to study and describe rapid changes in brain activity that enable neural locations to function in diverse ways and capture multiple functions (Cromwell and Panksepp, 2011). The reward of this effort is a more complicated, but more accurate, view of the role of feeling and motives in our lives.

Footnotes

The author list outside of the first, corresponding author is listed in alphabetical order. This strategy was used because of the similar workload and contribution among the authors in the production of this manuscript.

References

Abe, N., Greene, J.D., 2014. Response to anticipated reward in the nucleus accumbens predicts behavior in an independent test of honesty. J. Neurosci. 34, 10564–10572.

Adolphs, R., 2017. How should neuroscience study emotions? by distinguishing emotion states, concepts, and experiences. Soc. Cogn. Affect. Neurosci. 12, 24–31.

Adolphs, R., Spezio, M., 2006. Role of the amygdala in processing visual social stimuli. Prog. Brain Res. 156, 363–378.

Ainslie, G., 2001. Breakdown of Will. Cambridge University Press, Cambridge UK.

Albrecht, K., Abeler, J., Weber, B., Falk, A., 2014. PMC4166960; the brain correlates of the effects of monetary and verbal rewards on intrinsic motivation. Front. Neurosci. 8, 303.

Alcaro, A., Panksepp, J., 2011. The SEEKING mind: primal neuro-affective substrates for appetitive incentive states and their pathological dynamics in addictions and depression. Neurosci. Biobehav. Rev. 35, 1805–1820.

Anderson, S.W., Bechara, A., Damasio, H., Tranel, D., Damasio, A.R., 1999. Impairment of social and moral behavior related to early damage in human prefrontal cortex. Nat. Neurosci. 2, 1032–1037.

Atkinson, J.W., Heyns, R.W., Veroff, J., 1954. The effect of experimental arousal of the affiliation motive on thematic apperception. J. Abnorm. Psychol. 49, 405–410.

Averill, J.R., 1980. A constructionist view of emotion in Plutchik. In: Kellerman, H. (Ed.), Theories of Emotion. Academic, New York, pp. 305–339.

Baars, B.J., 1998. A Cognitive Theory of Consciousness. Cambridge University Press, Cambridge UK.

Baez, S., Santamaria-Garcia, H., Orozco, J., Fittipaldi, S., Garcia, A.M., Pino, M., Ibanez, A., 2016. Your misery is no longer my pleasure: reduced schadenfreude in Huntington's disease families. Cortex 83, 78–85.

Baez, S., Pino, M., Berrio, M., Santamaria-Garcia, H., Sedeno, L., Garcia, A.M., Fittipaldi, S., Ibanez, A., 2018. Corticostriatal signatures of schadenfreude: evidence from Huntington's disease. J. Neurol. Neurosurg. Psychiatry 89 (1), 112–116.

Baez-Mendoza, R., Harris, C.J., Schultz, W., 2013. Activity of striatal neurons reflects social action and own reward. Proc. Natl. Acad. Sci. U. S. A. 110, 16634–16639.

Baez-Mendoza, R., van Coeverden, C.R., Schultz, W., 2016. A neuronal reward inequity signal in primate striatum. J. Neurophysiol. 115, 68–79.

Baggio, H.C., Segura, B., Garrido-Millan, J., Marti, M.J., Compta, Y., Valldeoriola, F., Tolosa, E., Junque, C., 2015. Resting-state frontostriatal functional connectivity in Parkinson's disease-related apathy. Mov. Disord. 30, 671–679.

Bard, P., 1928. *A diencephalic mechanism for the expression of rage with special reference to the sympathetic nervous system*. Am. J. Physiol. 84 (3), 490–516. https://doi.org/10.1152/ajplegacy.1928.84.3.490.

Barker, T.V., Buzzell, G.A., Fox, N.A., 2019. Approach, avoidance, and the detection of conflict in the development of behavioral inhibition. New Ideas Psychol. 53, 2–12. https://doi.org/10.1016/j.newideapsych.2018.07.001.

Barrett, L.F., 2013. Psychological Construction: The Darwinian Approach to the Science of Emotion. Emotion Review 5, 379–389.

Barrett, L.F., 2017. The theory of constructed emotion: an active inference account of interoception and categorization. Social Cognitive and Affective Neuroscience 12, 1–23.

Barrett, K.C., Campos, J., 1987. Perspectives on emotional development II: a functionalist approach to emotions. In: Osofsky, J. (Ed.), Handbook of Infant Development. Wiley, New York, pp. 555–578.

Barrett, K.C., Morgan, G.A., 2018. Mastery motivation: retrospect, present, and future directions. In: In: Elliot, A. (Ed.), Advances in Motivation Science Vol. 5. Elsevier, Amsterdam, pp. 2–39.

Batson, C.D., Fultz, J., Schoenrade, P.A., 1987. Distress and empathy: two qualitatively distinct vicarious emotions with different motivational consequences. J. Personality 55, 19–39.

Baumeister, R.F., 1984. Choking under pressure: self-consciousness and paradoxical effects of incentives on skillful performance. J. Pers. Soc. Psychol. 46 (3), 610–620.

Bechara, A., 2004. Disturbances of emotion regulation after focal brain lesions. Int. Rev. Neurobiol. 62, 159–193.

Bechara, A., Damasio, H., Damasio, A.R., 2000. Emotion, decision making and the orbitofrontal cortex. Cereb. Cortex 10, 295–307.

Beck, A., Schlagenhauf, F., Wustenberg, T., Hein, J., Kienast, T., Kahnt, T., Schmack, K., Hagele, C., Knutson, B., Heinz, A., Wrase, J., 2009. Ventral striatal activation during reward anticipation correlates with impulsivity in alcoholics. Biol. Psychiatry 66, 734–742.

Beer, J.S., John, O.P., Scabini, D., Knight, R.T., 2006. Orbitofrontal cortex and social behavior: integrating self-monitoring and emotion-cognition interactions. J. Cogn. Neurosci. 18, 871–879.

Berhenke, A., Miller, A.L., Brown, E., Seifer, R., Dickstein, S., 2011. Observed emotional and behavioral indicators of motivation predict school readiness in Head Start graduates. Early Child. Res. Q. 26, 430–441. https://doi.org/10.1016/j.ecresq.2011.04.001.

Berridge, K.C., 2004. Motivation concepts in behavioral neuroscience. Physiol. Behav. 81, 179–209.

Berridge, K.C., 2018a. Evolving concepts of emotion and motivation. Front. Psychol. 9, 1647.

Berridge, K.C., 2018b. Evolving concepts of emotion and motivation. Front. Psychol. 9, 1647.

Berridge, K.C., 2019. Affective valence in the brain: modules or modes? Nat. Rev. Neurosci. 20, 225–234.

Berridge, K.C., Cromwell, H.C., 1990. Motivational-sensorimotor interaction controls aphagia and exaggerated treading after striatopallidal lesions. Behav. Neurosci. 104, 778–795.

Berridge, K.C., Kringelbach, M.L., 2015. Pleasure systems in the brain. Neuron 86, 646–664.

Berridge, K.C., Robinson, T.E., 2016. Liking, wanting, and the incentive-sensitization theory of addiction. Am. Psychol. 71, 670–679.

Binkley, K.A., Webber, E.S., Powers, D.D., Cromwell, H.C., 2014. Emotion and relative reward processing: an investigation on instrumental successive negative contrast and ultrasonic vocalizations in the rat. Behav. Processes 107, 167–174.

Bjork, J.M., Knutson, B., Fong, G.W., Caggiano, D.M., Bennett, S.M., Hommer, D.W.,

2004. Incentive-elicited brain activation in adolescents: similarities and differences from young adults. J. Neurosci. 24, 1793–1802.
Blakemore, R.L., Neveu, R., Vuilleumier, P., 2017. How emotion context modulates unconscious goal activation during motor force exertion. Neuroimage 146, 904–917.
Blanchard, T.C., Hayden, B.Y., 2014. Neurons in dorsal anterior cingulate cortex signal postdecisional variables in a foraging task. J. Neurosci. 34, 646–655.
Blasi, A., Mercure, E., Lloyd-Fox, S., Thomson, A., Brammer, M., Sauter, D., Deeley, Q., Barker, G.J., Renvall, V., Deoni, S., Gasston, D., Williams, S.C., Johnson, M.H., Simmons, A., Murphy, D.G., 2011. Early specialization for voice and emotion processing in the infant brain. Curr. Biol. 21, 1220–1224.
Botvinick, M., Braver, T., 2015. Motivation and cognitive control: from behavior to neural mechanism. Annu. Rev. Psychol. 66, 83–113.
Bourgeois, A., Chelazzi, L., Vuilleumier, P., 2016. How motivation and reward learning modulate selective attention. Prog. Brain Res. 229, 325–342.
Broca, P., 1878. Anatomie comparée des circonvolutions cérébrales: le grande lobe limbique et la scissure limbique dans la série des mammifères. Rev. D'Anthropol. 1, 385–498.
Brodaty, H., Altendorf, A., Withall, A., Sachdev, P., 2010. Do people become more apathetic as they grow older? A longitudinal study in healthy individuals. Int. Psychogeriatr. 22, 426–436.
Brosnan, S.F., 2006. Nonhuman species' reactions to inequity and their implications for fairness. Soc. Justice Res. 19 (2), 153–185.
Brudzynski, S.M., 2007. Ultrasonic calls of rats as indicator variables of negative or positive states: acetylcholine-dopamine interaction and acoustic coding. Behav. Brain Res. 182, 261–273.
Brudzynski, S.M., 2013. Ethotransmission: communication of emotional states through ultrasonic vocalization in rats. Curr. Opin. Neurobiol. 23, 310–317.
Buck, R., 1984. The Communication of Emotion. Guilford Press, New York.
Burgdorf, J., Knutson, B., Panksepp, J., 2000. Anticipation of rewarding electrical brain stimulation evokes ultrasonic vocalization in rats. Behav. Neurosci. 114, 320–327.
Burghardt, G., 2005. The Genesis of Play. MIT Press, Cambridge Mass.
Cabanac, M., 1971. Physiological role of pleasure. Science 173, 1103–1107.
Cabanac, M., 1999. Emotion and phylogeny. Jpn. J. Physiol. 49, 1–10.
Cannon, W.B., 1931. *Again the James-Lange and the thalamic theories of emotion".* Psychol. Rev. 38, 281–295. https://doi.org/10.1037/h0072957.
Carter, R.M., Macinnes, J.J., Huettel, S.A., Adcock, R.A., 2009. 2742668; Activation in the VTA and nucleus accumbens increases in anticipation of both gains and losses. Front. Behav. Neurosci. 3, 21.
Carver, C.S., Harmon-Jones, E., 2009. Anger is an approach-related affect: evidence and implications. Psychol. Bull. 135, 183–204.
Castro, D.C., Berridge, K.C., 2014. Advances in the neurobiological bases for food' liking' versus' wanting'. Physiol. Behav. 136, 22–30.
Castro, D.C., Berridge, K.C., 2017. Opioid and orexin hedonic hotspots in rat orbitofrontal cortex and insula. Proc. Natl. Acad. Sci. U. S. A. 114, E9134.
Cerqueira, M., Millot, S., Castanheira, M.F., Felix, A.S., Silva, T., Oliveira, G.A., Oliveira, C.C., Martins, C.I.M., Oliveira, R.F., 2017. Cognitive appraisal of environmental stimuli induces emotion-like states in fish. Sci. Rep. 7, 13181–13190.
Chevallier, C., Kohls, G., Troiani, V., Brodkin, E.S., Schultz, R.T., 2012. 3329932; the social motivation theory of autism. Trends Cogn. Sci. (Regul. Ed.) 16, 231–239.
Chib, V.S., Adachi, R., O'Doherty, J.P., 2018. Neural substrates of social facilitation effects on incentive-based performance. Soc. Cogn. Affect. Neurosci. 13 (4), 391–403.
Chiew, K., Braver, T., 2014. Dissociable influences of reward motivation and positive emotion on cognitive control. Cogn. Affect. Behav. Neurosci. 14, 509–529.
Clements, C.C., Zoltowski, A.R., Yankowitz, L.D., Yerys, B.E., Schultz, R.T., Herrington, J.D., 2018. Evaluation of the social motivation hypothesis of autism: a systematic review and meta-analysis. JAMA Psychiatry 75 (8), 797–808.
Cohen, E.J., Quarta, E., Bravi, R., Granato, A., Minciacchi, D., 2017. Neural plasticity and network remodeling: From concepts to pathology. Neuroscience 344, 326–345.
Craig, A.D., 2002. How do you feel? Interoception: the sense of the physiological condition of the body. Nat. Rev. Neurosci. 3, 655–666.
Crespi, Leo P., 1942. Quantitative variation of incentive and performance in the white rat. Am. J. Psychol. 55, 467–517.
Cromwell, H.C., 2018. Jaak Panksepp (1943-2017). Am. Psychol. 73, 202.
Cromwell, H.C., Atchley, R.M., 2015. Influence of emotional states on inhibitory gating: animals models to clinical neurophysiology. Behav. Brain Res. 276, 67–75.
Cromwell, H.C., Berridge, K.C., 1993. Where does damage lead to enhanced food aversion: the ventral pallidum/substantia innominata or lateral hypothalamus? Brain Res. 624, 1–10.
Cromwell, H.C., Panksepp, J., 2011. Rethinking the cognitive revolution from a neural perspective: how overuse/misuse of the term' cognition' and the neglect of affective controls in behavioral neuroscience could be delaying progress in understanding the BrainMind. Neurosci. Biobehav. Rev. 35, 2026–2035.
Cromwell, H.C., Ricker, J.M., 2018. Emotional State and motivation interactions: ultrasonic vocalizations during incentive contrast and free choice paradigms. In: Brudzynski, S.M. (Ed.), Handbook of Ultrasonic Vocalizations. Academic Press, Amsterdam NE, pp. 267–277.
Cromwell, H.C., Schultz, W., 2003. Effects of expectations for different reward magnitudes on neuronal activity in primate striatum. J. Neurophysiol. 89, 2823–2838.
Cromwell, H.C., Hassani, O.K., Schultz, W., 2005. Relative reward processing in primate striatum. Exp. Brain Res. 162, 520–525.
Cromwell, H.C., Tremblay, L., Schultz, W., 2018. Neural encoding of choice during a delayed response task in primate striatum and orbitofrontal cortex. Exp. Brain Res. 236, 1679–1688.
Dagher, A., Robbins, T.W., 2009. Personality, addiction, dopamine: insights from Parkinson's disease. Neuron 61, 502–510.
Damasio, A., 1994. Descartes' Error: Emotion, Reason and the Human Brain. Putnam Publishing, New York.
Damasio, A.R., 1996. The somatic marker hypothesis and the possible functions of the prefrontal cortex. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 351, 1413–1420.
Damasio, A.R., 2004. Emotions and Feelings: A Neurobiological Perspective. In: Manstead, S.R., Frijda, N., Fisher, A. (Eds.), Studies in Emotion and Social Interaction. Feelings and Emotions: The Amsterdam Symposium. Cambridge University Press, Cambridge U.K, pp. 49–57.
Darwin, C., 1859. On the Origin of Species. John Murray, London.
Davidson, R.J., 1994. Asymmetric brain function, affective style, and psychopathology: the role of early experience and plasticity. Dev. Psychopathol. 6, 741–758.
Davidson, R.J., 1998. Affective style and affective disorders: perspectives from affective neuroscience. Cogn. Emot. 12, 307–330.
Davidson, R.J., Fox, N.A., 1982. Asymmetrical brain activity discriminates between positive and negative affective stimuli in human infants. Science 218, 1235–1237.
De Waal, F., 2019. Mama's Last Hug. Norton Publishing, N.Y. N.Y.
de Wit, S., Corlett, P.R., Aitken, M.R., Dickinson, A., Fletcher, P.C., 2009. Differential engagement of the ventromedial prefrontal cortex by goal-directed and habitual behavior toward food pictures in humans. J. Neurosci. 29, 11330–11338.
Decety, J., Lamm, C., 2006. 5917291; Human empathy through the lens of social neuroscience. Sci. World J. 6, 1146–1163.
Deci, E.L., Ryan, R.M., 1985. Intrinsic Motivation and Self-determination in Human Behaviour. Plenum, New York.
Deckers, L., 2005. Motivation, 2nd ed. Pearson Education, Boston MA.
Di Domenico, S.I., Ryan, R.M., 2017. PMC5364176; the emerging neuroscience of intrinsic motivation: a new frontier in self-determination research. Front. Hum. Neurosci. 11, 145.
Dichter, G.S., Richey, J.A., Rittenberg, A.M., Sabatino, A., Bodfish, J.W., 2012. Reward circuitry function in autism during face anticipation and outcomes. J. Autism Dev. Disord. 42, 147–160.
DiFeliceantonio, A.G., Berridge, K.C., 2012. Which cue to' want'? Opioid stimulation of central amygdala makes goal-trackers show stronger goal-tracking, just as sign-trackers show stronger sign-tracking. Behav. Brain Res. 230, 399–408.
Dijksterhuis, A.J., Aarts, H.A.G., 2010. Goals, Attention, and (Un)Consciousness. Annu. Rev. Psychol. 61, 467–490.
Djamshidian, A., O'Sullivan, S.S., Doherty, K., Lees, A.J., Averbeck, B.B., 2011. Altruistic punishment in patients with Parkinson's disease with and without impulsive behaviour. Neuropsychologia 49 (1), 103–107.
Douglas, H.M., Halverstadt, B.A., Reinhart-Anez, P., Webber, E.S., Cromwell, H.C., 2018. A possible social relative reward effect: influences of outcome inequity between rats during operant responding. Behav. Processes 157, 459–469.
Dumontheil, I., Wolf, L.K., Blakemore, S.J., 2016. Audience effects on the neural correlates of relational reasoning in adolescence. Neuropsychologia 87, 85–95.
Dweck, C.S., 2017a. The journey to children's mindsets – and beyond. Child Dev. Perspect. 11 (2), 139–144.
Dweck, C.S., 2017b. From needs to goal and representations: foundations for a unified theory of motivation, personality, and development. Psych. Rev. 124, 689–719.
Ekman, P., 2003. Emotions Revealed: Recognizing Faces and Feelings to Improve Communication and Emotional Life. Times Books/Henry Holt and Co., New York NY.
Elliot, A.J., 2006. The hierarchical model of approach-avoidance motivation. Motiv. Emot. 30, 111–116.
Eshel, N., Roiser, J.P., 2010. Reward and punishment processing in depression. Biol. Psychiatry 68, 118–124. https://doi.org/10.1016/j.biopsych.2010.01.027.
Fareri, D.S., Gabard-Durnam, L., Goff, B., Flannery, J., Gee, D.G., Lumian, D.S., Caldera, C., Tottenham, N., 2015. Normative development of ventral striatal resting state connectivity in humans. Neuroimage 118, 422–437.
Faure, A., Richard, J.M., Berridge, K.C., 2010. Desire and dread from the nucleus accumbens: cortical glutamate and subcortical GABA differentially generate motivation and hedonic impact in the rat. PLoS One 5, e11223.
Finger, B.C., Dinan, T.G., Cryan, J.F., 2011. Behavioral satiety sequence in a genetic mouse model of obesity: effects of ghrelin receptor ligands. Behav. Pharmacol. 22, 624–632.
Flaherty, C.F., 1996. Incentive Relativity. Cambridge University Press, New York, NY, US.
Fox, N.A., 1991. If it's not left, it's right: electroencephalograph asymmetry and the development of emotion. Am. Psychol. 46, 863–872.
Fox, N.A., Rubin, K.H., Calkins, S.D., Marshall, T.R., Coplan, R.J., Porges, R.J., et al., 1995. Frontal activation asymmetry and social competence at four years of age. Child Dev. 66, 1770–1784.
Fox, N.A., Henderson, H.A., Marshall, P.J., Nichols, K.E., Ghera, M.M., 2005. Behavioral inhibition: linking biology and behavior within a developmental framework. Annu. Rev. Psychol. 56, 235–262.
Fragaszy, D.M., Visalberghi, E., 1990. Social processes affecting the appearance of innovative behaviors in capuchin monkeys. Folia Primatol. 54, 155–165.
Frijda, N.H., 1986. Studies in Emotion and Social Interaction. Cambridge University Press, New York N.Y.
Gainotti, G., 2019. Emotions and the right hemisphere: can new data clarify old models? Neuroscientist 25, 258–270. https://doi.org/10.1177/1073858418784342.
Gee, D.G., Humphreys, K.L., Flannery, J., Goff, B., Telzer, E.H., Shapiro, M., Hare, T.A., Bookheimer, S.Y., Tottenham, N., 2013. A developmental shift from positive to negative connectivity in human amygdala-prefrontal circuitry. J. Neurosci. 33, 4584–4593.
Geen, R.G., 1991. Social motivation. Ann Rev Psychol 42, 377–399.
Gendolla, G.H.E., Richter, M., 2006. Cardiovascular reactivity during performance under social observation: the moderating role of task difficulty. Int. J. Psychophysiol. 62, 185–192. https://doi.org/10.1016/j.ijpsycho.2006.04.002.
Gigerenzer, G., 2008. Why heuristics work. Perspect. Psychol. Sci. 3, 20–29.
Goldstein, B.L., Shankman, S.A., Kujawa, A., Torpey-Newman, D.C., Olino, T.M., Klein,

D.N., 2016. Developmental changes in electroencephalographic frontal asymmetry in young children at risk for depression. J. Child Psychol. Psychiatry 57, 1075–1082.
Graham, A.M., Pfeifer, J.H., Fisher, P.A., Carpenter, S., Fair, D.A., 2015. Early life stress is associated with default system integrity and emotionality during infancy. J. Child Psychol. Psychiatry 56, 1212–1222.
Gray, J.A., McNaughton, N., 2000. The Neuropsychology of Anxiety, second ed. Oxford University Press, New York.
Gruber, M.J., Gelman, B.D., Ranganath, C., 2014. PMC4252494; States of curiosity modulate hippocampus-dependent learning via the dopaminergic circuit. Neuron 84, 486–496.
Gunnar, M.R., Hostinar, C.E., Sanchez, M.M., Tottenham, N., Sullivan, R.M., 2015. Parental buffering of fear and stress neurobiology: Reviewing parallels across rodent, monkey, and human models. Soc. Neurosci. 10, 474–478.
Guyer, A.E., Nelson, E.E., Perez-Edgar, K., Hardin, M.G., Roberson-Nay, R., Monk, C.S., Bjork, J.M., Henderson, H.A., Pine, D.S., Fox, N.A., Ernst, M., 2006. Striatal functional alteration in adolescents characterized by early childhood behavioral inhibition. J. Neurosci. 26, 6399–6405.
Haber, S.N., Knutson, B., 2010. The reward circuit: linking primate anatomy and human imaging. Neuropsychopharmacology 35, 4–26.
Halford, J.C., Wanninayake, S.C., Blundell, J.E., 1998. Behavioral satiety sequence (BSS) for the diagnosis of drug action on food intake. Pharmacol. Biochem. Behav. 61, 159–168.
Hane, A.A., Fox, N.A., Henderson, H.A., Marshall, P.J., 2008. Behavioral reactivity and approach–withdrawal bias in infancy. Dev. Psychol. 44, 1491–1496. https://doi.org/10.1037/a0012855.
Happaney, K., Zelazo, P.D., Stuss, D.T., 2004. Development of orbitofrontal function: current themes and future directions. Brain Cogn 55, 1–10.
Hassani, O.K., Cromwell, H.C., Schultz, W., 2001. Influence of expectation of different rewards on behavior-related neuronal activity in the striatum. J. Neurophysiol. 85, 2477–2489.
Hayden, B.Y., 2016. Time discounting and time preference in animals: a critical review. Psychon. Bull. Rev. 23, 39–53.
Hayden, B.Y., Platt, M.L., 2007. Temporal discounting predicts risk sensitivity in rhesus macaques. Curr. Biol. 17, 49–53.
Henderson, H.A., Pine, D.S., Fox, N.A., 2015. Behavioral inhibition and developmental risk: a dual-processing perspective. Neuropsychopharmacol. Rev. 40, 207–224. https://doi.org/10.1038/npp.2014.189.
Henrich, J., Heine, S.J., Norenzayan, A., 2010. Most people are not WEIRD. Nature 466, 29.
Herrnstein, R.J., 1977. The evolution of behaviorism. Am. Psychol. 32 (8), 593–603. https://doi.org/10.1037/0003-066X.32.8.593.
Hikida, T., Yawata, S., Yamaguchi, T., Danjo, T., Sasaoka, T., Wang, Y., Nakanishi, S., 2013. Pathway-specific modulation of nucleus accumbens in reward and aversive behavior via selective transmitter receptors. Proc. Natl. Acad. Sci. U. S. A. 110, 342–347.
Hommel, B., Moors, A., Sander, D., Deonna, J., 2017. Emotion meets action: towards an integration of research and theory. Emot. Rev. 9, 295–298.
Hommer, D.W., Bjork, J.M., Gilman, J.M., 2011. Imaging brain response to reward in addictive disorders. Ann. N. Y. Acad. Sci. 1216, 50–61.
Ikemoto, S., Panksepp, J., 1999. The role of nucleus accumbens dopamine in motivated behavior: a unifying interpretation with special reference to reward-seeking. Brain Res. Brain Res. Rev. 31, 6–41.
Ikemoto, S., Yang, C., Tan, A., 2015. Basal ganglia circuit loops, dopamine and motivation: a review and enquiry. Behav. Brain Res. 290, 17–31.
Immordino-Yang, M.H., Yang, X.F., Damasio, H., 2014. Correlations between social-emotional feelings and anterior insula activity are independent from visceral states but influenced by culture. Front. Hum. Neurosci. 8, 728.
Ito, T.A., Larsen, J.T., Smith, N.K., Cacioppo, J.T., 1998. Negative information weighs more heavily on the brain: the negativity bias in evaluative categorizations. J. Pers. Soc. Psychol. 75, 887–900.
Iyengar, S.S., Lepper, M.R., 1999. Rethinking the value of choice: a cultural perspective on intrinsic motivation. J. Pers. Soc. Psychol. 76, 349.
Izard, C.E., 1971. The Face of Emotion. Appleton-Century-Crofts, East Norwalk CT.
Izuma, K., Saito, D.N., Sadato, N., 2010. Processing of the incentive for social approval in the ventral striatum during charitable donation. J. Cogn. Neurosci. 22, 621–631.
James, W., 1884. What is an Emotion? Mind 9, 188–205.
Józsa, K., Barrett, K., 2018. Affective and Social Mastery Motivation in Preschool As Predictors of Early School Success: a Longitudinal Study. Article accepted for publication, Early Childhood Research Quarterly. .
Kacelink, A., Bateson, M., 1996. Risky theories—the effects of variance on foraging decisions. Integr. Comp. Biol. 36, 402–434.
Kagan, J., Reznick, J.S., Clarke, C., Snidman, N., Garcia-Coll, C., 1984. Behavioral inhibition to the unfamiliar. Child Dev. 55, 2212–2225.
Kassam, K.S., Markey, A.R., Cherkassky, V.L., Loewenstein, G., Just, M.A., 2013. Identifying emotions on the basis of neural activation. PLoS One 8 (6), e66032. https://doi.org/10.1371/journal.pone.0066032. Published 2013 Jun 19.
Kaveri, S., Nakahara, H., 2014. Dual reward prediction components yield Pavlovian sign- and goal-tracking. PLoS One 9, e108142.
Kim, S.I., 2013. Neuroscientific model of motivational process. Front. Psychol. 4, 98.
Kim, E.J., Kim, E.S., Covey, E., Kim, J.J., 2010. Social transmission of fear in rats: the role of 22-kHz ultrasonic distress vocalization. PLoS One 5, e15077.
Kim, H.S., Sasaki, J.Y., 2014. Cultural neuroscience: biology of the mind in cultural contexts. Annu. Rev. Psychol. 65, 487–514.
Kitayama, S., Park, J., 2014. Error-related brain activity reveals self-centric motivation: culture matters. J. Exp. Psychol. Gen. 143 (1), 62.
Kitayama, S., Tompson, S., 2010. Envisioning the future of cultural neuroscience. Asian J. Soc. Psychol. 13 (2), 92–101.
Kitayama, S., Yanagisawa, K., Ito, A., Ueda, R., Uchida, Y., Abe, N., 2017. Reduced orbitofrontal cortical volume is associated with interdependent self-construal. Proc. Natl. Acad. Sci. 114 (30), 7969–7974.
Kiyokawa, Y., Takeuchi, Y., Mori, Y., 2007. Two types of social buffering differentially mitigate conditioned fear responses. Eur. J. Neurosci. 26, 3606–3613.
Klein, J.T., Shepherd, S.V., Platt, M.L., 2009. 3387539; Social attention and the brain. Curr. Biol. 19, 958.
Klimecki, O.M., Leiberg, S., Lamm, C., Singer, T., 2013. Functional neural plasticity and associated changes in positive affect after compassion training. Cereb. Cortex 23, 1552–1561.
Kloumann, I.M., Danforth, C.M., Harris, K.D., Bliss, C.A., Dodds, P.S., 2012. Positivity of the English language. PLoS One 7, e29484.
Knutson, B., Burgdorf, J., Panksepp, J., 2002. Ultrasonic vocalizations as indices of affective states in rats. Psychol. Bull. 128, 961–977.
Knutson, B., Fong, G.W., Adams, C.M., Varner, J.L., Hommer, D., 2001a. Dissociation of reward anticipation and outcome with event-related fMRI. Neuroreport 12, 3683–3687.
Knutson, B., Adams, C.M., Fong, G.W., Hommer, D., 2001b. Anticipation of increasing monetary reward selectively recruits nucleus accumbens. J. Neurosci. 21, RC159.
Knutson, B., Taylor, J., Kaufman, M., Peterson, R., Glover, G., 2005. Distributed neural representation of expected value. J. Neurosci. 25, 4806–4812.
Kohls, G., Chevallier, C., Troiani, V., Schultz, R.T., 2012. 3436671; Social' wanting' dysfunction in autism: neurobiological underpinnings and treatment implications. J. Neurodev. Disord. 4, 10.
Kohls, G., Perino, M.T., Taylor, J.M., Madva, E.N., Cayless, S.J., Troiani, V., Price, E., Faja, S., Herrington, J.D., Schultz, R.T., 2013. 3799969; the nucleus accumbens is involved in both the pursuit of social reward and the avoidance of social punishment. Neuropsychologia 51, 2062–2069.
Kolb, B., Gibb, R., 2011. Brain plasticity and behaviour in the developing brain. J. Can. Acad. Child. Adolesc. Psychiatry. 20, 265–276.
Kos, C., van Tol, M.J., Marsman, J.B., Knegtering, H., Aleman, A., 2016. Neural correlates of apathy in patients with neurodegenerative disorders, acquired brain injury, and psychiatric disorders. Neurosci. Biobehav. Rev. 69, 381–401.
Kostic, V.S., Filippi, M., 2011. Neuroanatomical correlates of depression and apathy in Parkinson's disease: magnetic resonance imaging studies. J. Neurol. Sci. 310, 61–63.
Krakauer, J.W., Ghazanfar, A.A., Gomez-Marin, A., MacIver, M.A., Poeppel, D., 2017. Neuroscience Needs Behavior: Correcting a Reductionist Bias. Neuron 93, 480–490.
Kruglanski, A.W., Fishbach, A., Woolley, K., Bélanger, J.J., Chernikova, M., Molinario, E., Pierro, A., 2018. A structural model of intrinsic motivation: on the psychology of means-ends fusion. Psychol. Rev. 125, 165–182.
Kurzban, R., Duckworth, A., Kable, J.W., Myers, J., 2013. An opportunity cost model of subjective effort and task performance. Behav. Brain Sci. 36, 661–679.
Lahvis, G.P., Panksepp, J.B., Kennedy, B.C., Wilson, C.R., Merriman, D.K., 2015. Social conditioned place preference in the captive ground squirrel (Ictidomys tridecemlineatus): social reward as a natural phenotype. J. Comp. Psychol. 129, 291–303.
Lamm, C., Singer, T., 2010. The role of anterior insular cortex in social emotions. Brain Struct. Funct. 214, 579–591.
Langford, D.J., Crager, S.E., Shehzad, Z., Smith, S.B., Sotocinal, S.G., Levenstadt, J.S., Chanda, M.L., Levitin, D.J., Mogil, J.S., 2006. Social modulation of pain as evidence for empathy in mice. Science 312, 1967–1970.
Larsen, B., Luna, B., 2015. In vivo evidence of neurophysiological maturation of the human adolescent striatum. Dev. Cogn. Neurosci. 12, 74–85.
LeDoux, J.E., 1996. The Emotional Brain: The Mysterious Underpinnings of Emotional Life. Simon and Schuster, New York.
LeDoux, J., 2012. Rethinking the emotional brain. Neuron 73, 653–676.
Lee, W., Reeve, J., 2013. Self-determined, but not non-self-determined, motivation predicts activations in the anterior insular cortex: an fMRI study of personal agency. Soc. Cogn. Affect. Neurosci. 8, 538–545.
Lee, W., Reeve, J., 2017. Identifying the neural substrates of intrinsic motivation during task performance. Cogn. Affect. Behav. Neurosci. 17, 939–953.
LeDoux, J.E., 2014. Coming to terms with fear. Proc. Natl. Acad. Sci. U. S. A. 111, 2871–2878.
Lee, J., Jimenez, A.M., Reavis, E.A., Horan, W.P., Wynn, J.K., Green, M.F., 2019. Reduced neural sensitivity to social vs nonsocial reward in Schizophrenia. Schizophr. Bull. 45 (3), 620–628.
Leszczuk, M.H., Flaherty, C.F., 2000. Lesions of nucleus accumbens reduce instrumental but not consummatory negative contrast in rats. Behav. Brain Res. 116, 61–79.
Likata, M., Paulus, M., Kuhn-Popp, N., Meinhardt, J., Sodian, B., 2015. Infant frontal asymmetry predicts child emotional availability. International Journal of Behavioral Development 39, 492–496.
Locke, E.A., Latham, G.P., 1990. A Theory of Goal Setting & Task Performance. Prentice-Hall, Englewood Cliffs N.J.
Logothetis, N.K., 2008. What we can do and what we cannot do with fMRI. Nature 453, 869.
Lorenz, K., 1981. The Foundations of Ethology. Springer Science, New York.
Lowel, S., Singer, W., 1992. Selection of intrinsic horizontal connections in the visual cortex by correlated neuronal activity. Science 255, 209–212.
MacLean, P.D., 1949. Psychosomatic disease and the 'visceral brain': recent developments bearing on the Papez theory of emotion. Psychosom. Med. 11, 338–353.
MacLean, P.D., 1952. Some psychiatric implications of physiological studies on fronto-temporal portion of limbic system (visceral brain). Electroenceph. Clin. Neurophysiol. 44, 407–418.
Markus, H.R., 2016. What moves people to action? Culture and motivation. Curr. Opin. Psychol. 8, 161–166.
Matsumoto, D., Yoo, S.H., Fontaine, J., 2008. Mapping expressive differences around the

world: the relationship between emotional display rules and individualism versus collectivism. J. Cross-Cult. Psychol. 39 (1), 55–74.
Meyza, K.Z., Bartal, I.B., Monfils, M.H., Panksepp, J.B., Knapska, E., 2017. The roots of empathy: Through the lens of rodent models. Neurosci. Biobehav. Rev. 76, 216–234.
Mikosz, M., Nowak, A., Werka, T., Knapska, E., 2015. Sex differences in social modulation of learning in rats. Sci. Rep. 5, 18114.
Miller, N.E., 1963. Some motivational effects of electrical and chemical stimulation of the brain. Electroencephalograph. Clin. Neurophysiol. (Suppl. 24), 247–259.
Miramontes, O., DeSouza, O., 1996. The nonlinear dynamics of survival and social facilitation in termites. J. Thor. Biol. 181 (4), 373–380.
Montague, P.R., Berns, G.S., 2002. Neural economics and the biological substrates of valuation. Neuron 36, 265–284.
Morales, M., Margolis, E.B., 2017. Ventral tegmental area: cellular heterogeneity, connectivity and behaviour. Nat. Rev. Neurosci. 18 (2), 73–85. https://doi.org/10.1038/nrn.2016.165. Epub 2017 Jan 5. Review.
Morewedge, C.K., Buechel, E.C., 2013. Motivated underpinnings of the impact bias in affective forecasts. Emotion 13 (6), 1023–1029.
Mu, Y., Kitayama, S., Han, S., Gelfand, M.J., 2015. How culture gets embrained: cultural differences in event-related potentials of social norm violations. Proc. Natl. Acad. Sci. 112 (50), 15348–15353.
Muller-Pinzler, L., Gazzola, V., Keysers, C., Sommer, J., Jansen, A., Frassle, S., Einhauser, W., Paulus, F.M., Krach, S., 2015. Neural pathways of embarrassment and their modulation by social anxiety. Neuroimage 119, 252–261.
Murayama, K., Matsumoto, M., Izuma, K., Matsumoto, K., 2010. PMC3000299; Neural basis of the undermining effect of monetary reward on intrinsic motivation. Proc. Natl. Acad. Sci. U. S. A. 107, 20911–20916.
Mutschler, I., Wieckhorst, B., Kowalevski, S., Derix, J., Wentlandt, J., Schulze- Bonhage, A., et al., 2009. Functional organization of the human anterior insular cortex. Neurosci. Lett. 457, 66–70. https://doi.org/10.1016/j.neulet.2009.03.101.
Myers, C.A., Wang, C., Black, J.M., Bugescu, N., Hoeft, F., 2016. PMC5040906; the matter of motivation: striatal resting-state connectivity is dissociable between grit and growth mindset. Soc. Cogn. Affect. Neurosci. 11, 1521–1527.
Nemmi, F., Nymberg, C., Helander, E., Klingberg, T., 2016. Grit Is Associated with Structure of Nucleus Accumbens and Gains in Cognitive Training. J. Cogn. Neurosci. 28, 1688–1699.
Nisbett, R.E., Wilson, T.D., 1977. Telling more than we can know: Verbal reports on mental processes. Psychological Review 84, 231–259.
O' Doherty, J.P., 2004. Reward representations and reward-related learning in the human brain: insights from neuroimaging. Curr. Opin. Neurobiol. 14, 769–776.
O'Brien, W.J., Browman, H.I., Evans, B.I., 1990. Search strategies of foraging animals. Am. Sci. 78, 152–160.
Oberliessen, L., Hernandez-Lallment, J., Schable, S., van Wingerden, M., Seinstra, M., Kalensher, T., 2016. Inequity aversion in rats, rattus norvegicus. Anim. Behav. 115, 157–166.
Oldham, S., Murawski, C., Fornito, A., Youssef, G., Yucel, M., Lorenzetti, V., 2018. The anticipation and outcome phases of reward and loss processing: a neuroimaging meta-analysis of the monetary incentive delay task. Hum. Brain Mapp. 39, 3398–3418.
Opendak, M., Gould, E., Sullivan, R., 2017. Early life adversity durig the infant sensitive period attachment: programming of behavioral neurobiology of threat processing and social behavior. Dev. Cogn. Neurosci. 25, 145–159.
Panksepp, J., 1998. Affective Neuroscience: The Foundations of Human and Animal Emotions. Oxford University Press, New York, NY, US.
Panksepp, J., 2005. Psychology. Beyond a joke: from animal laughter to human joy? Science 308, 62–63.
Panksepp, J., 2011. The basic emotional circuits of mammalian brains: do animals have affective lives? Neurosci. Biobehav. Rev. 35, 1791–1804.
Panksepp, J., Biven, L., 2012. The Archaeology of the Mind. W.W. Norton and Company, New York N.Y.
Panksepp, J., Panksepp, J.B., 2013. Toward a cross-species understanding of empathy. Trends Neurosci. 36 (8). https://doi.org/10.1016/j.tins.2013.04.009.
Panksepp, J., Siviy, S., Normansell, L., 1984. The psychobiology of play: theoretical and methodological perspectives. Neurosci. Biobehav. Rev. 8, 465–492.
Papez, J.W., 1937. A proposed mechanism of emotion. Arch. Neurol. Psych. 38, 725–743.
Papini, M.R., Penagos-Corzo, J.C., Perez-Acosta, A.M., 2019. Avian Emotions: Comparative Perspectives on Fear and Frustration. Front. Psychol. 9, 2707.
Park, H.R.P., Kostandyan, M., Boehler, C.N., Krebs, R.M., 2018. Smiling faces and cash bonuses: exploring common affective coding across positive and negative emotional and motivational stimuli using fMRI. Cogn. Affect. Behav. Neurosci. 18, 550–563.
Panksepp, J., 2003. Can anthropomorphic analyses of separation cries in other animals inform us about the emotional nature of social loss in humans? Comment on Blumberg and Sokoloff (2001). Psychol. Rev. 110, 376–396.
Paschke, L.M., Walter, H., Steimke, R., Ludwig, V.U., Gaschler, R., Schubert, T., Stelzel, C., 2015. Motivation by potential gains and losses affects control processes via different mechanisms in the attentional network. Neuroimage 111, 549–561.
Pawlisch, B.A., Riters, L.V., 2010. Selective behavioral responses to male song are affected by the dopamine agonist GBR-12909 in female European starlings (Sturnus vulgaris). Brain Res. 1353, 113–124.
Perez-Manrique, Gomila, 2017. The comparative study of empathy:sympathetic concern and empathicperspective-taking in non-human animals. Biol. Rev. https://doi.org/10.1111/brv.12342. pp. 000–000.1 doi:.
Pessoa, L., 2009. How do emotion and motivation direct executive control? Trends Cogn. Sci. (Regul. Ed.) 13, 160–166.
Pessoa, L., 2013. The Cognitive-emotional Brain: From Interactions to Integration. MIT Press, Cambridge.
Peterson, R.L., 2005. The neuroscience of investing: fMRI of the reward system. Brain Res. Bull. 67, 391–397.
Pizzagalli, D.A., 2014. Depression, stress, and anhedonia: toward a synthesis and integrated model. Annu. Rev. Clin. Psychol. 10, 393–423. https://doi.org/10.1146/annurev-clinpsy-050212-185606.
Qin, S., Young, C.B., Duan, X., Chen, T., Supekar, K., Menon, V., 2014. Amygdala subregional structure and intrinsic functional connectivity predicts individual differences in anxiety during early childhood. Biol. Psychiatry 75, 892–900.
Quirin, M., Meyer, F., Heise, N., Kuhl, J., Kustermann, E., Struber, D., Cacioppo, J.T., 2013. Neural correlates of social motivation: an fMRI study on power versus affiliation. Int. J. Psychophysiol. 88, 289–295.
Rademacher, L., Krach, S., Kohls, G., Irmak, A., Grunder, G., Spreckelmeyer, K.N., 2010. Dissociation of neural networks for anticipation and consumption of monetary and social rewards. Neuroimage 49, 3276–3285.
Radke, S., Seidel, E.M., Eickhoff, S.B., Gur, R.C., Schneider, F., Habel, U., Derntl, B., 2016. When opportunity meets motivation: neural engagement during social approach is linked to high approach motivation. Neuroimage 127, 267–276.
Range, F., Horn, L., Viranyi, Z., Huber, L., 2009. The absence of reward induces inequity aversion in dogs. Proc. Natl. Acad. Sci. U. S. A. 106 (1), 340–345.
Richard, J.M., Berridge, K.C., 2011. Nucleus accumbens dopamine/glutamate interaction switches modes to generate desire versus dread: D(1) alone for appetitive eating but D(1) and D(2) together for fear. J. Neurosci. 31, 12866–12879.
Richard, J.M., Castro, D.C., Difeliceantonio, A.G., Robinson, M.J., Berridge, K.C., 2013. Mapping brain circuits of reward and motivation: in the footsteps of Ann Kelley. Neurosci. Biobehav. Rev. 37, 1919–1931.
Ricker, J.M., Hatch, J.D., Powers, D.D., Cromwell, H.C., 2016. Fractionating choice: a study on reward discrimination, preference, and relative valuation in the rat (Rattus norvegicus). J. Comp. Psychol. 130, 174–186.
Riters, L.V., 2010. Evidence for opioid involvement in the motivation to sing. J. Chem. Neuroanat. 39, 141–150.
Riters, L.V., Spool, J.A., Merullo, D.P., Hahn, A.H., 2017. Song practice as a rewarding form of play in songbirds. Behav. Processes.
Roelofs, K., Minelli, A., Mars, R.B., van Peer, J., Toni, I., 2009. On the neural control of social emotional behavior. Soc. Cogn. Affect. Neurosci. 4, 50–58.
Rogers, C.E., Sylvester, C.M., Mintz, C., Kenley, J.K., Shimony, J.S., Barch, D.M., Smyser, C.D., 2017. Neonatal Amygdala Functional Connectivity at Rest in Healthy and Preterm Infants and Early Internalizing Symptoms. J. Am. Acad. Child Adolesc. Psychiatry 56, 157–166.
Ruff, C.C., Fehr, E., 2014. The neurobiology of rewards and values in social decision making. Nat. Rev. Neurosci. 15, 549–562.
Romanian Adoptees Study Team,Rutter, M., O'Conner, T.G., English, 2004. Are There Biological Programming Effects for Psychological Development? Findings From a Study of Romanian Adoptees. Developmental Psychology 40, 81–94.
Ryan, R.M., Deci, E.L., 2000a. Self-determination theory and the facilitation of intrinsic motivation, social development, and well-being. Am. Psychol. 55, 68–78.
Ryan, R.M., Deci, E.L., 2000b. Intrinsic and extrinsic motivations: classic definitions and new directions. Contemp. Educ. Psychol. 25, 54–67.
Rydell, A., Berlin, L., Bohlin, G., 2003. Emotionality, emotion regulation, and adaptation among 5- to 8-year-old children. Emotion 3, 30–47.
Saarimäki, H., Ejtehadian, L.F., Glerean, E., Jääskeläinen, I.P., Vuilleumier, P., Sams, M., Nummenmaa, L., 2018. Distributed affective space represents multiple emotion categories across the human brain. Soc. Cogn. Affect. Neurosci. 13 (5), 471–482. https://doi.org/10.1093/scan/nsy018.
Salamone, J.D., Correa, M., Ferrigno, S., Yang, J.H., Rotolo, R.A., Presby, R.E., 2018a. The psychopharmacology of effort-related decision making: dopamine, Adenosine, and insights into the neurochemistry of motivation. Pharmacol. Rev. 70, 747–762.
Salamone, J.D., Correa, M., Yang, J.H., Rotolo, R., Presby, R., 2018b. Dopamine, effort-based choice, and behavioral economics: basic and translational research. Front. Behav. Neurosci. 12, 52.
Schirmer, A., Escoffier, N., Zysset, S., Koester, D., Striano, T., Friederici, A.D., 2008. When vocal processing gets emotional: on the role of social orientation in relevance detection by the human amygdala. Neuroimage 40, 1402–1410.
SchoolerMauss, J.W., 2010. be happy and to know it: The experience and meta-awareness of pleasure, in Kringelbach. In: Berridge, K.C. (Ed.), Pleasures of the Brain. Oxford University Press, Oxford U.K, pp. 244–254.
Schröder, T., Thagard, P., 2013. The affective meanings of automatic social behaviors: three mechanisms that explain priming. Psychol. Rev. 120 (1), 255–280.
Schultz, W., 2010. Subjective neuronal coding of reward: temporal value discounting and risk. Eur. J. Neurosci. 31, 2124–2135.
Schultz, W., 2015. Neuronal reward and decision signals: from theories to data. Physiol. Rev. 95, 853–951.
Sharma, A., Satterthwaite, T.D., Vandekar, L., Katchmar, N., Daldal, A., Ruparel, K., Elliot, M.A., Baldassano, C., Thase, M.E., Gur, R.E., Kable, J.W., Wolf, D.H., 2016. Divergent relationship of depression severity to social reward responses among patients with bipolar versus unipolar depression. Psychiatry Res. Neuroimaging 254, 18–25.
Shenhav, A., Musslick, S., Lieder, F., Kool, W., Griffiths, T.L., Cohen, J.D., Botvinick, M.M., 2017. Toward a rational and mechanistic account of mental effort. Annu. Rev. Neurosci. 40, 99–124.
Siddharthan, A., Cherbuin, N., Eslinger, P.J., Kozlowska, K., Murphy, N.A., Lowe, L., 2018. WordNet-Feelings: A Linguistic Categorisation of Human Feelings. pp. 22 Retrieved from arXiv:1811.02435.
Singer, T., Klimecki, O.M., 2014. Empathy and compassion. Curr. Biol. 24, R878.
Singer, T., Seymour, B., O'Doherty, J.P., Stephan, K.E., Dolan, R.J., Frith, C.D., 2006. 2636868; Empathic neural responses are modulated by the perceived fairness of others. Nature 439, 466–469.
Skidmore, F.M., Yang, M., Baxter, L., von Deneen, K., Collingwood, J., He, G., Tandon, R.,

Korenkevych, D., Savenkov, A., Heilman, K.M., Gold, M., Liu, Y., 2013. Apathy, depression, and motor symptoms have distinct and separable resting activity patterns in idiopathic Parkinson disease. Neuroimage 81, 484–495.
Smith, K.S., Berridge, K.C., 2007. Opioid limbic circuit for reward: interaction between hedonic hotspots of nucleus accumbens and ventral pallidum. J. Neurosci. 27, 1594–1605.
Spreckelmeyer, K.N., Krach, S., Kohls, G., Rademacher, L., Irmak, A., Konrad, K., Kircher, T., Grunder, G., 2009. 2686229; Anticipation of monetary and social reward differently activates mesolimbic brain structures in men and women. Soc. Cogn. Affect. Neurosci. 4, 158–165.
Stellar, E.M., 1954. The physiology of motivation. Psychol. Rev. 154, 5–22.
Strauss, B., 2002. Social facilitation in motor tasks: a review of research and theory. Psychol. Sport Exerc. 3 (3), 237–256.
Takahashi, H., Kato, M., Matsuura, M., Mobbs, D., Suhara, T., Okubo, Y., 2009. When your gain is my pain and your pain is my gain: neural correlates of envy and schadenfreude. Science 323, 937–939.
Tang, J., Chrzanowski-Smith, O.J., Hutchinson, G., Kee, F., Hunter, R.F., 2018. Relationship between monetary delay discounting and obesity: a systematic review and meta-regression. Int. J. Obes. (Lond).
Teitelbaum, P., Epstein, A.N., 1962. The lateral hypothalamic syndrome: recovery of feeding and drinking after lateral hypothalamic lesions. Psychol. Rev. 69, 74–90.
Thorndike, E.L., 1898. Animal intelligence: An experimental study of the associative processes in animals. Psychological Monographs: General and Applied 2, i–109.
Toates, F., 1986. Motivational Systems. Cambridge University Press, Cambridge UK.
Tom, R.L., Ahuja, A., Maniates, H., Freeland, C.M., Robinson, M.J.F., 2018. Optogenetic activation of the central amygdala generates addiction-like preference for reward. Eur. J. Neurosci.
Tomasello, M., 2009. Why we Cooperate. MIT Press, Cambridge MA.
Tomkins, S.S., 1984. Affect theory. Approaches to Emotion. pp. 163–195 163.
Tomkins, S.S., 1991. Affect, Imagery, Consciousness. Vol. III. The Negative Affects: Anger and Fear. Springer, New York, NY.
Tottenham, N., Gabard-Durnam, L.J., 2017. The developing amygdala: a student of the world and a teacher of the cortex. Curr. Opin. Psychol. 17, 55–60.
Tsutsui, K., Grabenhorst, F., Kobayashi, S., Schultz, W., 2016. A dynamic code for economic object valuation in prefrontal cortex neurons. Nat. Commun. 7, 12554.
Ulfig, N., Setzer, M., Bohl, J., 2003. Ontogeny of the human amygdala. Ann. N. Y. Acad. Sci. 985, 22–33.
van Reekum, R., Stuss, D.T., Ostrander, L., 2005. Apathy: why care? J. Neuropsychiatry Clin. Neurosci. 17, 7–19.
Vanderveldt, A., Oliveira, L., Green, L., 2016. Delay discounting: pigeon, rat, human–does it matter? J. Exp. Psychol. Anim. Learn. Cogn. 42, 141–162.
Verdejo-Garcia, A., Alcazar-Corcoles, M.A., Albein-Urios, N., 2018. Neuropsychological interventions for decision-making in addiction: a systematic review. Neuropsychol. Rev.
Veroff, J., 1957. Development and validation of a projective measure of power motivation. J. Abnorm. Psychol. 54, 1–8.
Visalberghi, E., Addessi, E., 2001. Acceptance of novel foods in capuchin monkeys: do specific social facilitation and visual stimulus enhancement play a role? Anim. Behav. 62 (3), 567–576.
Walter, H., Heckers, S., Kassubek, J., Erk, S., Frasch, K., Abler, B., 2010. PMC2821181; Further evidence for aberrant prefrontal salience coding in schizophrenia. Front. Behav. Neurosci. 3, 62.
Waltz, J.A., Gold, J.M., 2016. Motivational deficits in schizophrenia and the representation of expected value. Curr. Top. Behav. Neurosci. 27, 375–410.
Watson, J.B., 1913. Psychology as the behaviorist views it. Psychological Review 20, 158–177.
Webber, E.S., Chambers, N., Kostek, J., Mankin, D.E., Cromwell, H.C., 2015. Relative Reward Effects on Operant Behavior: Incentive Contrast, Inhibition and Variety Effects Behavioral Processes. https://doi.org/10.1016/j.beproc.2015.05.003.
Webber, E.S., Mankin, D.E., Cromwell, H.C., 2016. Striatal activity and reward relativity: neural signals encoding dynamic outcome valuation. eNeuro 3 (5). https://doi.org/10.1523/ENEURO.0022-16.2016. ENEURO.0022-16.2016.
Wee, C.Y., Tuan, T.A., Broekman, B.F., Ong, M.Y., Chong, Y.S., Kwek, K., Shek, L.P., Saw, S.M., Gluckman, P.D., Fortier, M.V., Meaney, M.J., Qiu, A., 2017. Neonatal neural networks predict children behavioral profiles later in life. Hum. Brain Mapp. 38, 1362–1373.
White, R.W., 1959. Motivation reconsidered: the concept of competence. Psychol. Rev. 66, 297–333.
White, L.K., Degnan, K.A., Henderson, H.A., Pérez-Edgar, K., Walker, O.L., Shechner, T., Leibenluft, E., Bar-Haim, Y., Pine, D.S., Fox, N.A., 2017. Developmental relations among behavioral inhibition, anxiety, and attention biases to threat and positive information. Child Dev. 88, 141–155. https://doi.org/10.1111/cdev.12696.
Whiten, A., van de Waal, E., 2017. Social learning, culture and the 'socio-cultural brain 'of human and non-human primates. Neurosci. Biobehav. Rev. 82, 58–75.
Wilson, R.P., Colizzi, M., Bossong, M.G., Allen, P., Kempton, M., Bhattacharyya, S., 2018. The neural substrate of reward anticipation in health: a meta-analysis of fMRI findings in the monetary incentive delay task. Neuropsychol. Rev. 28, 496–506.
Wohr, M., Seffer, D., Schwarting, R.K., 2016. Studying Socio-Affective Communication in Rats through Playback of Ultrasonic Vocalizations. Curr. Protoc. Neurosci. 75, 8.35.1–8.35.17.
Wrase, J., Schlagenhauf, F., Kienast, T., Wustenberg, T., Bermpohl, F., Kahnt, T., Beck, A., Strohle, A., Juckel, G., Knutson, B., Heinz, A., 2007. Dysfunction of reward processing correlates with alcohol craving in detoxified alcoholics. Neuroimage 35, 787–794.
Yoshie, M., Nagai, Y., Critchley, H.D., Harrison, N.A., 2016. Why I tense up when you watch me: inferior parietal cortex mediates an audience's influence on motor performance. Sci. Rep. 6, 19305.
Younes, N., Reips, U.D., 2019. Guideline for improving the reliability of Google Ngram studies: evidence from religious terms. PLoS One 14 (3), e0213554. https://doi.org/10.1371/journal.pone.0213554. eCollection 2019.
Yu, R., Mobbs, D., Seymour, B., Rowe, J.B., Calder, A.J., 2014. The neural signature of escalating frustration in humans. Cortex 54, 165–178.
Zajonc, R.B., 1965. Social facilitation. Science 149 (3681), 269–274.
Zajonc, R.B., 1980. Feeling and thinking: Preferences need no inferences. American Psychologist 35, 151–175.
Zajonc, R.B., Herman, E.M., 1969. Social enhancement and impairment of performance in the cockroach. J. Pers. Soc. Psychol. 13, 83–92.
Zaki, J., 2014. Empathy: a motivated account. Psychol. Bull. 140, 1608–1647.