

Cognitive-emotional interactions

The role of social cognition in emotion

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Although recent research has shown that social cognition and emotion engage overlapping regions of the brain, few accounts of this overlap have been offered. What systems might be commonly or distinctively involved in each? The close functional relationship between social cognition and emotion might be understood in terms of a central role for mental state attribution in the understanding, learning and regulation of emotion. In each of these cases, mental state attributions might be supported by either stimulus-driven or more reflective processes.

Exploring the role of mental state attribution in emotion

Whether viewed from a phylogenetic or an ontogenetic perspective, it is clear that the abilities to understand, learn from and behave appropriately towards one another were as essential for our hominid ancestors as they are for a developing child [1]. In the past decade, insight into the neural mechanisms supporting these abilities has been provided by two burgeoning fields of research: social cognitive neuroscience and affective neuroscience. Although these fields developed largely independently [2], for multiple reasons the boundaries between the phenomena they study are becoming increasingly blurred (Box 1). Perhaps chief among them is the finding that ostensibly different types of social cognitive or emotional abilities recruit similar suites of cortical and subcortical neural systems. Although this fact has been noted [3], to date few accounts of the apparent interdependence of social cognition and emotion have been advanced.

Here, we review recent work suggesting that this relationship can be understood – at least in part – in terms of a fundamental role of one type of social cognitive capacity in processing emotion: the ability to explain behavior in terms of intentional mental states, which we will refer to as mental state attribution (MSA; Box 2). The role of MSA can be considered in three domains: (i) understanding emotion, (ii) learning emotionally significant information and (iii) regulation of emotional responses. For each domain, we discuss the roles in emotion processing of systems supporting MSAs that vary in their degree of representational complexity and reflective control. Based on this review, we propose a neural framework for understanding the role of social cognition in emotion that can guide future research.

Understanding emotions in self and others

The ability to understand both another person's and one's own emotional states is essential for virtually all aspects of social behavior and crucially depends upon MSA. Indeed, emotion understanding – by definition – requires a causal attribution about the intentions behind an action. Evidence suggests that MSA contributes to emotion understanding through the operation of both rapid stimulus-driven processes [4,5] and more deliberative, reflective and conceptually driven processes [6–8].

Evidence for the neural bases of stimulus-driven MSA came initially from imaging studies showing that some motor regions respond during both the execution and observation of specific movements [4]. The idea was that if motor regions code the intentions behind one's own action, then if activated when observing another person engaging in the same action, they could support a direct experiential understanding of that person's intention [4,9].

This 'shared representation' logic guided subsequent studies of the direct experience and observation of pain or emotion that also showed activation of overlapping neural systems, including most prominently the two cortical regions that receive ascending viscerosensory inputs: the anterior insula (AI) and the midportion of the anterior cingulate cortex (mACC) [4,7,10–15]. The AI is believed to support affective experience in part through interoceptive awareness of these body state inputs [16,17], whereas the ACC is thought to code affective attributes of pain, such as the perceived unpleasantness (as opposed to sensory-discriminative properties, such as location and intensity) [18–20] and motivate appropriate behavior through projections to motor and autonomic centers [16,21]. The engagement of the AI, ACC and other regions is thought to facilitate the automatic sharing of – and hence direct experiential understanding of the intentions behind – affective states, which in turn might provide a substrate for empathic connection [7,13].

Emotion understanding is not always so simple, however, because nonverbal cues to emotion are often ambiguous. In such cases, additional information is needed to constrain attributions about a person's intentions and hence their emotional state. One source of information is our prior experience with that person and knowledge about antecedent events. For example, wide open eyes could mean that someone is either afraid or surprised – and elicit amygdala activity accordingly – depending on what one knows has just happened to them [22]. Similarly, activation of shared representations – and presumably empathic connection – might be blocked if one perceives another to be a past or potential competitor [23,24].

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Box 1. Investigating social cognition and emotion: separate approaches to inseparable phenomena?

The fact that social cognition and emotion depend upon highly overlapping neural systems might seem at odds with the fact that behavioral work on these topics has historically proceeded in largely independent disciplines. Close inspection of their respective theoretical and methodological approaches, however, suggests that social cognition and emotion researchers might often be studying intertwined aspects of the same phenomenon.

To understand these relationships, consider how each field would approach study of a man and woman on their first date. A social cognition researcher might ask how they make attributions about the situational or dispositional causes of each other's behavior, and how such judgments are influenced by their motivations, attitudes, moods, group memberships and available cognitive resources [53,72,73]. By contrast, an emotion researcher might be interested in describing the cognitive antecedents and/or expressions of each person's affective experience, emotion-related behavior and autonomic arousal, with an emphasis on understanding their cross-species or cross-cultural consistencies [74,75].

Two types of similarities between social cognition and emotion can be highlighted here. The first is that the attributions of interest to social cognition researchers might determine how one responds emotionally. In the present example, whether you think someone is anxious by nature, or because anyone would be on a first date, could determine how you respond emotionally to them [53]. The second is that the stimuli used to study social cognition and emotions are often related, if not identical, especially in neuroscience research on these topics. Stimuli in both emotion and social cognition experiments include real, simulated, described or photographed social interactions, in addition to images of faces and facial expressions, all of which might evince both social cognitive attributions and emotional responses to varying degrees.

It might not be surprising, therefore, that social cognition and emotion depend upon similar neural systems, given that social information carries great emotional and motivational significance. Of course, we can respond emotionally to non-social stimuli (e.g. odors, nature, etc.), and some emotions, such as pity and shame, might require social cognitive attributions; space constraints prevent further discussion of this topic here, but it is discussed by Harris and Fiske [64] and by Scherer *et al.* [75]. It is not clear, however, when and how social interaction can be devoid of emotion or affect. One goal for future neuroscience research should be to incorporate behavioral methods that could differentiate the roles of social cognition and emotion in social interaction.

Engagement of control processes that support more cognitively complex MSAs might enable understanding of the emotional state of a target when stimulus-triggered processing of situational information is not sufficient. These controlled MSAs enable us actively to take other peoples' perspectives and make judgments about their emotions or diagnostic elements of stable emotional dispositions, thereby changing empathic responding [25] and activation in the AI and mACC [8]. By and large, they depend on a network of regions, including the right temporal parietal junction (TPJ) and dorsal-rostral regions of the medial prefrontal cortex (MPFC), including Brodmann area (BA) 10 [6,26,27]. Interestingly, a recent meta-analysis singles out BA 10 – which is especially developed in humans – as being particularly sensitive to tasks involving both emotions and MSA [28]. If the mACC and AI support direct experiential awareness of intentional states, it is possible that the MPFC network supports meta-cognitive reflective awareness of them.

Strikingly, only one study of stimulus-triggered empathy showing mACC and AI activity has also shown MPFC

Box 2. MSA

As used here, MSA is an umbrella term encompassing the various ways in which we use mental state concepts to describe, understand and predict behavior, and corresponds to the 'intentional stance', as described by philosophers [76]. MSA has figured importantly but differently in four types of behavioral work that have provided springboards for current imaging research.

Social cognition

Although social cognition research has not explicitly focused on unpacking the mechanisms of MSA, it has appreciated that MSA is central to the goal of understanding the causes of behavior. Social cognition researchers have asked, for example, how much behavior is due to internal (e.g. beliefs, intentions, dispositions and attitudes) as opposed to situational forces, in addition to how we weigh the contributions of each when judging the causes of either our own behavior or the behavior of others [53,77].

Emotion

In the study of emotion, MSA figures prominently, if not focally, in appraisal theories, which specify how cognitive interpretations can shape emotions. MSAs about intentionality of another's action, for example, will determine if one feels anger, and are central to secondary appraisals of one's ability to cope with current stressors. MSAs are also used to introspect upon and describe one's current or past emotions [75].

Development

Developmental psychologists coined the term 'theory of mind' (TOM) to explain a child's emerging use of MSAs to explain behavior, and have debated whether TOM involves learning to simulate another's mind or the acquisition of abstract theoretical knowledge about mental states [1,9,56]. Efforts to identify the age of TOM onset has led to the development of false belief tasks thought to be diagnostic of the ability to use MSAs, as opposed to other schemes, for explaining behavior [78].

Social cognitive and affective neuroscience

Functional imaging and lesion work has informed the study of MSA by identifying a network of associated brain systems and the somewhat inconsistent deficits in MSA that follow from lesions to some of its components. In general, these data have illustrated how neuroscience is useful for understanding how complex abilities, such as MSA, might fractionate into component computational systems. A primary goal of current work is to characterize these computations and describe how they give rise to different types of MSAs [6,26,27,68].

activity [29]. In this study, MPFC was active for the perception of pain in self and others versus perceiving damage to artificial limbs, which makes it unclear whether MPFC involvement is related to mental attributions specific to empathy, non-empathy-related attributions or both. The lack of clear findings of MPFC activation could indicate a functional distinction between the affective experience of directly sharing another's feelings and the meta-cognitive task of thinking about and rating them [6,30], which is consistent with the observation that MPFC activity during others' pain (although not significantly greater than baseline) might be positively related to self-rated empathic concern [13]. Alternatively, it is possible that experiential and reflective processing do work together but only in certain circumstances. This possibility is supported by a recent study examining functional connectivity of mACC and AI regions commonly active during the direct experience and observation of pain [15]. Here, mACC and AI activity was correlated with activity in pain-related brainstem nuclei during self-pain

and with the MPFC when observing others in pain (Figure 1a, b). The fact that these regions were not identified in the vast majority of standard contrasts suggests that MPFC involvement might have been missed in prior work examining activity averaged across subjects and time points. The coactivation of these networks suggests that emotion understanding might in some cases involve the use of reflective cognition drawing on the MPFC to interpret activity in networks supporting experiential processing of emotions.

Interestingly, some of the same regions involved in reflecting upon others' emotional states are involved in reflecting upon our own emotions [6,26], consistent with theories suggesting that in some cases we treat ourselves as an 'other' when making self-judgments [31]. The reverse might also be true: we use information about our own states and traits when we reflect upon the states and traits of others who seem to be like ourselves. Thus, judgments about known or similar, as compared with less familiar or dissimilar, others draw on medial frontal regions similar to those used for self-referential processing [6,27]. Exactly

when, and how, we use similar processes for judging ourselves and others, and the extent to which these processes are dedicated to the processing of social information as opposed to more general meta-cognitive functions used when categorizing and re-representing affective and other types of input in a symbolic format, is currently a matter of debate [6,32].

In sum, the research surveyed in this section suggests that understanding the emotions of others through MSA is supported by a distributed functional network including cingulate and insula regions that are important for stimulus-driven processing of social cues and their underlying intentions, in addition to a network of regions centered on the MPFC used to reflect upon and reason about them.

Emotional learning

The role of MSA in emotion is not limited to understanding emotions in the present moment but additionally helps us to learn about emotion-eliciting events and also to form lasting impressions of others' emotionally relevant

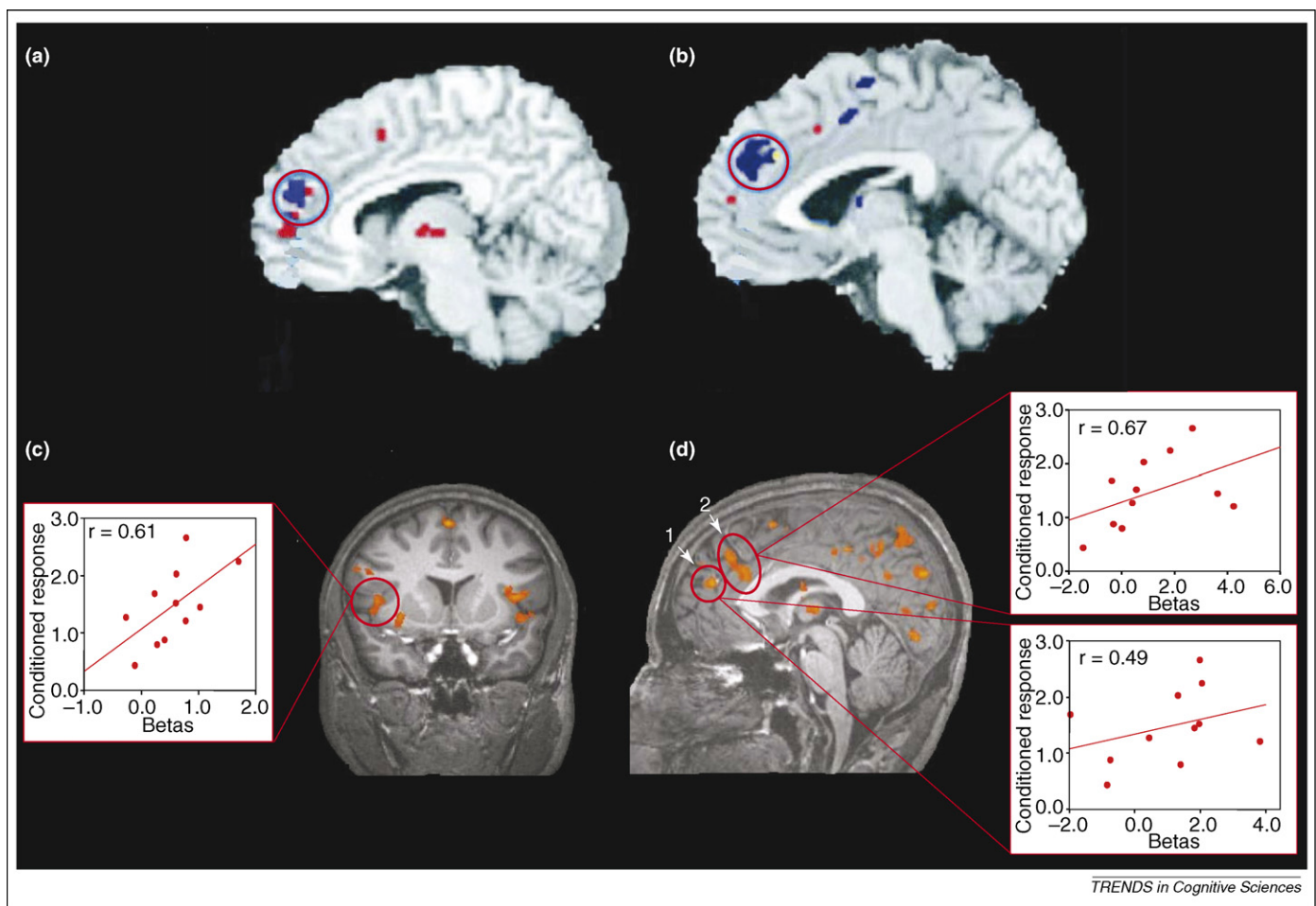


Figure 1. (a, b) Sagittal views of areas with increased connectivity with seed regions commonly active during self and other pain in the (a) AI and (b) ACC [15]. Activations during the direct experience of pain are marked in red, and during the observation of others' pain are marked in blue. Importantly, when observing others' pain, activation in the MPFC (circled) co-varied with activation in seed regions in both the AI {6,40,24}^{*} and ACC {12,48,12}^{*}. (c,d) Functional activation during an observational fear learning task [35]; (c) shows a coronal view of activation in the right AI {-28, 15, -4}¹ when observing the pain response of a learning model to a shock. The adjacent graph shows that the magnitude of this activation predicts the strength of the conditioned response (indexed by the skin conductance response) at a later time to a cue associated with the pain of the learning model ($P < 0.05$). (d) A sagittal view of activation in the (1) MPFC {1,46,24}¹ and (2) ACC {3,27,32}¹ during the observation of the pain response of a learning model to a shock. As in (c), adjacent graphs display the positive relationship between the magnitude of activation during observation and the subsequent conditioned response ($P = 0.08$ and $P < 0.05$ for 1 and 2, respectively).¹x, y, z coordinates for local maxima in Montreal Neurological Institute (MNI) space; ²x, y, z coordinates for local maxima in Talairach space; ³after one individual who was an outlier was removed.

dispositions. For example, watching another's fear expression to an unfamiliar dog could provide valuable information about potential danger, that individual's anxious disposition or both. These abilities to learn from and about others crucially depend on understanding others' emotions using both stimulus-driven and reflective MSAs.

Learning from others

Neuroscience models of emotional learning are based primarily on studies of fear conditioning showing that the amygdala is crucial for learning through direct experience which stimuli predict aversive outcomes [33,34]. Emotional learning can also take place through indirect means, however, such as verbal communication and observation. Although these social-emotional routes to learning are crucial to everyday life for most humans [35], their neural bases have only recently begun to be explored [36,37].

A common example is observational fear learning in which one vicariously learns to fear a stimulus that elicits expressions of fear in a conspecific. Cross-species research demonstrates that learning fear through observing others shares behavioral [38,39] and neural features with conditioned fear, including involvement of the amygdala [37,40]. Although this suggests that low-level stimulus-driven processes have an important role in observational fear learning across species, recent work in humans suggests that, in addition to explicit knowledge about the stimulus contingencies, fear learning through observation might also involve higher-level reflective MSAs. Olsson *et al.* [37] found that overlapping regions of the amygdala, AI and ACC were active during both observational learning and subsequent expression of fear responses, whereas the dorsal MPFC was active only during observation of another's distress. Importantly, the magnitude of the conditioned response was predicted by activity in the AI, ACC and dorsal MPFC (Figure 1c,d). This suggests that shared representations supporting experiential understanding of emotion – in addition to regions supporting reflective MSAs – jointly support social-emotional learning (Figure 1c,d).

Learning about others

The two types of MSAs that support learning from others also provide crucial diagnostic information about others' stable social-emotional dispositions. Consider a social interaction that unfolds over time. During the initial moments of contact, stimulus-driven systems might assess the affective value of social targets with varying degrees of complexity. For example, the simple perception or evaluation of either attractive or potentially threatening and untrustworthy faces activates either striatal regions implicated in reward and reinforcement learning [41] or the amygdala and AI regions implicated in aversive learning, as described earlier [42–45]. With repeated interaction, imaging studies suggest that the striatum might encode which actions produce desired social outcomes, consistent with its general role in reinforcement learning [41,46]. Striatum activity accompanies both cooperation and trust [46–49] – but also punishing a previously unfair partner

[50] or knowing that they are in pain [24] – perhaps because of an expectation that the partner's behavior will be brought back in line with expected norms. It should be noted, however, that growing evidence suggests that the amygdala and striatum are not simply 'fear' and 'reward' systems, and instead are sensitive to the arousal-related and motivational properties of valenced stimuli in general [51,52].

The affective value of a social target is determined, of course, both by their dispositions and by situational variables [53]. An identical punch might be taken as aggressive or playful, for example, depending on one's assessment of the puncher's intent. Contextual information that precedes or follows initial stimulus-driven assessments might flexibly constrain and update them using bidirectional interconnections between the amygdala, striatum and orbitofrontal cortex (OFC) [54–56]. For example, OFC damage might cause an individual to be unable to appreciate *faux pas*, or to consider that the amount they tease someone, or are praised by them, is contextually inappropriate [54,56,57]. In such situations, OFC damage impairs the ability quickly and implicitly to use MSAs (e.g. my girlfriend is embarrassed...) to regulate moment-to-moment behavior (...so I should stop teasing her). By contrast, rostral and dorsal MPFC might support explicit MSAs used when reflecting upon the intentions behind and consequences of actions, as evidenced by its activation during strategic games [50,58] and when forgiving others' transgressions [59].

Taken together, current work suggests that both rapid and reflective MSAs support emotional learning from and about others. As the complexity of required MSAs increases, processing might move from stimulus-driven subcortical to orbitofrontal regions and on to rostral and dorsal MPFC regions if processing becomes explicitly evaluative or reflective.

Regulation of emotional responses

The MSA processes used for emotion understanding and learning also enable us adaptively to regulate our own emotional responses. To date, studies have investigated primarily the use of higher-level MSAs to regulate emotion in two ways.

The first 'situation focused' or 'other focused' strategy involves reinterpreting the situational meaning of others' intentions or feelings, as when, for example, thinking positively or negatively about the dispositions (she is hearty or weak) and future emotions (she will feel fine or get worse) experienced by someone who is sick and in pain [60–62]. Interestingly, recent work suggests that simply making an attribution about the feelings of another person can have the unintended consequence of disrupting amygdala-mediated negative evaluations of them [63,64]. One reason for this might be that MSAs can direct attention to the nonthreatening intentions (e.g. thinking about their food preferences) of a social target, thereby disambiguating them as potential sources of threat.

The second 'self-focused' strategy involves mentally manipulating one's personal connection to an emotionally charged situation, as when, for example, one experiences aversive events from the simulated perspective of an

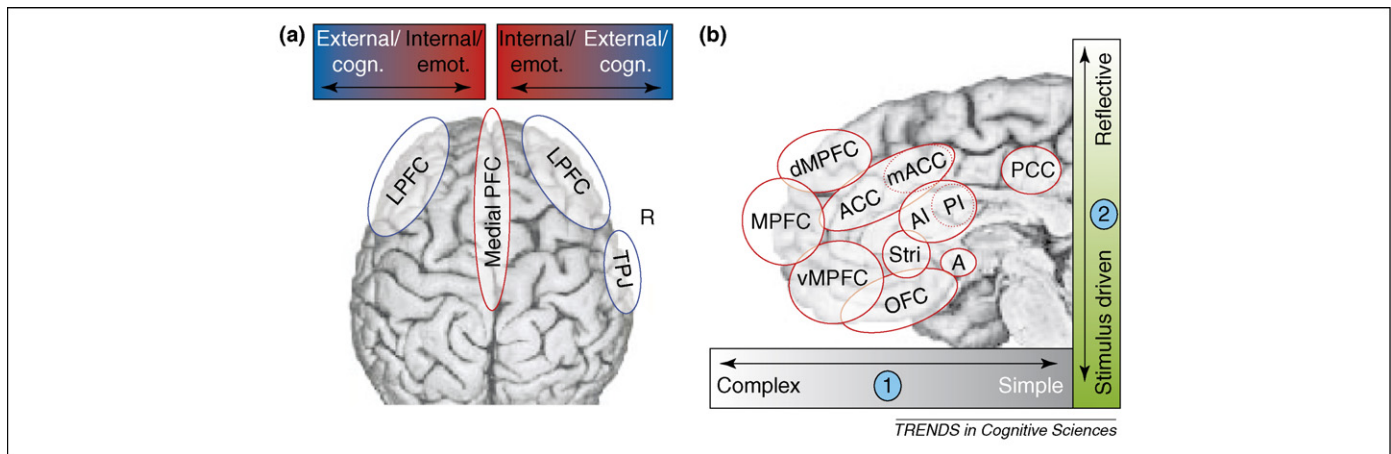


Figure 2. A functional-anatomical organization of regions supporting the role of MSA in emotion. (a) Midline regions (e.g. MPFC) interconnected with emotion centers support representations of internal states and might be coding emotional qualities of MSAs. By contrast, lateral regions [e.g. the lateral prefrontal cortex (LPFC) and TPJ] interconnected with visuospatial centers support externally generated representations and might be coding cognitive aspects of MSA. (b) Closely aligned to the midline section along with the insula (1), posterior regions [e.g. the posterior cingulate cortex (PCC), posterior insula (PI) and the mACC] support simple 'first-order' sensory aspects of MSA, whereas representational complexity increases as the information is re-represented in more anterior regions (e.g. MPFC); (2) ventral regions [e.g. the amygdala (A), OFC, striatum (Stri) and ventral MPFC (vMPFC)] are predominantly engaged in stimulus-driven processes, whereas dorsal regions [e.g. dorsal MPFC (dMPFC) and LPFC] support performance monitoring and reflective processes of MSA. Abbreviation: cogn, cognitive; R, right.

objective and detached third person observer [65–67]. Although each strategy can modulate stimulus-driven amygdala activity, they seem to depend differentially upon complementary PFC regions: the MPFC – which receives direct inputs about the internal state of the body – might be relatively more important for self-focused regulation, whereas other-focused regulation might depend more on ventrolateral PFC regions used to select from memory information that helps to interpret others' feelings [6].

In sum, it seems that MSAs can regulate emotion either through reinterpretations of others' feelings or by simulating what it would be like to be experiencing the event from a third person perspective. These strategies might differentially depend on medial and lateral regions of the PFC, respectively.

A neural framework for the role of social cognition in emotion

One way to understand the relationship between social cognition and emotion is to delineate the way in which the processes and mental representations underlying them are distributed along general functional axes in the brain [30,68]. Based on the preceding review, we propose that the role of social cognition – and MSA in particular – in emotion can be understood in terms of three related but distinct dimensions of functional-anatomic organization. The proposed framework should be viewed as complementary to previously formulated functional-anatomical models, which have attempted to capture a broader array of social cognitive phenomena and have often done so along two dimensions [30,68]. According to the scheme proposed here (Figure 2, Box 3), lateral regions preferentially process information about external inputs, whereas medial regions have an essential role in MSA by representing information about internal states [68]. Along with the AI, posterior medial regions such as the mACC represent body state information that is represented with increasing complexity as processing moves anteriorly towards the frontal pole and BA 10 [30]. BA 10 has a

key role integrating information about the internal state of the body with higher-level mental state knowledge needed to categorize affective states. Finally, as processing moves from ventral to dorsal regions, it becomes less stimulus driven and increasingly controlled and reflective, enabling one to judge explicitly and be aware of one's own or others' emotional states. Given the early stages of research in this area, of course, the functional distinctions drawn between medial-lateral, posterior-anterior and ventral-dorsal regions are by necessity highly simplified and heuristic. It is expected that continued research will be crucial for their further specification.

Future directions

This survey of research on the neural bases of MSA in emotion understanding, learning and regulation provides a framework for understanding current work but also highlights how much there remains to be clarified in future research. At least four types of question will be important to address.

The first concerns the fact that research has focused on how the average person perceives emotions in static social stimuli, but less is known about how dispositional or situational motivations (e.g. to seek affiliation or fear rejection, or be empathic versus competitive) might influence the neural systems supporting emotion understanding, learning and regulation during real-time social interaction. Methods and approaches are now being developed to address these issues [48,69].

Second, an interactive approach will also be important for the analysis of data, to clarify how different components of the functional networks supporting MSA work together in social cognitive and emotional attributions. Indeed, the fact that both simple and complex MSAs can be impaired following damage to just one of the regions described earlier [54,70,71], and that each region might have general functional roles beyond MSA [26,32], makes it clear that understanding time- and context-varying interactions between regions will be essential [15].

Box 3. A three-dimensional neural framework for understanding the role of MSA in social cognition and emotion

The role of social cognition – and MSA in particular – in emotion can be broadly understood in terms of three related but distinct dimensions of functional–anatomical organization that generally follow patterns of inter-regional connectivity and neurodevelopmental trends in cortical evolution.

The first concerns the medial–lateral axis (Figure 2a), with midline regions interconnected with visceral centers and stimulus-driven emotion centers such as the amygdala and striatum [79]. Whereas the midline regions are important for representing information about internal states, lateral regions interconnected with visuospatial centers are important for externally generated representations. In this view, medial and lateral regions might be more engaged by, respectively, the emotional and cognitive qualities of MSAs [51], such that attributions about feelings recruit the MPFC, and complex elaborations of MSA dependent on abstract rules and retrieving information from memory recruit the LPFC [6,68,80]. Interestingly, similar functional–anatomical distinctions have been drawn previously in relation to both social cognitive processes [68] and other nonsocial domains, such as response selection and motor behavior [81] and hedonic experiences [55].

The second involves the midline posterior–anterior axis and concerns the degree of complexity of MSA-related information (Figure 2b), which in the frontal lobe follows a radial pattern of cortical evolution, whereby a three-layered cingulate cortex developed into a six-layered rostral MPFC [82]. Posterior regions provide the ‘first-order’ perceptual substrate of the socio-emotional processing stream by initially representing nonverbal [superior temporal sulcus (STS)] and body state (posterior insula and middle ACC) cues. As this information is passed anteriorly along the insula and MPFC, it is re-represented with increasingly complexity [30,31,80] in a ‘second-order’ format that supports awareness of, and explicit judgments about, the meaning of affective mental states. A similar distinction has been outlined by Amodio and Frith [30].

The third dimension tracks the frontal midline from its ventral regions predominantly engaged in stimulus-driven processes to its dorsal regions supporting performance monitoring and reflective processes (Figure 2b). At present, this division is perhaps the most speculative, and is intended to distinguish the amygdala, striatum and OFC, which support stimulus-driven MSAs, from dorsomedial and lateral PFC regions, which support explicit and reflective MSAs [6,83].

Using this framework, it can be seen that different neural systems might support MSAs, depending upon the task and processing demands: subcortical (amygdala and striatum) and posterior (STS, mACC and insula) systems will support emotion understanding, learning and regulation unless it becomes necessary to engage anterior medial and lateral PFC regions to categorize and reason about affective states [83].

Third, careful comparisons of human and non-human animal models of social–emotional behavior will be useful for understanding what processes uniquely characterize each species. In some areas of research – such as social–emotional learning – it remains to be seen whether strong homologies between species belie the use of common MSA processes or a reliance on variants of the same basic Observational Fear Learning paradigms. In other areas of work – such as the use of MSA to regulate emotion – the mapping might be complicated because humans are capable of complex attributions about mental states that might be difficult to capture in animal models.

Fourth, basic work on the role of social cognition in emotion is particularly well suited for translational efforts. Myriad psychological disorders, ranging from

schizophrenia to anxiety disorders and depression, are characterized by impaired social cognition in addition to emotion understanding, learning and regulation. Examining possible deficits in core neural systems supporting MSA might be crucial to understanding better the etiology and possible therapies for these disorders.

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