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Large-scale brain networks in affective and social neuroscience: towards an integrative functional architecture of the brain

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Understanding how a human brain creates a human mind ultimately depends on mapping psychological categories and concepts to physical measurements of neural response. Although it has long been assumed that emotional, social, and cognitive phenomena are realized in the operations of separate brain regions or brain networks, we demonstrate that it is possible to understand the body of neuroimaging evidence using a framework that relies on domain general, distributed structure–function mappings. We review current research in affective and social neuroscience and argue that the emerging science of large-scale intrinsic brain networks provides a coherent framework for a domain-general functional architecture of the human brain.

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One overarching goal in human brain imaging research is to understand the physical responses of neurons (e.g., electrical, magnetic, blood flow or chemical measures related neurons firing) in mental (i.e., psychological) terms. At its inception, brain-imaging research not only started with psychological ‘faculties’ such as emotions (e.g., anger, disgust, fear, etc.), social cognitions and perceptions (the self, person perception, etc.), as well as non-social cognitions (e.g., memory, attention, etc.) and perceptions (visual images, auditory sounds), and searched for their correspondence in topographically distinct swaths of brain tissue (often on the assumption that each constitutes its own mental ability as a specific process). This faculty psychology tradition, bolstered by often-implicit assumptions of modularity [1], carved up human brain imaging research into at least three sister disciplines — affective, social, and cognitive neuroscience. Increasingly, this paradigm in the human

neurosciences has been criticized [2^{*},3^{*},4,5^{**},6,7], in large part because the brain imaging research it inspired reveals it to be misguided. Experimental tasks ranging widely across the various neuroscience disciplines produce patterns of results that are more similar than a faculty psychology approach would suggest. Assumptions about modularity, even in sensory cortices, are also in question.

Faculty psychology is not quite dead, however. Recent methodological shifts have moved from topographical attempts to locate faculties towards a systems neuroscience approach (for a recent review, see [5^{**},8^{**}]), sometimes involving correspondingly misguided attempts to map emotions, social cognitions, and non-social cognitions and perceptions to distinct brain networks. Understanding the functions of the human brain in psychological terms requires not only methodological sophistication, however; it also demands a different psychological conceptualization and set of constructs for understanding how the brain accomplishes its emotional, social, and cognitive/perceptual feats (cf., [2^{*},5^{**}]). Over two decades of brain imaging data point towards a framework where the human brain is intrinsically organized into domain-general, distributed functional networks. Emotions, social cognitions, and non-social cognitions (and perceptions, which for this paper we include in the category ‘cognition’) can be thought of as mental events (prompted by specific experimental tasks, or arising as naturally occurring states) that are constructed from interactions within and between these networks that compute domain-general functions. In this paper, we review recent research within affective and social neuroscience that points towards this constructionist cognitive architecture of the brain that relies on distributed structure–function mappings.

Affective neuroscience: the nature of emotion

In the field of affective neuroscience, no topic has received more attention than the brain basis of emotion. Until recently, scientists were largely convinced that anger, fear, sadness, happiness, and disgust, as emotional faculties, arise from separate, innate, culturally universal neural modules in the brain (for a review see [5^{**},9^{**}]). In the typical brain imaging study of emotion, participants are asked to cultivate an emotional experience from viewing images or movies, by remembering previous experiences or perceiving an emotion in posed facial expressions (such as smiles, scowls, pouts, etc.), in non-linguistic vocalizations (such as sighs, shouts, etc.) or in body postures during brain imaging. Recently, two

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Figure 1



Each pie chart depicts the relative frequency with which various mental functions are discussed in the context of increased activation within the 'executive control' network (top left), the 'salience' network (top right), the 'mirroring' network (bottom left), and the 'mentalizing network' (bottom right) as obtained using the Neurosynth database including over 6000 publications from over 50 journals [107].

large-scale statistical summaries (i.e., meta-analyses) of human neuroimaging studies (covering studies published between 1993 and 2011) have demonstrated that anger, sadness, fear, disgust, and happiness cannot be localized to activity in specific topographical regions of the human brain using such tasks [9••,10•].¹ Brain regions such as the amygdala, anterior insula, pregenual and subgenual anterior cingulate cortex, and orbitofrontal cortex (once considered to be the brain locations of fear, disgust, sadness, and anger, respectively) demonstrate remarkably consistent increases in activity during a variety of emotional states indicating that these regions lack the

specificity that is the hallmark of an emotion faculty perspective (see Figure 6 in [9••]).²

Nonetheless, the belief that emotions can be localized somewhere in the brain is very strong (see [11•,12•] for discussions), and efforts at topographical localization have given way to the hypothesis that emotions can be localized to specific brain networks (e.g., [13,14]). According to an emotion faculty approach, emotions are homologous in non-human mammals and universally inherited in humans, so the corresponding hypothesis would be that

¹ Vytal and Hamann [10•] interpret their findings as evidence that different emotions are localized to distinct topographical regions of the brain, but their results show spatial overlap in activations that preclude such an interpretation. Instead, studies that require participants to cultivate different emotions produce consistent activations that overlap significantly with one another.

² It is tempting to assume that this lack of specificity is a function of coarse spatial and temporal resolution in brain imaging experiments on the grounds that careful optogenetic, lesion, and molecular neuroscience research has revealed the circuitry that supports 'emotional' behaviors such as freezing, attack, and withdrawal; but there are a number of empirical and philosophical arguments regarding why the circuitry for certain behaviors cannot be understood as evidence for the neurobiology of emotions per se (for a discussion, see [11•,12•]).

Box 1 Networks that are intrinsic to the brain's architecture

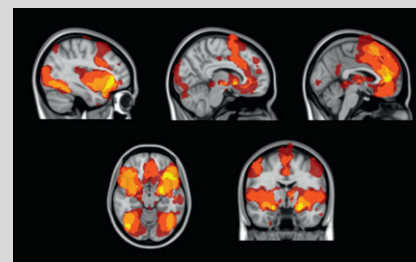
The human brain is organized into large-scale 'intrinsic' networks reflecting strong temporally-organized coupling of activity across widely distributed brain regions, taking up a large proportion of the brain's metabolic budget [90*,91]. Intrinsic networks have been observed during mental states that arise independent of any task or external stimulus ([16,92,93*], for a review see [8**]), that arise in response to specific tasks, and that occur during various states of consciousness, including sleep and sedation (e.g., [94–96]). And importantly for questions about the nature of emotion, intrinsic networks are structured by anatomical connectivity [97,98*,99,100] influencing oscillations within the gamma frequency range [101], with several networks identified in non-human primates [102–105,106*]. A major focus of current research is to understand how these networks are related to psychological functions. We propose that these networks underlie domain general functions that cut across the boundaries stipulated by faculty psychology (i.e. the boundaries presupposed by social, affective, cognitive, and perceptual neurosciences). Instead, activity across networks and interactions between them give rise to the experienced mental states as Gestalts that are then categorized as one or the other of these faculties.

emotion networks should be anatomically constrained (and can therefore be inherited) and are homologous with networks that exist within the brains of other animals. The science of 'intrinsic' network connectivity represents a prime candidate for identifying emotion networks according to these criteria (see [Box 1](#)). Recent research from our lab casts doubt on the specific emotion network hypothesis, however. Using a 'seed and discovery' process for revealing intrinsic brain networks in task-independent (i.e., resting-state) fMRI BOLD data from 389 individuals, we demonstrated that distributed, anatomically-constrained networks for each emotion do not exist within the intrinsic architecture of the human brain [15]. Instead, the most reliable sources of activation during states of anger, sadness, fear, and disgust (as obtained from meta-analytic results) each produced a discovery map whose spatial overlap yielded the intrinsic network referred to as the 'salience' network [16] or the ventral attention network [17,18] (see [Box 2](#)). A recent fMRI study from our lab confirms that nodes within the 'salience' network (see [Table 1](#)) independently track feelings of pleasure and distress (medial orbitofrontal cortex) and feelings of arousal (amygdala) during both pleasant and unpleasant instances of happiness, sadness, and fear [19**].

The nodes within the 'salience' network not only lack specificity for discrete emotions, but also are not specific to the broader domain of emotion per se (see [Figure 1](#)), consistent with criticisms of the limbic system concept. For example, regions within the amygdala are not only engaged during emotional states, but also show reliable increases in activity when people are asked to process novel material, even when such material is neutral and not explicitly affectively evocative (e.g., [20*,21**,22]). The amygdala also shows degeneration that is equivalent to hippocampal degeneration in the early stages of Alzheimer's disease [23*]. Together, these findings suggest a

Box 2 Intrinsic connectivity in the human brain does not reveal emotion networks

Using a seed-based analysis approach, we [15] designed a method for revealing intrinsic networks within the human brain, first demonstrating that this method can recover the brain's well-known 'default' mode network but does not produce spurious evidence of networks. First, we treated pre-defined nodes of the 'default' mode network as seeds (e.g., medial prefrontal cortex and posterior cingulate cortex, following [47**]). For each seed, we estimated a 'discovery map' that contained the voxels whose time-course correlated with the timecourse of voxels within the seed region. A conjunction of these 'discovery' maps recovered the 'default' mode network as single map of their spatial overlap. Using a similar 'seed and discover' method, we then ran a control analysis to show that nodes from auditory, visual, and motor cortices produce a conjunction map that is empty, indicating that our method would not produce spuriously results. Finally, we used our 'seed and discover' method on meta-analytic activation peaks that were consistently activated for anger as reported in [10*] because this meta-analysis was explicitly designed to reveal maximally distinct neural patterns for different emotion categories; the conjunction of all the 'discovery maps' was empty, indicating that a distributed, anatomically-inspired networks for anger does not exist within the intrinsic architecture of the human brain. We repeated this analysis, with the same result, for the peaks that consistently activated during sadness, fear, disgust, and happiness. Furthermore, a conjunction of the discovery maps derived from the largest meta-analytic peaks for each negative emotion (anger, disgust, fear, and sadness) reproduced the 'salience' network, indicating that this network is a common contributor to at least four unpleasant emotional states.



Note: The conjunction map ($N = 89$) for meta-analytic ally inspired anger, disgust, fear, and sadness discovery maps. Yellow indicates spatial overlap for all negative emotion maps. Light orange indicates spatial overlap for three of the four maps. Orange indicates spatial overlap for two of the maps. Red indicates no spatial overlap.

role for the amygdala in the processes supporting encoding and retrieval, even for material that is 'non-emotional' or is not explicitly potent affectively. Other research shows that the amygdala is important for processes supporting perception and attention [24]. Furthermore, the amygdala has also long been implicated in social cognition, both within humans (e.g., [25]) and in comparative studies of non-human primates [26]. Recent research has demonstrated that humans with larger amygdalae characterized by stronger intrinsic connectivity to other brain regions such as the ventromedial prefrontal cortex, superior temporal sulcus, and fusiform gyrus are able to form and maintain larger and more complex social networks, both in face-to-face [27**,28*] and online [29*]

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Figure 2

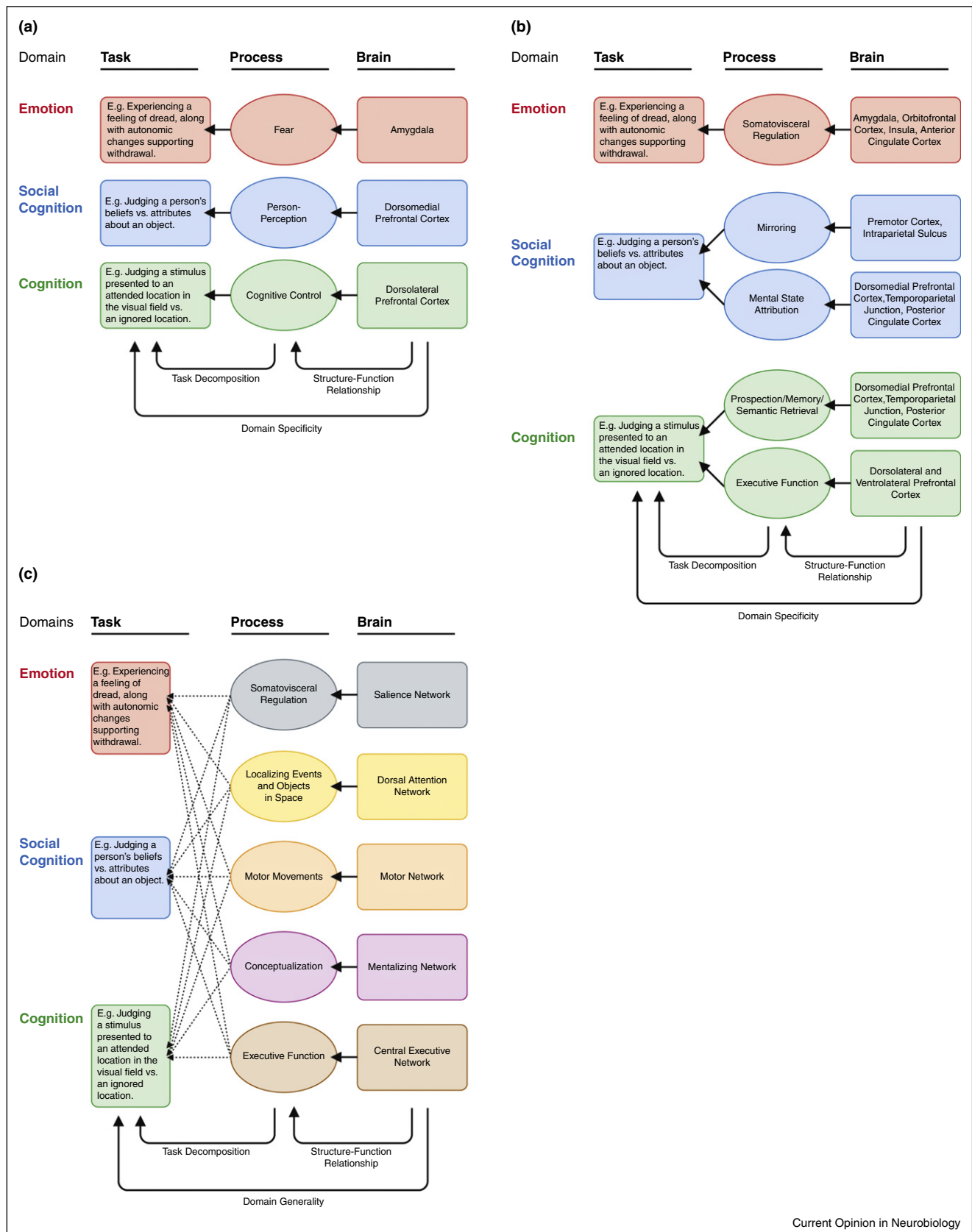


Table 1

Distributed structure–function mappings for selected intrinsic networks

Network	Major nodes	Functional description
'Salience'/'Ventral Attention' [16–18,92,93*]	Anterior cingulate cortex (ACC), bilateral anterior insula	Dorsal subnetwork: using representations of homeostatic and metabolic information from the body to guide attention and motor behavior Ventral subnetwork: representing homeostatic and metabolic information as affective feelings that are a basic feature of all conscious states
'Default'/'Mentalizing' [47**,50,92,93*]	Medial prefrontal cortex, retrosplenial area, posterior cingulate cortex/precuneus, medial temporal lobe (hippocampus, entorhinal cortex), bilateral superior temporal sulcus	Conceptualization by representing prior experiences (i.e., memory and category knowledge) to construct a mental model of the past, the present moment, or the future Dorsal subnetwork: an emphasis on abstract, third-person experience Ventral subnetwork: an emphasis on first-person, embodied experience
'Executive Control' [16,92,93*]	Bilateral dorsolateral prefrontal cortex, inferior parietal lobe, inferior parietal sulcus, precuneus, and middle cingulate cortex (mCC)	Increasing or decreasing the firing rate of neurons in accordance with current goals
'Dorsal Attention' [17,92,93*]	Bilateral frontal eye fields, dorsal posterior parietal cortex, fusiform gyrus, area MT+	Visuospatial attention
Limbic [93*]	Medial temporal lobe, anterior cingulate cortex, medial and lateral orbitofrontal cortex, amygdala, ventral striatum, periaqueductalgray	Regulation and representation of the body's core (i.e., visceromotor regulation and representation)

Note: In the interest of space, not all intrinsic networks are listed here. Other networks not listed include sensorimotor, motor, and visual networks [92,93*] and a language network [51]. The analysis identifying the 'limbic' network [93*] does not include subcortical structures that are known to be involved in visceromotor regulation based on their known anatomical connections, including the basal ganglia, which are involved in orchestrating effortful behavior and motor control, the central nucleus of the amygdala, which is involved in regulating autonomic responses, and the midbrain periaqueductal gray, which is involved in coordinating coherent physiological and behavioral responses. The 'mirroring' network is not listed here because it is a collection of regions that show task-related functional connectivity rather than a network that is intrinsic to the brain's architecture; it shares roughly half of its spatial topography with the 'dorsal attention' network (associated with sensory orienting) as well nodes within the motor network. It was defined initially by a class of 'mirror neurons' which respond both when the self performs an action (e.g. ripping a piece of paper, grasping a pair of scissors) and when perceiving another person perform the same action [[62*,63], but see [67]]. Some authors [63] also posit a 'limbic mirror system' that they believe is devoted to perceiving affective behavior, but the regions of this network largely overlap with the 'salience' network.

groupings. There is even some indication that increases in amygdala volume occur as the result of pressures associated with living in larger social groupings [30**].

More broadly, nodes within the 'salience' network are engaged during a variety of psychological domains, including during empathy (e.g., [31,32,33*]), language and executive function tasks [34], and during attention allocation [17]. These nodes are thought to play some role in the brain's 'switching' or 'reorienting' between 'internal' and 'external' events [17,35]. The spatial topography of the 'salience' network is highly similar to an 'aversion' network whose major hub is in the amygdala (see Figure 3

in [27**]). It is possible that the 'salience' network supports a variety of different psychological mechanisms (cf. [8**]). Such multiple functions make it all but impossible to infer the presence of a single process from a neural response in nodes of the network (called reverse inference; [36]). In addition, the lack of domain specificity in 'salience' network engagement suggests the possibility that brain imaging is too spatially and temporally coarse to permit meaningful functional interpretation.

Yet an intriguing possibility is that the anatomic connections within the nodes of the 'salience' network, along with their temporal dynamics, together perform a

The progression from a faculty psychology/modular approach towards a constructionist/distributed structure approach to brain-function inferences. In (a), individual brain regions specifically compute a domain-specific psychological faculty that could be isolated with a domain-specific behavioral task. In (b), domain-specific brain networks interact to produce responses within domain-specific tasks. (c) Functional motifs within domain-general intrinsic brain networks interact to produce a wide variety of tasks; dotted lines indicate that every network is not necessarily engaged to support every task response. Constellations of subprocesses likely underlie each higher order functional description (e.g. 'motor movements' can be broken down into layers of motor selection, involving lateral inhibition, etc.). We utilize the higher order process descriptions in this figure to highlight the point that even at a higher order of description, the processes comprising 'somatovisceral regulation' are domain-general processes that are not specific to emotion, the processes comprising 'mentalizing' are not specific to social cognition, and so on.

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domain-general function supporting a range of tasks crossing the boundaries of emotion, social cognition, and non-social cognition. For example, anatomical connections indicate that nodes within the ‘salience’ network are important for autonomic and hormonal regulation and representation [37,38[•],39–42], making it reasonable to hypothesize that in a given moment, the ‘salience’ network functions to orient the brain’s processing capacity towards the most homeostatically-relevant and metabolically-relevant information — it performs a body-based source of attention within the human brain. If a stimulus or event has homeostatic or metabolic implications (or the brain predicts these implications based on prior experience; [43[•]]), then the ‘salience’ network will be engaged, helping to allocate processing resources towards that stimulus.

The idea that the ‘salience’ network might be domain-general does not preclude the possibility that it contains spatial gradients or subnetworks that are relatively more engaged for certain types of tasks. For example, the dorsal subnetwork of the ‘salience’ network (most clearly involving connections between the dorsal anterior insula and dorsal ACC) seems to be especially important for spatial orientation and selecting motor actions (i.e., response selection) necessary for executing goal directed behavior (e.g., [44^{••}]); the ventral subnetwork (involving connections between ventral anterior insula and pregenual ACC extending to the subgenual ACC) appears to be important for directing selection in the ‘visceromotor’ (or autonomic nervous system) responses that support motor actions, maintain homeostasis, and serve as the basis of affective feelings. This hypothesis is consistent with our recent finding that the strength of intrinsic connectivity within the ventral ‘salience’ subnetwork is uniquely correlated with the intensity of affective experience, whereas connectivity within the more dorsal subsystem is uniquely correlated to motor control and changing mental sets [45^{••}].

Evidence from our meta-analyses on the brain basis of emotion more broadly supports a domain-general approach to distributed structure–function mappings. Some of the voxel clusters showing consistent increases in activation during anger, sadness, fear, disgust, and happiness appear within nodes of several of the brain’s intrinsic networks that are typically not considered to fall within the emotion domain (Table 1; also see [9^{••}]). For example, during emotional states, activity consistently increases within the ventromedial and dorsomedial prefrontal cortex and in the posterior cingulate cortex/precuneus regions — key nodes within the brain’s ‘mentalizing’ network [46], also referred to as the ‘default mode’ network [47^{••}]; this network routinely and robustly engaged when remembering personal events (autobiographical memory), when imagining the future (prospection), during moral cognition and reasoning, when accessing memory for word meanings (semantic memory), during scene construction and context-based object perception [47^{••},48,49[•],50] and during

instances of social affiliation (discussed in [27^{••}]). In addition, our emotion meta-analysis revealed consistent increases of activity in the lateral prefrontal cortex, which is a key node within ‘central executive’ and ‘language’ networks [16,17,51]. These nodes within the ‘mentalizing’, ‘executive’, and ‘language’ networks show a consistent increase in activation during a range of different emotions and more general affective states [9^{••},52^{••}]. A recent fMRI study from our lab found that several of these nodes produced consistent increases in activation during anger and fear experiences that occur when imagining a variety of social threat and physical danger scenarios [53], and show increased network cohesion when watching movies designed to evoke sadness [54]. Moreover, a recent neuroimaging study that directly compared patterns of network activity during emotions, thoughts, and bodily feelings confirmed that nodes within these networks are engaged across these different psychological domains [55].

Taken together, the search for the distinct brain correlates of different emotions, inspired by faculty psychology, has produced evidence of an entirely different functional architecture of the brain — one with broadly distributed functional networks that interact to produce a range of emotional states. In the next section, we discuss how these networks are not limited to constructing instances of anger, sadness, fear, disgust, and happiness.

Social neuroscience: person perception and the self

In the domain of social neuroscience, a key question concerns how one person’s mind creates the perception of another person as having intentions, beliefs, morals, traits, and so on. Much of this research has been guided by prominent social cognition theories developed in the 1980s and 1990s, referring to these abilities as ‘person perception’, ‘mind perception’, ‘ordinary personology’, or ‘mental state attribution’ [56–59]. Although early research in social neuroscience attempted to locate social cognitive processes in individual brain regions, such as the dorsomedial prefrontal cortex or the temporoparietal junction, the move towards a systems neuroscience approach quickly developed as dozens of studies showed that the neural correlates of person perception spanned regions that appeared to organize themselves into networks. Several meta-analyses [60[•],61[•]] indicate that studies of person perception consistently report increased activation in regions comprising the ‘mentalizing’ network mentioned above, and in a ‘mirroring’ network, (which shows an increase in activation when a person is detecting the goal-directed, voluntary movement of body parts, and includes the premotor cortex, superior temporal sulcus, and inferior parietal lobule; [62[•],63]) (see note in Table 1).

Currently, an overarching goal in social neuroscience has been to understand the distinct functional contributions of the ‘mentalizing’ and ‘mirroring’ networks during

instances of person perception. For example, studies suggest that the ‘mirroring’ network appears to be more associated with representing instrumental motor movements (e.g. facial movements and bodily gestures) while making inferences about their mental meaning, whereas the ‘mentalizing’ network is more strongly associated with representing context information that allows mental state inference to occur [64[•]]. The ‘mirroring’ network also appears to be relatively more engaged when physical movements are perceived as discrete behaviors (called ‘action identification’; e.g., someone shredding paper), whereas the ‘mentalizing’ network is relatively more engaged when making inferences about the goals of those actions (e.g., ‘destroying evidence’) [65[•],66^{••}]. This research has inspired hypotheses for how the two networks communicate and interact with each other. One hypothesis is that the networks act in parallel, at times cooperating and other times competing during person perception [64[•]]. Another hypothesis is that the two are hierarchically related, with the ability to form abstract mental state attributions being dependent on the ability to observe and represent actions in more concrete terms first [65[•],66^{••}]. Interestingly, observed actions appear to engage the ‘mirroring’ system after their meaning has been inferred (cf. [67]), perhaps within the neural context of an active ‘mentalizing’ network.

Network approaches to understanding person perception have, in a sense, revived domain-general insights in social perception from over fifty years ago. For example, a recent study of emotion perception [68^{••}] finds that perceiving physical actions as emotional expressions involves an interaction between nodes of both the ‘mirroring’ and ‘mentalizing’ networks, placing emotion perception within the more general domain of person perception (as originally suggested by [69]). This social perception framework has been recently extended to understand how people construct emotional experiences by making mental state inferences about bodily changes [11[•],70]. The hypothesis is that people are engaging in a form of mental state inference when they simultaneously categorize their (interoceptive) bodily sensations using conceptual knowledge about emotion.³ Taking this perspective, a recent study has shown that making mental state attributions about one’s own affective states (e.g. ‘I feel good’) indeed involves nodes within the ‘mentalizing’ network, the ‘executive control’ network, and the ‘salience’ network [71^{••}].

³ The broader hypothesis is that people use conceptual knowledge to categorize incoming sensory input from the body (interoceptive input) and from the world (exteroceptive input) to create a ‘situated conceptualization’ — a perception of these sensations as meaningfully referring to something in a particular context. A situated conceptualization is a conceptual act, producing perceptions of emotion in the self (e.g., a feeling of anger), perceptions of emotion in others (e.g., a smile as an anger expression), as well as a range of other cognitive and perceptual events.

A sense of personal identity (referred to as ‘the self’) is another topic of interest in social neuroscience [e.g. [72,73]]. Early theorizing in social cognition conceived of the self as resulting from a powerful, domain-general memory system [74], and foreshadowed recent meta-analytic discoveries that report consistent activation in the ‘mentalizing’ network when people create mental state inferences and trait judgments about the self (i.e. judging the self as an object, as when self-reflecting [60[•],61[•],75,76], also see [77,78]), including when processing one’s own name or seeing one’s own face (termed ‘self-specific activity’; [79]). Moreover, autobiographical memory (which routinely engages the ‘mentalizing’ network; [50,79]) has been discussed as a precondition for mental states that create a sense of self [80].

Just as with the ‘salience’ network, a variety of functions have been attributed to the ‘mentalizing’ network (see [47^{••},50]), but it is possible that the network is performing one basic function across social, affective, and cognitive domains. We hypothesize that the nodes of the mentalizing network interact to create an inferential, conceptual system [2[•]] that creates situated conceptualizations: these are the multimodal simulations that are strongly situated in a particular background context making meaning of sensory input and supporting specific courses of action [11[•],70,81]. Our hypothesis is that the ‘mentalizing’ network orchestrates the associative recombination of stored information (both abstract and embodied) to create not only instances of cognition but also instances of emotions and perceptions of people and events in the world. Such a proposal is consistent with the view that every waking moment of life is an instance of the ‘remembered present’ [82]. It is also consistent with the hypothesis that the ‘mentalizing’ network constructs mental models or simulations that facilitate future behavior [50]. Remembering, thinking about the future, taking another person’s perspective, as well as understanding the cause and consequences of your own bodily feelings all depend on the ability to draw on stored experiences to create a meaningful mental moment in the present. Sometimes, the present moment is created with minimal input from the senses (as in mindwandering or prospection); studies of internally-driven or endogenous mentation (i.e. mentation that is not sustained by a concrete task set forth by the experimenter) have robustly demonstrated the engagement of the ‘mentalizing’ network. At other times, the brain’s task is to make meaning of the current sensory array (to understand what sensations stand for in the world); brain imaging evidence indicates that this network is also engaged when the brain’s task is to create predictions about what sensory input refers to in the moment (e.g., during object perception, person perception, or emotion; e.g., [9^{••},48,83]).

By explicitly comparing ‘mentalizing’ network activations during judgments of self versus others [[61[•]], also see

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[73]], it is possible to hypothesize that a dorsal ‘mentalizing’ subnetwork is relatively more engaged in creating situated conceptualizations when abstract, ‘third-person’ information is required to make a judgment (such as knowledge about mental state categories, scene construction, etc.), whereas a more ventral ‘mentalizing’ subnetwork appears to be relatively more engaged when more embodied, ‘first-person’ information is required to make a judgment (e.g., bodily sensations or feelings related to homeostasis), referred to as the ‘dorsomedial’ and ‘medial temporal lobe’ subnetworks, respectively [47^{••}]. In support of this view, there is a spatial gradient within the medial prefrontal cortex (a key node of the ‘mentalizing’ network), with more ventral activations in evidence during self-related judgments, during autonomic and endocrine regulation, and during the processing of pain and rewarding stimuli, whereas more dorsal activations are relatively more in evidence during other-related judgments, as well as during occasions of memory and mind-wandering which often involve viewing and evaluating the self as an object [61[•],84]. Similarly, nodes within the dorsal subnetwork of the ‘mentalizing’ network are relatively more engaged when perceivers create abstract representations of other people (sometimes termed ‘meta-cognition’), whereas the more ventral nodes are relatively more engaged when people use their own internal state as a way of inferring what someone else is thinking or feeling (termed ‘self-projection’; [85]). Interestingly, we predict that during mental states that require first-person information, we might see more inter-network connectivity between the ventral ‘mentalizing’ subnetwork and the ‘salience’ network. Consistent with this hypothesis, two meta-analyses report increase in activation for several nodes within the ‘salience’ network, including the insula and the anterior cingulate cortex, particularly for self-related judgments [61[•],86[•]].

A constructionist functional architecture of the brain

Figure 2 summarizes the transition in human neuroscience research away from the search for domain-specific neural modules towards the discovery of large-scale, domain general networks that are distributed in both their structure and function. There are three take-away hypotheses from this figure. First, a psychological faculty, such as fear, or the ability to perceive the traits or mental states of another person (or other faculties we have not discussed here, such as working memory [87]), is not a *process* that can be probed in an unadulterated way by a single task; each faculty represents a category of phenomena — a collection of instances — that are constructed via the interaction of more basic, domain general processes, which themselves map to networks that emerge from neural integration across time and space within the brain. Second, the experimental tasks that are currently in use within affective, social, and cognitive neuroscience do not themselves reflect individual processes; the responses to

those tasks are constructed via the interaction of more basic, domain-general processes and their corresponding distributed networks. Third, scientific progress will be speeded not by trying to localize psychological faculties to topographical brain regions or even to individual networks, but instead by modeling responses to experimental tasks as high-dimensional brain states (reflecting the engagement of domain general networks, their internal operations, and their interactions).⁴

From this perspective, then, the distinction between social, affect, and cognitive neuroscience is artificial. There is no ‘affective’ brain, ‘social’ brain, or ‘cognitive’ brain. Each human has one brain whose functional properties can be understood differently for different time scales and levels of organization. At the level of human brain imaging, we are suggesting that the data point towards a single systems neuroscience framework that spans psychological domains. In such a framework, the brain contains a set of intrinsic networks that can be understood as performing domain-general operations; these operations serve as the functional architecture for how mental events and behaviors are constructed. We are not suggesting that all neurons within a network have exactly the same (general) receptive field, or that all neurons within a network fire every time the network is engaged. Instead, we are suggesting that, at the level of brain imaging, a neuron’s function can be understood in the context of neural responses within the network (i.e., the function is distributed across the assembly of neurons within the network that are active at a given point in time), and this function is domain-general. Each of these “core systems” in the brain does not produce one distributed pattern of response. Instead, instance by instance, the function of the core system corresponds to a set of ‘functional motifs’ arising from the ‘structural motif’ that undergirds each network (for a discussion of motifs, see [88]). A similar approach has recently been proposed for improving the characterization and treatment of psychopathology and neurodegenerative diseases [89[•]].

By shifting the empirical emphasis from the search for mental faculties as unified neurobiological categories towards developing a more componential, constructionist functional architecture of the human brain, the overlap in empirical findings across psychological domains is not a problem for reverse inference, but becomes the engine that drives a more valid approach to reverse inference. Debates about whether emotions are a special case of social cognition, or whether person-perceptions are a special case of memory recede to be replaced an approach that attempts to build a domain-general understanding of how the brain creates the mind.

⁴ An alternative approach would be to craft more elemental behavioral methods that target and isolate particular domain-general functions.

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- of special interest
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