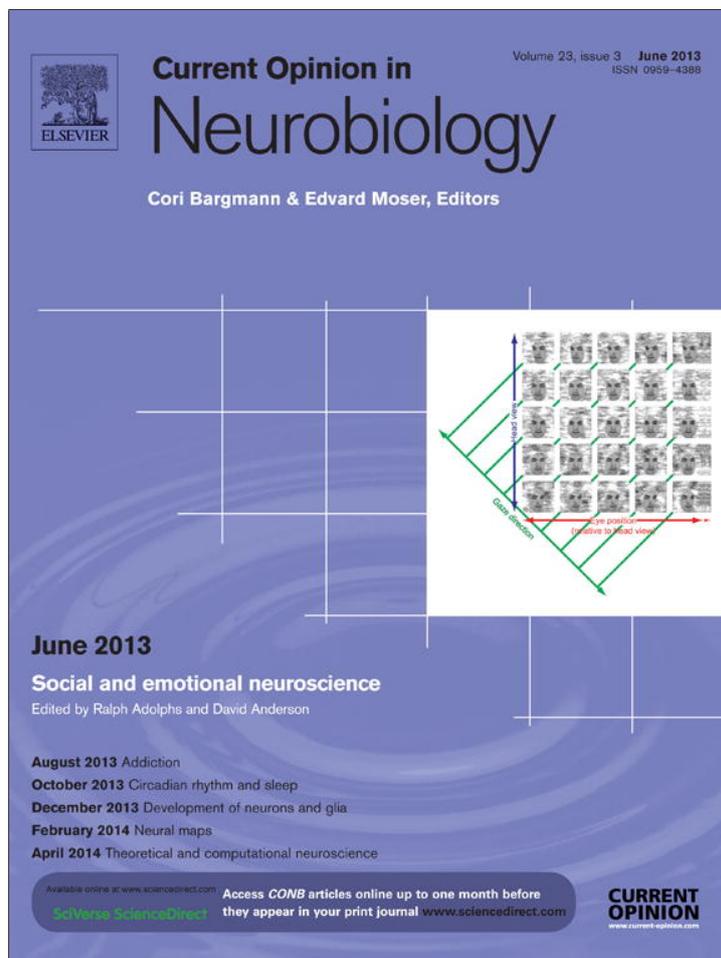


Provided for non-commercial research and education use.  
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/authorsrights>



ELSEVIER

Available online at [www.sciencedirect.com](http://www.sciencedirect.com)

SciVerse ScienceDirect

Current Opinion in

Neurobiology

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

Lisa Feldman Barrett<sup>1</sup> and Ajay Bhaskar Satpute<sup>2</sup>

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.

### Addresses

<sup>1</sup> Northeastern University, Massachusetts General Hospital/Harvard Medical School, United States

<sup>2</sup> Northeastern University, United States

Corresponding author: Barrett, Lisa Feldman ([l.barrett@neu.edu](mailto:l.barrett@neu.edu))

**Current Opinion in Neurobiology** 2013, **23**:361–372

This review comes from a themed issue on **Social and emotional neuroscience**

Edited by **Ralph Adolphs** and **David Anderson**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 23rd January 2013

0959-4388/\$ – see front matter, © 2013 Elsevier Ltd. All rights reserved.

<http://dx.doi.org/10.1016/j.conb.2012.12.012>

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<sup>•</sup>,3<sup>•</sup>,4,5<sup>••</sup>,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<sup>••</sup>,8<sup>••</sup>]), 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<sup>•</sup>,5<sup>••</sup>]). 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<sup>••</sup>,9<sup>••</sup>]). 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

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<sup>••</sup>,10<sup>•</sup>].<sup>1</sup> 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

<sup>1</sup> Vytal and Hamann [10<sup>•</sup>] 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.

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

Nonetheless, the belief that emotions can be localized somewhere in the brain is very strong (see [11<sup>•</sup>,12<sup>•</sup>] 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

<sup>2</sup> 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<sup>•</sup>,12<sup>•</sup>]).

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

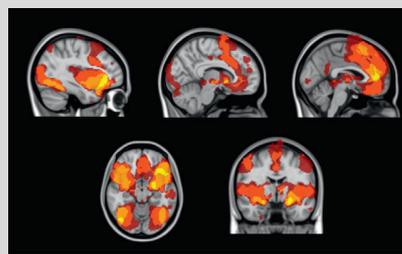
The human brain is organized into large-scale 'intrinsic' networks reflecting strong temporally-organized coupling of activity across widely distributed brain regions, taking up a large proportion of the brain's metabolic budget [90\*,91]. Intrinsic networks have been observed during mental states that 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**

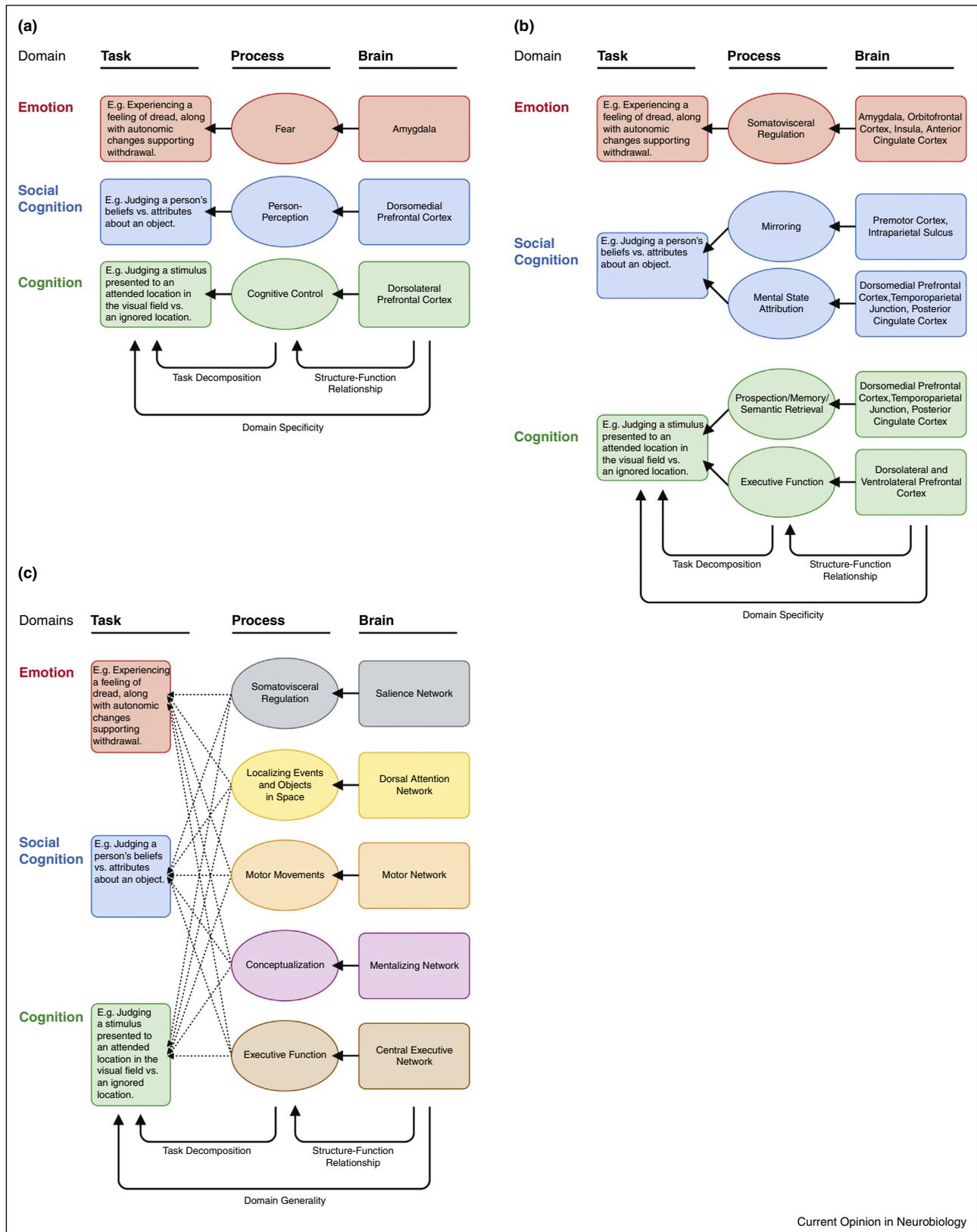
Using a seed-based analysis approach, we [15] designed a method for revealing intrinsic networks within the human brain, first demonstrating that this method can recover the brain's well-known 'default' mode network but does not produce spurious evidence of networks. First, we treated pre-defined nodes 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\*]

Figure 2



Current Opinion in Neurobiology

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 necessary 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.

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<sup>\*</sup>]. 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<sup>\*</sup>,66<sup>\*\*</sup>]. 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<sup>\*</sup>]. 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<sup>\*</sup>,66<sup>\*\*</sup>]. 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<sup>\*\*</sup>] 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<sup>\*</sup>,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.<sup>3</sup> 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<sup>\*\*</sup>].

<sup>3</sup> 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<sup>\*</sup>,61<sup>\*</sup>,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<sup>\*\*</sup>,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<sup>\*</sup>] 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<sup>\*</sup>,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<sup>\*\*</sup>,48,83]).

By explicitly comparing 'mentalizing' network activations during judgments of self versus others [[61<sup>\*</sup>], also see

[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<sup>••</sup>]. 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<sup>•</sup>,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<sup>•</sup>,86<sup>•</sup>].

### 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).<sup>4</sup>

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<sup>•</sup>].

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.

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

## Acknowledgments

We thank Paul Gade, Ian Kleckner, and Ralph Adolphs for their comments on an earlier version of this manuscript, and Tal Yakoni for his assistance with using NeuroSynth to construct Figure 1, Alexandra Touroutoglou for her assistance with constructing the figure accompanying Box 2, and Aaron Scott for his assistance in constructing Figures 1 and 2. Preparation of this manuscript was supported by a National Institute of Health Director's Pioneer Award (DPIOD003312) and by the U.S. Army Research Institute for the Behavioral and Social Sciences (contract W5J9CQ-11-C-0046) to Lisa Feldman Barrett. The views, opinions, and/or findings contained in this article are solely those of the author(s) and should not be construed as an official Department of the Army or DOD position, policy, or decision.

## References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
  - of outstanding interest
1. Fodor JA: *The Modularity of Mind: An Essay on Faculty Psychology*. Cambridge, MA: MIT Press; 1983.
  2. Barrett LF: **The future of psychology: connecting mind to brain**.
    - *Perspect Psychol Sci* 2009, **4**:326-339.
 Introduces the concept of a 'psychological primitive' and its relation to a systems neuroscience approach in studying mind:brain correspondence.
  3. Duncan S, Barrett LF: **Affect is a form of cognition: a neurobiological analysis**. *Cogn Emot* 2007, **21**:1184-1211.
 

Introduces the hypothesis that emotion and cognition are not categories that can be distinguished at the level of the brain and that affect, as one component of an emotion, is in fact a basic element of all conscious experiences regardless of whether they are considered cognitive, perceptual, or emotional.
  4. Fuster JM: **The module: crisis of a paradigm**. *Neuron* 2000, **26**:51-53.
  5. Lindquist KA, Barrett LF: **A functional architecture of the human brain: emerging insights from the science of emotion**. *Trends Cogn Sci* 2012, **16**:533-540.
 

Reviews recent research on the science of emotion to demonstrate the limitations of using folk psychology categories as a way of understanding brain function; discusses how the science of large-scale brain networks offers a powerful paradigm for creating a functional architecture of the brain.
  6. Pessoa L: **On the relationship between emotion and cognition**. *Nat Rev Neurosci* 2008, **9**:148-158.
  7. Uttal WR: *The New Phrenology: The Limits of Localizing Cognitive Processes in the Brain*. Cambridge, MA: The MIT press; 2001.
  8. Bressler SL, Menon V: **Large-scale brain networks in cognition: emerging methods and principles**. *Trends Cogn Sci* 2010, **14**:277-290.
 

Reviews current research on structural and functional contributions to large-scale brain networks that provide a framework for understanding cognition.
  9. Lindquist KA, Wager TD, Kober H, Bliss-Moreau E, Barrett LF: **The brain basis of emotion: a meta-analytic review**. *Behav Brain Sci* 2012, **35**:121-143.
 

Reports a quantitative meta-analytic summary of neuroimaging research on emotion spanning two decades, finding that both limbic and non-limbic regions show consistent but non-specific increases in activation during anger, sadness, fear, disgust and happiness; discusses an alternative 'constructionist' approach of interpreting these activations in terms of a framework of large-scale distributed networks.
  10. Vytal K, Hamann S: **Neuroimaging support for discrete neural correlates of basic emotions: a voxel-based meta-analysis**. *J Cogn Neurosci* 2010, **22**:2864-2885.
 

Reports a quantitative meta-analytic summary of neuroimaging research on emotion, finding that both limbic and non-limbic regions show consistent but non-specific increases in activation during anger, sadness, fear, disgust and happiness; findings are interpreted as evidence that emotions are biologically basic categories, despite the lack of specificity in the observed activations. Also see Hamann S: Mapping discrete and dimensional emotions onto the brain: controversies and consensus. *Trends Cogn Sci* 2012, **16**:458-466, which points towards the need for more complex, network-based representations of emotion.
  11. Barrett LF: **Emotions are real**. *Emotion* 2012, **12**:413-429.
    - Outlines a theoretical framework for guiding scientific investigations of how physical actions (such as freezing, or attack) and somatovisceral changes within the core of the body are experienced as emotions; identifies several neurobiological ingredients of an emotional response and discusses why the neural circuitry supporting physical actions does not, in and by itself, constitute evidence for the brain basis of emotion, but instead is one ingredient in constructing emotional states.
  12. LeDoux J: **Rethinking the emotional brain**. *Neuron* 2012, **73**:653-676.
 

Reviews research on the neurobiology of safety responses, and discusses how these responses are not, in and of themselves, not emotional responses. The implication is that aversive learning is not "fear" learning, and the circuitry that supports aversive learning and freezing behaviors is not "fear" circuitry. Presents a theoretical model of how safety behaviors are a basic ingredient in "fear", which is similar to Barrett LF: Emotions are real. *Emotion* 2012, **12**:413-429. Barrett LF: Solving the emotion paradox: categorization and the experience of emotion. *Pers Soc Psychol Rev* 2006, **10**:20-46.
  13. Murphy FC, Ewbank MP, Calder AJ: **Emotion and personality factors influence the neural response to emotional stimuli**. *Behav Brain Sci* 2012, **35**:156-157.
  14. Panksepp J: **The basic emotional circuits of mammalian brains: do animals have affective lives?** *Neurosci Biobehav Rev* 2011, **35**:1791-1804.
  15. Touroutoglou A, Lindquist K, Hollenbeck M, Dickerson B, Barrett LF: **Intrinsic connectivity networks related to basic emotions**. *Society for Neuroscience; New Orleans, LA: 2012*.
  16. Seeley WW, Menon V, Schatzberg AF, Keller J, Glover GH, Kenna H, Reiss AL, Greicius MD: **Dissociable intrinsic connectivity networks for salience processing and executive control**. *J Neurosci* 2007, **27**:2349-2356.
  17. Corbetta M, Patel G, Shulman GL: **The reorienting system of the human brain: from environment to theory of mind**. *Neuron* 2008, **58**:306-324.
  18. Eckert MA, Menon V, Walczak A, Ahlstrom J, Denslow S, Horwitz A, Dubno JR: **At the heart of the ventral attention system: the right anterior insula**. *Hum Brain Mapp* 2009, **30**:2530-2541.
  19. Wilson-Mendenhall C, Barrett LF, Barsalou LW: **Neural evidence that human emotions share core affective properties**. *Psychol Sci*, in press
 

Affective feelings of positivity versus negativity (valence) and activation versus quiescence (arousal) differentially correlate with BOLD activation in the medial orbitofrontal cortex and amygdala, respectively, regardless of whether participants were reliving pleasant or unpleasant happiness (e.g., remembering a birthday party versus remembering a painful event that is thankfully now over), pleasant or unpleasant fear (e.g., reliving a rollercoaster ride versus a walk down a dark alley), or pleasant or unpleasant sadness (e.g., nostalgia about an old lover versus losing a job).
  20. Moriguchi Y, Negreira A, Weierich M, Dautoff R, Dickerson BC, Wright CI, Barrett LF: **Differential hemodynamic response in affective circuitry with aging: an fMRI study of novelty, valence, and arousal**. *J Cogn Neurosci* 2011, **23**:1027-1041.
 

Reports on an fMRI study showing that stimulus novelty reliably engages the amygdala and other nodes within the salience network, and examines not only age-related differences in the shape of the hemodynamic response within the amygdala, but also differences in its functional connectivity.
  21. Weierich MR, Wright CI, Negreira A, Dickerson BC, Barrett LF: **Novelty as a dimension in the affective brain**. *Neuroimage* 2010, **49**:2871-2878.
 

Reports on an fMRI study demonstrating that anger experienced in social and physical threat situations differ in their neural correlates, as does fear experienced in these two contexts; a common set of activations was observed across all instances of emotion, however, in key nodes of the default and executive control networks.
  22. Wright CI, Negreira A, Gold AL, Britton JC, Williams D, Barrett LF: **Neural correlates of novelty and face-age effects in young and elderly adults**. *Neuroimage* 2008, **42**:956-968.

23. Poulin SP, Dautoff R, Morris JC, Barrett LF, Dickerson BC:  
 • **Amygdala atrophy is prominent in early Alzheimer's disease and relates to symptom severity.** *Psychiatry Res* 2011, **194**:7-13.  
 Compares the magnitude of amygdala atrophy to that of the hippocampus in two samples of people with mild Alzheimer's disease (versus age-matched controls) and finds that the magnitude of amygdala atrophy is comparable to that of the hippocampus.
24. Pessoa L: **Emotion and cognition and the amygdala: from "what is it?" to "what's to be done?"**. *Neuropsychologia* 2010, **49**:681-694.
25. Adolphs R: **The social brain: neural basis of social knowledge.** *Annu Rev Psychol* 2009, **60**:693-716.
26. Barton RA: **Primate brain evolution: integrating comparative, neurophysiological, and ethological data.** *Evol Anthropol* 2006, **15**:224-236.
27. Bickart KC, Hollenbeck MC, Barrett LF, Dickerson BC: **Intrinsic amygdala-cortical functional connectivity predicts social network size in humans.** *J Neurosci* 2012, **32**:14729-14741.  
 Reports evidence from resting-state fMRI that individual differences in the strength of the amygdala's intrinsic connectivity in two of three large-scale networks predict social network size over and above variations in amygdala volume.
28. Bickart KC, Wright CI, Dautoff RJ, Dickerson BC, Barrett LF:  
 • **Amygdala volume and social network size in humans.** *Nat Neurosci* 2011, **14**:163-164.  
 Reports evidence from structural MRI that individual differences in amygdala volume within humans, adjusting for intracranial volume, predict the size and complexity of social network size and complexity.
29. Kanai R, Bahrami B, Roylance R, Rees G: **Online social network size is reflected in human brain structure.** *Proc Biol Sci* 2012, **279**:1327-1334.  
 Reports the neural correlates of variation in online social network size.
30. Sallet J, Mars RB, Noonan MP, Andersson JL, O'Reilly JX, Jbabdi S, Coxson PL, Jenkinson M, Miller KL, Rushworth MF:  
 • **Social network size affects neural circuits in macaques.** *Science* 2011, **334**:697-700.  
 Reports a neuroimaging study of 23 monkeys who were assigned to living groups of different sizes (because they were involved in different experiments), and finds that living in larger groups produces changes in brain structure; fails to rule out the hypothesis that volumetric changes are attributable to the experimental tasks to which monkeys were exposed.
31. Decety J, Jackson PL: **The functional architecture of human empathy.** *Behav Cogn Neurosci Rev* 2004, **3**:71-100.
32. Singer T, Seymour B, O'Doherty J, Kaube H, Dolan RJ, Frith CD:  
 • **Empathy for pain involves the affective but not sensory components of pain.** *Science* 2004, **303**:1157-1162.
33. Fan Y, Duncan NW, de Greck M, Northoff G: **Is there a core neural network in empathy? An fMRI based quantitative meta-analysis.** *Neurosci Biobehav Rev* 2011, **35**:903-911.  
 Shows that empathy is not a unitary phenomenon, but instead involves multiple systems corresponding to different kinds of empathy. Proposes engagement of a core system that underlies diverse forms of empathy, and separate systems for empathy driven by cognitive-evaluative and affective-perceptual sources.
34. Nelson SM, Dosenbach NU, Cohen AL, Wheeler ME, Schlaggar BL, Petersen SE: **Role of the anterior insula in task-level control and focal attention.** *Brain Struct Funct* 2010, **214**:669-680.
35. Menon V, Uddin LQ: **Saliency, switching, attention and control: a network model of insula function.** *Brain Struct Funct* 2010, **214**:655-667.
36. Poldrack RA: **Inferring mental states from neuroimaging data: from reverse inference to large-scale decoding.** *Neuron* 2011, **72**:692-697.
37. Craig AD: **How do you feel? Interoception: the sense of the physiological condition of the body.** *Nat Rev Neurosci* 2002, **3**:655-666.
38. Craig AD: **How do you feel — now? The anterior insula and human awareness.** *Nat Rev Neurosci* 2009, **10**:59-70.  
 Reviews neurobiological evidence for functions of the anterior insula which builds on Craig's [37] review.
39. Mesulam MM, Mufson EJ: **Insula of the old world monkey. I. Architectonics in the insulo-orbito-temporal component of the paralimbic brain.** *J Comp Neurol* 1982, **212**:1-22.
40. Mesulam MM, Mufson EJ: **Insula of the old world monkey. III: Efferent cortical output and comments on function.** *J Comp Neurol* 1982, **212**:38-52.
41. Ongur D, Ferry AT, Price JL: **Architectonic subdivision of the human orbital and medial prefrontal cortex.** *J Comp Neurol* 2003, **460**:425-449.
42. Vogt BA: **Pain and emotion interactions in subregions of the cingulate gyrus.** *Nat Rev Neurosci* 2005, **6**:533-544.
43. Barrett LF, Bar M: **See it with feeling: affective predictions during object perception.** *Philos Trans R Soc Lond B: Biol Sci* 2009, **364**:1325-1334.  
 Summarizes neuroanatomical connections which support the hypothesis that affective feelings arising from autonomic and hormonal changes in the core of the body makes up part of the brain's prediction of what the visual sensations stand for in the present, including how to act on them in the near future.
44. Shackman AJ, Salomons TV, Slagter HA, Fox AS, Winter JJ, Davidson RJ: **The integration of negative affect, pain and cognitive control in the cingulate cortex.** *Nat Rev Neurosci* 2011, **12**:154-167.  
 Proposes a revised understanding of the role of the anterior cingulate cortex from being involved in 'cold' cognition to a hub for engaging in control across 'hot' domains too, including pain and negative affect.
45. Touroutoglou A, Hollenbeck M, Dickerson BC, Feldman Barrett L:  
 • **Dissociable large-scale networks anchored in the right anterior insula subserve affective experience and attention.** *Neuroimage* 2012, **60**:1947-1958.  
 Analyzes two samples of resting state fMRI data to show that the 'salience' network can be functionally dissociated into dorsal and ventral subnetworks, whose connectivity strength is correlated to individual differences in the ability to select motor responses and the intensity of affective experience, respectively.
46. Amodio DM, Frith CD: **Meeting of minds: the medial frontal cortex and social cognition.** *Nat Rev Neurosci* 2006, **7**:268-277.
47. Andrews-Hanna JR, Reidler JS, Sepulcre J, Poulin R, Buckner RL:  
 • **Functional-anatomic fractionation of the brain's default network.** *Neuron* 2010, **65**:550-562.  
 Uses a combination of connectivity-based and activation-based methods to show that the default network can be fractionated into two subnetworks, a dorsal medial prefrontal cortex subsystem and a medial temporal lobe subsystem.
48. Bar M: **The proactive brain: using analogies and associations to generate predictions.** *Trends Cogn Sci* 2007, **11**:280-289.
49. Schilbach L, Bzdok D, Timmermans B, Fox P, Laird AR, Vogeley K, Eickhoff SB: **Introspective minds: using ALE meta-analyses to study commonalities in the neural correlates of emotional processing, social, & unconstrained cognition.** *PLoS ONE* 2012, **7**.  
 Finds that regions in the default network are engaged in common by emotion processing, social, and unconstrained cognition. Supports the common involvement of the default network across diverse domains.
50. Buckner RL, Andrews-Hanna JR, Schacter DL: **The brain's default network: anatomy, function, and relevance to disease.** *Ann N Y Acad Sci* 2008, **1124**:1-38.
51. Tomasi D, Volkow ND: **Language network: segregation, laterality and connectivity.** *Mol Psychiatry* 2012, **17**:759.
52. Kober H, Barrett LF, Joseph J, Bliss-Moreau E, Lindquist K, Wager TD: **Functional grouping and cortical-subcortical interactions in emotion: a meta-analysis of neuroimaging studies.** *Neuroimage* 2008, **42**:998-1031.  
 Reports a quantitative meta-analysis of 162 neuroimaging studies of emotion and affect, focused on identifying brain regions that are consistently activated across all studies, as well as discovering their functional organization into consistent groupings, independent of semantically defined emotion categories; results describe six distributed functional groupings that resemble parts of intrinsic brain networks.
53. Wilson-Mendenhall CD, Barrett LF, Simmons WK, Barsalou LW: **Grounding emotion in situated conceptualization.** *Neuropsychologia* 2011, **49**:1105-1127.

54. Raz G, Winetraub Y, Jacob Y, Kinreich S, Maron-Katz A, Shaham G, Podlipsky I, Gilam G, Soreq E, Hendler T: **Portraying emotions at their unfolding: a multilayered approach for probing dynamics of neural networks.** *Neuroimage* 2012, **60**:1448-1461.
55. Oosterwijk S, Lindquist KA, Anderson E, Dautoff R, Moriguchi Y, Barrett LF: **States of mind: emotions, body feelings, and thoughts share distributed neural networks.** *Neuroimage* 2012, **62**:2110-2128.
56. Gilbert DT: **Ordinary personology.** In *The Handbook of Social Psychology*, vol 1 and 2. Edited by Fiske ST, Gardner L. McGraw-Hill; 1998:89-150.
57. Ross M, Fletcher GJO: **Attribution and social perception.** *The Handbook of Social Psychology*. 1985: 73-122.
58. Vallacher RR, Wegner DM: **What do people think they're doing? Action identification and human behavior.** *Psychol Rev* 1987, **94**:3-15.
59. Kozak MN, Marsh AA, Wegner DM: **What do I think you're doing? Action identification and mind attribution.** *J Pers Soc Psychol* 2006, **90**:543-555.
60. Van Overwalle F, Baetens K: **Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis.** *Neuroimage* 2009, **48**:564-584.  
A meta-analytic study showing that not only regions associated with mirroring but also the mentalizing network are often engaged while making inferences about actions but are rarely co-active. Suggests that these regions serve complementary roles in person perception.
61. Denny BT, Kober H, Wager TD, Ochsner KN: **A meta-analysis of functional neuroimaging studies of self- and other judgments reveals a spatial gradient for mentalizing in medial prefrontal cortex.** *J Cogn Neurosci* 2012, **24**:1742-1752.  
Meta-analysis showing that many regions in the 'mentalizing' network are not only engaged when making judgments about the self and about others, but also showed evidence for a gradient from ventromedial prefrontal cortex to dorsomedial prefrontal cortex that tracked with whether people are making judgments about the self or about others.
62. Iacoboni M: **Neurobiology of imitation.** *Curr Opin Neurobiol* 2009, **19**:661-665.  
Outlines the core regions associated with mirroring and proposes that this network developed as an extension from the motor system.
63. Cattaneo L, Rizzolatti G: **The mirror neuron system.** *Arch Neurol* 2009, **66**:557-560.
64. Zaki J, Hennigan K, Weber J, Ochsner KN: **Social cognitive conflict resolution: contributions of domain-general and domain-specific neural systems.** *J Neurosci* 2010, **30**:8481-8488.  
Finds that accurate identification of another person's affect state involves the coordinated activity of multiple networks, including regions involved in mirroring, the mentalizing network, and the executive function network.
65. Spunt RP, Satpute AB, Lieberman MD: **Identifying the what, why, and how of an observed action: an fMRI study of mentalizing and mechanizing during action observation.** *J Cogn Neurosci* 2011, **23**:63-74.  
Illustrates the engagement of both mirroring and mentalizing networks while observing others perform actions. Shows that the mentalizing network is modulated based on whether actions are described using intention-based words, but that regions associated with mirroring are not.
66. Spunt RP, Falk EB, Lieberman MD: **Dissociable neural systems support retrieval of how and why action knowledge.** *Psychol Sci* 2010, **21**:1593-1598.  
Illustrates that mentalizing and mirroring systems are both important for making inferences about other people's behaviors, but are differentially associated with different components of this ability. The mentalizing network is associated with focusing upon 'why' an action is being performed, and regions associated with mirroring are more active when focusing upon 'how' an action is being performed.
67. Lingnau A, Gesierich B, Caramazza A: **Asymmetric fMRI adaptation reveals no evidence for mirror neurons in humans.** *Proc Natl Acad Sci U S A* 2009, **106**:9925-9930.
68. Spunt RP, Lieberman MD: **An integrative model of the neural systems supporting the comprehension of observed emotional behavior.** *Neuroimage* 2012, **59**:3050-3059.  
Embeds emotion perception into a more general model of person perception.
69. Bruner JS, Tagiuri R: **The perception of people.** In *Handbook of Social Psychology*. Edited by Lindzey G. Cambridge, MA: Addison-Wesley; 1954:634-654.
70. Barrett LF: **Solving the emotion paradox: categorization and the experience of emotion.** *Pers Soc Psychol Rev* 2006, **10**:20-46.
71. Satpute AB, Shu J, Weber J, Roy M, Ochsner KN: **The functional neural architecture of self-reports of affective experience.** *Biol Psychiatry* 2012.  
Reports the involvement of functionally-distinct networks in constructing verbal judgments about affective states. Dissociates the functional contributions of sets of regions in fashioning self-reports.
72. Lieberman MD, Jarcho JM, Satpute AB: **Evidence-based and intuition-based self-knowledge: an fMRI study.** *J Pers Soc Psychol* 2004, **87**:421-435.
73. Mitchell JP, Macrae CN, Banaji MR: **Dissociable medial prefrontal contributions to judgments of similar and dissimilar others.** *Neuron* 2006, **50**:655-663.
74. Greenwald AG, Banaji MR: **The self as a memory system: powerful, but ordinary.** *J Pers Soc Psychol* 1989, **57**:41.
75. Van Overwalle F: **Social cognition and the brain: a meta-analysis.** *Hum Brain Mapp* 2009, **30**:829-858.
76. Northoff G, Heinzel A, de Greck M, Bermpohl F, Döbrowolny H, Panksepp J: **Self-referential processing in our brain — a meta-analysis of imaging studies on the self.** *Neuroimage* 2006, **31**:440-457.
77. Legrand D, Ruby P: **What is self-specific? Theoretical investigation and critical review of neuroimaging results.** *Psychol Rev* 2009, **116**:252-282.
78. Uddin LQ, Iacoboni M, Lange C, Keenan JP: **The self and social cognition: the role of cortical midline structures and mirror neurons.** *Trends Cogn Sci* 2007, **11**:153-157.
79. Qin P, Northoff G: **How is our self related to midline regions and the default-mode network?** *Neuroimage* 2011, **57**:1221-1233.
80. Prebble SC, Addis DR, Tippett LJ: **Autobiographical memory and sense of self.** *Psychol Bull*, in press
81. Barrett LF: **Variety is the spice of life: a psychological construction approach to understanding variability in emotion.** *Cogn Emot* 2009, **23**:1284-1306.
82. Edelman G: *The Remembered Present: A Biological Theory of Consciousness.* New York: Basic; 1989.
83. Greicius MD, Menon V: **Default mode activity during a passive sensory task: uncoupled from deactivation but impacting activation.** *J Cogn Neurosci* 2004, **16**:1484-1492.
84. Roy M, Shohamy D, Wager TD: **Ventromedial prefrontal-subcortical systems and the generation of affective meaning.** *Trends Cogn Sci* 2012, **16**:147-156.
85. Waytz A, Mitchell JP: **Two mechanisms for simulating other minds: dissociation between mirroring and self projection.** *Curr Direct Psychol Sci* 2011, **20**:197-200.
86. Qin P, Liu Y, Shi J, Wang Y, Duncan N, Gong Q, Weng X, Northoff G: **Dissociation between anterior and posterior cortical regions during self-specificity and familiarity: a combined fMRI-meta-analytic study.** *Hum Brain Mapp* 2012, **33**:154-164.  
Uses meta-analytic data and results from two focused experimental studies to dissociate neural processes correlated with self-related processing from those associated with familiarity-related processing.
87. Fuster JM, Bressler SL: **Cognit activation: a mechanism enabling temporal integration in working memory.** *Trends Cogn Sci* 2012, **16**:207-218.
88. Sporns O, Kötter R: **Motifs in brain networks.** *PLoS Biol* 2004, **2**:e369.
89. Menon V: **Large-scale brain networks and psychopathology: a unifying triple network model.** *Trends Cogn Sci* 2011, **15**:483-506.

Reviews evidence that large-scale brain networks offer a powerful paradigm for investigating dysfunctions in psychiatric and neurological disorders.

90. Raichle ME: **Two views of brain function.** *Trends Cogn Sci* 2010, **14**:180-190.  
Integrates evidence not only from cognitive and systems neuroscience but also from cellular and molecular neuroscience in support of the hypothesis that brain function can be largely understood in terms of intrinsic networks for interpreting, responding to, and predicting environmental demands.
91. Raichle ME, Mintun MA: **Brain work and brain imaging.** *Annu Rev Neurosci* 2006, **29**:449-476.
92. Smith SM, Fox PT, Miller KL, Glahn DC, Fox PM, Mackay CE, Filippini N, Watkins KE, Toro R, Laird AR *et al.*: **Correspondence of the brain's functional architecture during activation and rest.** *Proc Natl Acad Sci U S A* 2009, **106**:13040-13045.
93. Yeo BT, Krienen FM, Sepulcre J, Sabuncu MR, Lashkari D, Hollinshead M, Roffman JL, Smoller JW, Zollei L, Polimeni JR *et al.*: **The organization of the human cerebral cortex estimated by intrinsic functional connectivity.** *J Neurophysiol* 2011, **106**:1125-1165.  
Reports a clustering analysis of resting state fMRI data from 1000 participants to reveal functional connectivity networks that are intrinsic to the human brain.
94. Greicius MD, Kiviniemi V, Tervonen O, Vainionpaa V, Alahuhta S, Reiss AL, Menon V: **Persistent default-mode network connectivity during light sedation.** *Hum Brain Mapp* 2008, **29**:839-847.
95. Horowitz SG, Braun AR, Carr WS, Picchioni D, Balkin TJ, Fukunaga M, Dwyer JH: **Decoupling of the brain's default mode network during deep sleep.** *Proc Natl Acad Sci U S A* 2009, **106**:11376-11381.
96. Vanhaudenhuyse A, Noirhomme Q, Tshibanda LJ, Bruno MA, Boveroux P, Schnakers C, Soddu A, Perlberg V, Ledoux D, Brichant JF *et al.*: **Default network connectivity reflects the level of consciousness in non-communicative brain-damaged patients.** *Brain* 2010, **133**:161-171.
97. Greicius MD, Supekar K, Menon V, Dougherty RF: **Resting-state functional connectivity reflects structural connectivity in the default mode network.** *Cereb Cortex* 2009, **19**:72-78.
98. Deco G, Jirsa VK, McIntosh AR: **Emerging concepts for the dynamical organization of resting-state activity in the brain.** *Nat Rev Neurosci* 2011, **12**:43-56.  
Presents modeling evidence that intrinsic networks closely relate to anatomical connectivity but cannot be understood exclusively in anatomical terms.
99. Hagmann P, Cammoun L, Gigandet X, Meuli R, Honey CJ, Wedeen VJ, Sporns O: **Mapping the structural core of human cerebral cortex.** *PLoS Biol* 2008, **6**:e159.
100. van den Heuvel MP, Mandl RC, Kahn RS, Hulshoff Pol HE: **Functionally linked resting-state networks reflect the underlying structural connectivity architecture of the human brain.** *Hum Brain Mapp* 2009, **30**:3127-3141.
101. Cabral J, Hugues E, Sporns O, Deco G: **Role of local network oscillations in resting-state functional connectivity.** *Neuroimage* 2011, **57**:130-139.
102. Kojima T, Onoe H, Hikosaka K, Tsutsui K, Tsukada H, Watanabe M: **Default mode of brain activity demonstrated by positron emission tomography imaging in awake monkeys: higher rest-related than working memory-related activity in medial cortical areas.** *J Neurosci* 2009, **29**:14463-14471.
103. Margulies DS, Vincent JL, Kelly C, Lohmann G, Uddin LQ, Biswal BB, Villringer A, Castellanos FX, Milham MP, Petrides M: **Precuneus shares intrinsic functional architecture in humans and monkeys.** *Proc Natl Acad Sci U S A* 2009, **106**:20069-20074.
104. Rilling JK, Barks SK, Parr LA, Preuss TM, Faber TL, Pagnoni G, Bremner JD, Votaw JR: **A comparison of resting-state brain activity in humans and chimpanzees.** *Proc Natl Acad Sci U S A* 2007, **104**:17146-17151.
105. Vincent JL, Patel GH, Fox MD, Snyder AZ, Baker JT, Van Essen DC, Zempel JM, Snyder LH, Corbetta M, Raichle ME: **Intrinsic functional architecture in the anaesthetized monkey brain.** *Nature* 2007, **447**:83-86.
106. Hayes DJ, Northoff G: **Identifying a network of brain regions involved in aversion-related processing: a cross-species translational investigation.** *Front Integr Neurosci* 2011, **5**:49.  
Proposes a cross-species network of regions that are consistently associated during aversive states.
107. Yarkoni T, Poldrack RA, Nichols TE, Van Essen DC, Wager TD: **Large-scale automated synthesis of human functional neuroimaging data.** *Nat Methods* 2011, **8**:665-670.