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The neuroscience of construction: What neuroimaging approaches can tell us about how the brain creates the mind

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One of the most defining characteristics of mental life is that it changes from moment to moment. One can ponder the groceries needed for dinner and in the next moment feel angry because an important ingredient is sold out, or vividly remember the last time the same recipe was prepared. These mental events are experienced with different subjective qualities. Anger is experienced differently than thinking about a grocery list, and emotions and thoughts are experienced differently than remembering a previous moment in time. This subjective quality of emotions and other mental states is one of the central phenomena that psychological science seeks to measure and explain (Barrett, 2012).

For many years, psychologists took a "faculty psychology approach" (cf. Lindquist & Barrett, 2012; Uttal, 2001; Barrett, Wilson-Mendenhall, & Barsalou, Chapter 4, this volume) to the mind, assuming that the subjective quality of different mental states gives evidence of separate and distinct psychological processes, such as emotion, cognition, memory, and perception. In modern neuroscience, scientists have tried to map these faculties to specific locations in the brain (e.g., Barrett, 2009; Lindquist & Barrett, 2012). For example, neuroscientists have sought the neural modules of mental constructs, such as "fear" (e.g., Whalen et al., 1998), "theory of mind" (Saxe & Kanwisher, 2003), "episodic memory" (Rugg, Otten, & Henson, 2002), and "face perception" (e.g., Kanwisher, McDermott, & Chun, 1997). Faculty psychology beliefs are specifically striking in the field of emotion. Descartes (1985) believed that emotions emerge from the pineal gland, a small gland in the middle of the brain. Cannon (1927) argued that the thalamus is the neural center for emotion. Later, Papez (1937/1995) and MacLean (1952) argued that emotions emerge from the limbic system, a set of phylogentically "old" subcortical and allocortical structures. In recent years, scientists have carried faculty psychology forward, particularly in the domain of neuroimaging, in which they sought evidence

for emotion modules in the brain, not only for fear, (Sprengelmeyer et al., 1999; Whalen et al., 1998) but also disgust (the insula; Wicker et al., 2003). Twenty years of neuroimaging research has revealed, however, that the brain does not respect common-sense emotion categories, or any faculty psychology categories for that matter (Barrett, 2009; Barrett & Satpute, 2013; Duncan & Barrett, 2007; Gonsalves & Cohen, 2010; Lindquist & Barrett, 2012; Lindquist, Wager, Kober, Bliss, & Barrett, 2012; Pessoa, 2008; Poldrack, 2010; Uttal, 2001). In this chapter, we discuss how neuroscience data, and in particular, neuroimaging data, are beginning to yield evidence for a constructionist approach to emotion, and more broadly, to mind–brain correspondence. We begin our chapter by elaborating on specific constructionist hypotheses for mind–brain correspondence. Then we discuss how these hypotheses are supported by meta-analyses of the neuroimaging literature, by studies revealing the brain's intrinsic functional networks, and by individual neuroimaging studies that explicitly have tested constructionist hypotheses. We close with a discussion of how these findings might shape the way scientists understand how the brain creates the mind.

Constructionist Hypotheses for Mind–Brain Correspondence

Unlike a faculty psychology approach, constructionist models of the mind propose that emotions, thoughts, memories, and perceptions are mental states constructed out of more basic, domain-general psychological processes. This framework moves away from an attempt to localize mental events to specific areas or networks and instead aims to understand mental events by focusing on the interaction of large-scale distributed brain networks that support basic psychological processes (Barrett, 2009, 2011; Barrett & Satpute, 2013; Lindquist & Barrett, 2012; for a similar view, see Fox & Friston, 2012; Fuster, 2006; Mesulam, 1998). According to our constructionist view of the mind, the brain can be described as engaging in three domains of basic mental

processes at any given point in time: (1) representing basic sensory information from the world; (2) representing basic interoceptive sensations from the body; and (3) making meaning of internal and external sensations by activating stored representations of prior experience. We refer to these three processes as *core affect, exteroception,* and *conceptualization,* respectively. (For further discussions of core affect in this volume, see Barrett et al., Chapter 4; Russell, Chapter 8; Kleckner & Quigley, Chapter 12; and Ortony & Clore, Chapter 13. For discussions of conceptualization and acts of meaning in this volume, see Barrett et al., Chapter 4; Cunningham, Dunfield, & Stillman, Chapter 7; and Ortony & Clore, Chapter 13.)

We hypothesize that these basic processes combine in different patterns to generate specific mental content—for instance, when people experience a specific emotion, think about their plans for the day, remember an event, focus on a sensation, ruminate on someone's intentions, or attend to their bodily state. A person experiences a different mental state depending on the relative weight given to these processes in any given instance, and on which source of information is being represented in conscious awareness. As a result, executive control is another important basic psychological process that shapes mental experiences, because it helps to determine which information is prioritized and which is inhibited for representation in conscious experience. The result is that a mental state is experienced as unified (for a discussion see Barrett, Tugade, & Engel, 2004; Lindquist et al., 2012).

According to our constructionist model, whichever source of information is at the forefront of attention in a given moment is made meaningful by using the two other sources of information (Barrett, 2009). For instance, when a shift in core affect is at the forefront of attention and made meaningful using exteroceptive sensations and conceptualization, a person is said to be experiencing an emotion (e.g., fear or anger). When exteroceptive sensations are at the

forefront of attention and made meaningful using core affect and conceptualization, a person is said to be experiencing a perception. Finally, when representations of prior experiences are at the forefront of attention and comprise representations of exteroceptive sensations and core affect, a person is said to be having a memory about past core affective and exteroceptive sensations, or a thought about future core affective and exteroceptive sensations. All three sources of information are present all the time; it is the relative weight given to the processes depending on contextual and situational factors that gives rise to unique subjective experiences.

Brain-Based Hypotheses of Constructionism

According to our constructionist view, we hypothesize that each of these basic "domains of processing" maps on to a distributed network (or networks) in the brain. We focus on broadscale, distributed networks, since growing evidence indicates that brain regions do not act in isolation; rather, the psychological function of a set of brain regions exists as the interaction of those regions (see McIntosh, 2000, 2004). Table 5.1 lists seven networks identified within the brain's intrinsic architecture (Yeo et al., 2011; see also Seeley et al., 2007; Vincent, Kahn, Snyder, Raichle, & Buckner, 2008; Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Corbetta & Shulman, 2002; Fox & Raichle, 2007) that are likely candidates to support the basic building blocks of the mind. We hypothesize that emotions (and all mental states, for that matter) are constructed from the moment-to-moment interaction of these networks (cf. Barrett, 2009; Lindquist et al., 2012; Oosterwijk et al., 2012; for similar views, see Fuster, 2006; Goldman-Rakic, 1988; McIntosh, 2000; Mesulam, 1998; also see Bullmore & Sporns, 2009).

We hypothesize that one basic domain, core affect (experienced as feelings of pleasure or displeasure with some degree of arousal), is produced via a network of "limbic" tissue that is involved in visceromotor control, as well as representing visceromotor information within the

brain. This *limbic network,* which includes the basal ganglia, periaqueductal gray, central nucleus of the amygdala, and ventromedial prefrontal cortex, supports the brain's ability to generate and/or represent the somatovisceral changes that are experienced as the core affective tone that is common to every mental state (for a discussion, see Barrett, Mesquita, Ochsner, & Gross, 2007; Lindquist & Barrett, 2012; Oosterwijk et al., 2012). We hypothesize that this core affective function is further supported by the *salience network,* which comprises regions involved in interoception (Critchley, Elliott, Mathias, & Dolan, 2000; Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004) and shifts of attention resulting from body-based signals (Corbetta, Kincade, & Shulman, 2002; Eckert et al., 2009), including the anterior insular cortex, anterior midcingulate cortex (aMCC), and the temporoparietal junction (TPJ). In particular, we hypothesize that the salience network performs the psychological function of directing attention and behavior using core affective information from the body. By contrast, networks that comprise modal sensory brain areas, their respective association cortices, and the thalamus support the brain's ability to represent exteroceptive sensations occurring outside the body (see the somatomotor and visual network in Table 5.1).

Key to our constructionist approach is the idea that both core affective and exteroceptive sensations are made meaningful in a given context when representations of prior experiences are brought online. We hypothesize that this conceptualization function is supported by the *default network",* which comprises the medial prefrontal cortex (mPFC), medial temporal lobe, posterior cingulate cortex, ventrolateral prefrontal cortex (vlPFC; pars triangularis) and lateral temporal lobe (superior temporal gyrus extending into the anterior temporal lobe). In particular, we hypothesize that this network is involved in integrating activations in sensorimotor regions that support concept knowledge and memories (Barsalou, 2009) into rich, embodied representations

that are specifically tied to the situation at hand. Midline posterior aspects of the default network

(e.g., posterior cingulate, precuneus, hippocampus) may be involved particularly in the

integration of visuospatial aspects of concept knowledge (Cavanna & Trimble, 2006); midline

anterior aspects of the default network (e.g., mPFC) may be involved in integration of the

affective, social, and self-relevant aspects of concept knowledge (Gusnard, Akbudak, Shulman,

& Raichle, 2001); and lateral prefrontal and temporal regions may be involved in amodal aspects

of concept representation (e.g., as in language; Smith et al., 2012).

Finally, we hypothesize that a *frontoparietal network* that comprises the dorsolateral

prefrontal cortex (dlPFC), inferior parietal lobe, inferior parietal sulcus, and aspects of the

middle cingulate cortex (mCC), supports executive function by modulating activity in other

functional networks to help construct an instance of a mental state. The *dorsal attention network,*

which comprises the frontal eye fields, dorsal posterior parietal cortex, fusiform gyrus, and visual

area MT+ appears to play a similar role by directing attention to visual exteroceptive sensations

in particular. Together, these networks contribute to the executive control processes involved in

foregrounding certain types of information in conscious awareness.

The hypothesized networks we have just outlined (or some variation on them) provide a fruitful

avenue to understand how the brain creates emotions and other subjective mental states. In the

next sections we will discuss neuroscientific findings that demonstrate that these networks

appear across meta-analyses of neuroimaging studies on emotion, as intrinsic functional

networks in the brain, and within individual functional neuroimaging studies.

Meta-Analyses of Emotion Give Evidence That Favors Constructionism, Not Faculty Psychology

One avenue for testing constructionist hypotheses about the brain basis of emotion is the meta-

analysis. Meta-analytic summaries are useful tools for understanding mind–brain

correspondence, because they can identify the brain regions that are consistently and specifically activated across many studies of a mental phenomenon. Therefore, meta-analyses weigh in on whether mental states are best conceived of as emergent events that map onto functional assemblies of brain networks that support more basic psychological processes, or as faculties that map onto specific locations or networks. In theory, this information might be gleaned from single neuroimaging studies, but there are several reasons why the meta-analytic whole is greater than the sum of its parts. First, meta-analyses can weed out false positives (which occur frequently in neuroimaging studies; see Wager, Lindquist, & Kaplan, 2007; Yarkoni, 2009); thus, interpretation focuses on activations that are *consistently* observed across a number of studies. Second, meta-analyses can provide a picture of whether the consistent activation observed across studies is general to a number of mental states or *specific* to a single mental state. Individual studies rarely, if ever, do so, because most studies do not have enough comparison conditions to allow a proper test of the specificity hypothesis. Thus, meta-analyses can compare activity that occurs consistently for two mental states within the same superordinate category (e.g., fear vs. anger within the domain of emotion) or even two mental states that are thought to be members of different superordinate categories (e.g., fear from the superordinate category of emotion vs. memory from the superordinate category of cognition). Finally, meta-analyses allow the comparison of data across methods. For instance, as we describe in the next section, the findings from a meta-analysis of task-related neuroimaging studies (in which brain activity correlates with a mental task) can be compared to the intrinsic brain networks that are derived from analyses of task-independent brain activity (when participants lie at rest in the scanner).

Recent meta-analyses of the neuroimaging literature on emotion (Kober et al., 2008; Lindquist et al., 2012; Vytal & Hamann, 2010) provide evidence that favors a constructionist

view of the mind and calls into question the faculty psychology views that have dominated the

emotion literature to date. First and foremost, meta-analyses of the emotion literature reveal that

many of the brain regions that have a consistent increase in activity across studies of emotion are

the same regions that have been associated with other mental states, such as memory

(hippocampus, entorhinal cortex, medial prefrontal cortex), perception (primary and associative

visual cortex, auditory cortex), attention (dlPFC) and language (vlPFC, anterior temporal lobe).

These brain regions together form the "neural reference space for discrete emotion" (Lindquist et

al., 2012, p. 126 ; for a visual depiction, see their Fig. 4), which is the set of brain regions that

shows a consistent increase across all studies of emotion experience and perception.[1] These

findings echo recent observations that the brain basis of "emotion" versus "cognition" is not as

distinct as was once assumed (Barrett & Satpute, 2013; Barrett & Bar, 2009; Duncan & Barrett,

2007; Pessoa, 2008). Indeed, meta-analyses of different types of mental content (e.g., semantic

judgments: Binder, Desai, Graves, & Conant, 2009; autobiographical memory, prospection about

the future, theory of mind: Spreng, Mar, & Kim, 2009) produce a surprisingly similar neural

reference space, suggesting that the same mental "ingredients" may contribute to a number of

different types of mental states.

　　　　Another important finding from meta-analyses of the neuroimaging literature on emotion

is that instances of an emotion category (e.g., *fear*) are not *consistently* and *specifically*

associated with increased activity in a particular brain region (or a set of regions within an

anatomically inspired network), consistent with a constructionist account and contrary to faculty

psychology approaches. *Consistency* refers to the fact that a brain region shows increased

activity for every instance of an emotion category (e.g., the amygdala shows increased activity

each time a person experiences an instance of the category *fear*). *Specificity* refers to the fact that

a given brain region is active for instances of one (and only one) emotion category (e.g., the

amygdala does not show increased activity when a person is experiencing an instance of *anger*,

disgust, *happiness,* or *sadness*). Rather than exhibiting consistency and specificity for a given

emotion category, the same brain region(s) are involved in realizing instances of several emotion

categories.[2] For instance, in our most recent meta-analysis (Lindquist et al., 2012), we found that

the amygdala, which has been associated with fear (e.g., Whalen et al., 1998; also see Ohman &

Mineka, 2000), had increased activity in not only the perception of fear but also every other type

of emotion experience and perception (Lindquist et al., 2012). The insula, which has been

associated with disgust (e.g., Wicker et al., 2003; also see Calder, 2003), had increased activity

in not only the perception of disgust but also most other types of emotion experiences and

perceptions. The anterior cingulate cortex (ACC), which has been associated with sadness (e.g.,

Murphy, Nimmo-Smith, & Lawrence, 2003), had increased activity in not only sadness but also

several other types of emotion experiences and perceptions. This lack of specificity would have

been difficult to observe in single neuroimaging studies alone, since no existing neuroimaging

studies assess both the experience and perception of five different emotion categories.

  Finally, and most important to a constructionist view, our meta-analytic findings revealed

evidence of brain networks associated with domain-general, basic psychological functions in our

constructionist account. For instance, the general activity that we observed in the basal ganglia,

periaqueductal gray, ventromedial prefrontal cortex, amygdala, ACC, insula, and TPJ across

different instances of emotion is consistent with the limbic and the salience network that, we

hypothesize, support the psychological ingredient of "core affect." We also observed consistent

increases in the medial prefrontal cortex, hippocampus and medial temporal lobe, lateral

temporal lobe (superior temporal gyrus into the anterior temporal lobe), TPJ (angular gyrus) and

vlPFC (pars triangularis) that comprise the default network linked to our basic ingredient of conceptualization. Finally, we observed consistent activation in areas of visual, auditory, and somatosensory cortex linked to exteroception (somatomotor network), and areas of dorsolateral and vlPFC linked to executive control.

Consistent with the constructionist view that these domain-general networks act as functional networks that together create instances of emotion, a very similar set of networks is observed when the meta-analytic data are analyzed in an inductive, theory-free manner assessing how brain regions functionally cluster together across studies (Kober et al., 2008). A series of cluster analyses and multidimensional scalings reveal functional clusters of voxels that are consistently coactivated across studies of emotion experience and perception, and provide convergent evidence for the basic psychological "ingredients" proposed by our constructionist account (for a visual depiction, see Kober et al., 2008, Fig. 7). For instance, we found a functional cluster of brain regions that comprised the amygdala, hypothalamus, ventral striatum, and periacqueductal gray, and contained aspects of the limbic network that we hypothesize is generating bodily states across studies of emotion experience and perception. A paralimbic group that comprises the anterior and midinsula, putamen, and posterior orbitofrontal cortex (OFC) contains aspects of the salience network thought to represent core affective states and to use them to guide behavior and attention. Groups in medial prefrontal cortex and medial posterior cortex together resemble the default network that we hypothesize is performing a conceptualization function. A visual group that comprises primary and secondary visual cortex is consistent with the visual network that supports exteroception in the visual modality. Finally, a group in the lateral prefrontal cortex resembles the frontoparietal network that we hypothesize is performing an attentional function. Such findings are not unique to meta-analyses of emotion;

other meta-analyses show similar brain networks involved across diverse types of psychological

tasks (Binder et al., 2009; Smith et al., 2009; Spreng et al., 2009; Lenartowicz, Kalar, Congdon,

& Poldrack, 2010; Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011).

Of course, it remains a possibility that the domain-general networks we observed in our

meta-analyses reflect the limitations of task-related neuroimaging in which participants are asked

to engage in a psychological task in the scanner that involves other psychological processes

(executive attention, concepts, etc.). But there are two reasons why this interpretation is unlikely.

First, even data from single-cell recordings, electrical stimulation, and lesion studies provide

evidence consistent with the constructionist view that brain regions are part of networks that

support more general psychological functions (for a discussion, see Lindquist et al., 2012). For

instance, cells in rhesus monkey auditory cortex show increased activity in response to the

screams of other monkeys (indicating threat), but they also show increased activity in response to

the sounds of coos (affiliative sounds) and sounds indicating aggression (Kuraoka & Nakamura,

2007), suggesting that even individual cells do not respond to individual emotions. Electrical

stimulation of the same site within the temporal lobe of the human brain produces not only

emotions but also bodily sensations and cognitions; sometimes it produces no mental state at all

(Halgren, Walter, Cherlow, & Crandall,1978; Sem-Jacobson, 1968; Valenstein, 1974; for a

discussion, see Barrett et al., 2007). Although lesion findings have long been taken as evidence

that a particular brain region serves a particular mental faculty, there is growing evidence that

lesions in a given brain region impair a more general psychological function that itself

contributes to a certain mental state. For instance, researchers assumed for years that the

amygdala supports fear, because a patient (S. M.) with bilateral amygdala lesions could not

perceive fear on the faces of others (e.g., Adolphs, Tranel, Damasio, & Damasio, 1994; 1995;

Adolphs et al., 1999). Yet more recent findings demonstrate that amygdala lesions cause an inability to focus on the socially relevant features of a face. Patient S. M. is capable of perceiving fear when her attention is explicitly directed to the eyes of a face (Adolphs et al., 2005) or when viewing caricatures of fearful body postures (Atkinson, Heberlein, & Adolphs, 2007). These findings, along with lesion evidence linking the amygdala to impaired processing of novel stimuli (e.g., Bliss-Moreau, Toscano, Bauman, Mason, & Amaral, 2010) and blunted affect more generally (Bliss-Moreau, Bauman, & Amaral, 2011), are consistent with the idea that the amygdala is part of a more general network involved in detecting motivationally salient stimuli in the environment (cf. Cunningham & Brosch, 2012; Seeley et al., 2007; Touroutoglou, Hollenbeck, Dickerson, & Barrett, 2012).

Second, the domain-general networks hypothesized in a constructionist view and observed in meta-analyses of emotion studies are unlikely to reflect merely the limitations of task-related neuroimaging, because these networks are also observed as task-independent, intrinsic connectivity that is grounded by anatomical connections in healthy, functioning brains (Fox & Raichle, 2007; Vincent et al., 2008; Yeo et al., 2011). We now demonstrate how the science of intrinsic connectivity provides further evidence of the brain's basic networks and is consistent with a constructionist view of mind–brain correspondence.

Intrinsic Functional Connectivity Provides Evidence of the Brain's Basic Networks

The science of intrinsic functional connectivity is another emerging source of knowledge from cognitive neuroscience that can shed light on the basic psychological functions that comprise the mind and speak to a constructionist model of mind–brain correspondence. Intrinsic functional networks are broadscale networks that span the cortex and subcortex, and comprise brain regions that show a similar time course of activation, even when a person is "at rest" in the scanner and

not engaging in an external psychological task. Methods for measuring this so-called "resting-state functional connectivity MRI" (rs-fcMRI) of regions distributed across the brain have been developed over the past decade but have undergone an explosion in the past 3-5 years. rs-fcMRI reflects the temporal correlations between low-frequency BOLD signal fluctuations of brain areas and as such provides a basis for understanding the large-scale intrinsic organization of brain networks (Buckner, 2010; Deco, Jirsa, & McIntosh, 2010; Fox & Raichle, 2007; Vincent et al., 2008). In this method, a region of interest is selected (i.e., a seed region) and low-frequency BOLD signal fluctuations are extracted within that region. Next, correlations are computed between the low-frequency signal fluctuations within the seed region and all voxels in the brain. The resulting map is an intrinsic connectivity network of functionally related regions that is present in the absence of task, that is, during resting-state conditions.

rs-fcMRI has been widely used by many different laboratories to generate large-scale neuroanatomical intrinsic networks (Smith et al., 2009; Yeo et al., 2011) subserving critical brain functions, such as visual, auditory, and language processes (Cordes et al., 2000), as well as motor function (Biswal, Yetkin, Haughton, & Hyde, 1995), episodic memory (Vincent et al., 2006), executive control and salience processing (Seeley et al., 2007), affective experience (Touroutoglou et al., 2012), and attention (Fox, Corbetta, Snyder, Vincent, & Raichle, 2006). The spatial topography of these networks is consistent across individuals and scans, resting conditions (Van Dijk et al., 2010), and levels of consciousness (Greicius et al., 2008), demonstrating the specificity and robustness of the intrinsic functional correlations within large-scale brain networks. See Table 5.1 for a functional description of seven networks identified by Yeo and colleagues (2011), derived from the largest sample of participants (1,000) in any study of intrinsic functional connectivity to date, that likely reflect the most stable estimates of intrinsic

networks. Importantly, relevant to the psychology of individual differences, the magnitude of intrinsic connectivity within a given network predicts differences in behavior related to the function of that network. For example, participants with stronger intrinsic connectivity in the ventral subnetwork of the salience network (comprising ventral anterior insula (AI) and pregenual ACC, lateral OFC, thalamus, and basal ganglia) reported feeling more aroused during the viewing of negative evocative images than did individuals with weaker connectivity (Touroutoglou et al., 2012). Taken together, these findings suggest that patterns of rs-fcMRI likely represent the intrinsic functional architecture of the brain (Fox & Raichle, 2007) or regions of the brain that are commonly used together to produce a distributed function (Barrett & Satpute, 2013; Deco et al., 2010). In so doing, the intrinsic functional connectivity is particularly useful for examining psychological construction hypotheses about the mind.

In the context of rs-fcMRI, an important question, however, is how do we infer the functional interpretation of a given intrinsic connectivity network, assuming that it is defined independent of tasks and other experimental stimuli? Traditionally this is done by examining the tasks that either engage individual regions within a network of interest or the network as a whole during task-related fMRI studies (e.g., Barrett & Satpute, 2013). Because the intrinsic networks are independent of experimental context, they can also be compared with task-related functional connectivity networks activated during tasks across different studies. Additionally, more recently Laird et al. (2011) provided a means to assess the link between intrinsic connectivity networks and behaviors in a more direct way. By quantifying the relationship between intrinsic connectivity networks and behavioral domains coded in the BrainMap database—the largest fMRI and positron emission tomography (PET) database of task-related activation studies to date—Laird et al. were able to map intrinsic connectivity networks to specific groups of

functional ontology, including reasoning, language, social cognition, attention, and emotion. For example, the connectivity within the salience network was found to be strongly related to the behavioral domain of emotion and interoception. Other projects that map distributed brain activity to functional categories are the Neurosynth database (Yarkoni et al., 2011) and the Cognitive Atlas Project (Poldrack et al., 2011). These projects will no doubt prove useful as research in this area continues.

More recently, our laboratory used rs-fcMRI to gain insight into the nature of emotion, contributing to the long-standing scientific debate between psychological construction and basic emotion approaches to emotion. Basic emotion accounts hypothesize that happiness, sadness, anger, disgust, and fear arise from innate, culturally universal neural modules in the brain (Panksepp, 1998), which leads to the prediction that there are intrinsic connectivity networks specific to each distinct emotion category. In contrast, our psychological constructionist hypothesis that emotions (like all other complex mental states) are constructed from more basic core systems that correspond to functional networks in the brain predicts that domain-general intrinsic connectivity networks, such as salience detection, language, or executive control networks, would subserve all different emotions. Intrinsic connections are influenced by the anatomy and activation history of a given network (Buckner, 2010; Deco & Corbetta, 2011; Fox & Raichle, 2007), and some intrinsic connections are also homologous in other primate species (Hayes & Northoff, 2011; Vincent et al., 2007; Kojima et al., 2009; Rilling et al., 2007). The science of intrinsic connectivity therefore has the potential to enhance our understanding of a fundamental question: Do inherited emotion networks really exist in the brain?

To answer the question whether anger, disgust, fear, sadness and happiness are each associated with an anatomically given intrinsic brain network, Touroutoglou, Lindquist,

Dickerson, and Barrett (in press) used meta-analytic peaks of these emotion categories (Vytal &

Hamann, 2010) as rs-fcMRI seeds and generated a whole-brain rs-fcMRI map for each seed.

Each seed, then, was a location of voxels that was consistently activated at levels greater than

chance during that emotion. Using a spatial similarity index between every pair of rs-fcMRI

maps, the study showed very low similarity between maps within each emotion category (i.e., the

maps anchored by all anger seeds were not found to be part of the same spatially similar map),

indicating that there was no intrinsic connectivity network specific to each emotion. Consistent

with a psychological construction approach, intrinsic networks identified in other studies (Shirer,

Ryali, Rykhlevskaia, Menon, & Greicius, 2012) instead accounted for variance in the derived rs-

fcMRI maps, indicating that domain-general intrinsic networks are important for all emotions.

Furthermore, the rs-fcMRI maps anchored in seeds that are commonly considered to be

specifically related to distinct emotions (i.e., amygdala for fear, basal ganglia for happiness,

insula for disgust, OFC for anger) were found to converge in regions of the ventral portion of the

salience network (Touroutoglou et al., 2012). These results support the psychological

construction hypothesis that emotions are not subserved by heritable anatomical networks;

instead the voxels that are consistently active during a given emotion are part of a variety of

large-scale intrinsic networks that are important, but not limited, to emotions. In addition, and

consistent with a constructionist account, Laird and colleagues (2011) found that the intrinsic

connectivity between AI and ACC, two major nodes of the salience network (Seeley et al.,

2007), is linked to a variety of general psychological processes, such as language, executive

function, and affective and interoceptive processes, thus calling into question the traditional

distinction between emotion and cognition. Similarly, both Seeley et al. and Touroutoglou et al.

(2012) found that parts of the AI and ACC overlapped with both the executive function and salience network.

These analyses provide an example of how the science of intrinsic connectivity has the potential to identify the functional architecture of the brain that corresponds to the basic core operations of the mind. However, intrinsic connectivity MRI cannot determine how basic psychological processes combine in a given instance to produce the variety of mental states that characterize human life. To this end, task-related fMRI studies, carefully designed to manipulate the basic ingredients of the mind, are better suited to examine relationships between the interaction of neural networks supporting these ingredients and the emergence of mental states. In the next section, we report on two recent neuroimaging studies that examined how large-scale distributed networks in the brain combine when people construct different mental states in the fMRI scanner.

Functional Neuroimaging as an Explicit Tool to Test Constructionist Hypotheses

Based on the research reviewed thus far, it is possible to formulate and test specific hypotheses about the relative involvement of domain-general networks when mental states are constructed in real time. Although individual behavioral studies have explicitly tested a constructionist approach by manipulating the ingredients hypothesized to produce emotions and testing the behavioral outcome (e.g., Lindquist & Barrett, 2008), individual neuroimaging studies are perhaps even better suited for testing constructionist hypotheses for several reasons. First of all, mental states are emergent phenomena. This means that when a subjective experience has manifested itself in consciousness, it cannot be subjectively reduced to its underlying parts (cf. Barrett, 2011, 2012; Coan & Gonzalez, Chapter 9, this volume). That is, people cannot report on the underlying processes that shape their mental state, just as they cannot report on the

underlying processes that create a conscious percept (e.g., the visual features of contrast, color,

edges, etc., that contribute to the perception of a red vase). Furthermore, the processes that

combine to form emergent states typically operate unconsciously and automatically (Barrett,

2006; Wilson-Mendenhall, Barrett, Simmons, & Barsalou, 2011). Since functional neuroimaging

is not restricted by conscious or volitional report, this technique is particularly suitable to study

how these processes combine in real time. Second, individual neuroimaging studies can

explicitly test hypotheses that have been formulated (based in part on the data reviewed earlier)

about the regions and networks involved in conceptualization, core affect, and other basic

processes that create mental states (see Barrett, 2009; Lindquist et al., 2012; Kober et al., 2008;

Touroutoglou et al., in press).

In a recent experiment (Oosterwijk et al., 2012), we tested a constructionist model of the

mind using fMRI by asking participants to generate three categories of mental states (emotions,

body feelings, or thoughts) while examining similarities and differences in patterns of network

activity. We used a scenario immersion method developed in our laboratory (Wilson-Mendenhall

et al., 2011) to immerse participants in sensory-rich, vivid scenarios of unpleasant situations.

Critically, before each scenario was presented, participants were asked to experience the

situation as a body feeling (e.g., increased heartbeat, touch of an object against the skin, smells,

unpleasantness), as an emotion (e.g., fear, anger, guilt) or as a thought (e.g., plan, reflection).

Each trial started with a cue, followed by the scenario (the "immersion" phase), followed by an

"experience" phase in which participants could further construct and elaborate on the body

feeling, emotion, or thought (see also Addis, Wong, & Schacter, 2007). Taking a network-based

model of the mind as our starting assumption, we hypothesized that body feelings, emotions, and

thoughts are constructed from the interaction of large-scale distributed networks (Fox & Friston,

2012; Fuster, 2006; Goldman-Rakic, 1988; McIntosh, 2000; Mesulam, 1998; also see Bullmore & Sporns, 2009). In our study we focused specifically on the previously discussed intrinsic networks identified by Yeo and colleagues (2011). For a functional description of each of these networks see Table 5.1.

First, we found experimental support for the hypothesis that body feelings, emotions, and thoughts, although subjectively distinct, each involve participation of the same distributed brain networks. Most notably, a conjunction analysis that reveals overlapping patterns of brain activation across different tasks demonstrated common engagement of the salience network. We hypothesize that this network is involved in directing attention and behavior using core affective information from the body (Barrett & Satpute, 2013; Lindquist & Barrett, 2012; see also Seeley et al., 2007). The finding that the salience network was commonly active during the experience of a variety of mental states involving negative information is consistent with the role for this network in stress (Hermans et al., 2011), the experience of unpleasant affect (Hayes & Northoff, 2011), and tasks requiring the allocation of attention to evocative or behaviorally relevant stimuli (Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002; Nelson et al., 2010; Seeley et al., 2007). Moreover, several regions within the salience network, specifically the AI and the aMCC have been associated in the literature with interoception (Critchley et al., 2003, 2004) and subjective experiences more generally (Craig, 2002, 2009). The finding in our study that the salience network was engaged across all mental states suggests that representations of body sensations play a role when people experience body states or emotions *and* when they objectively think about a negative situation. This is consistent with several suggestions in the literature that cues from the body are a fundamental component of all mental life, including perception (Barrett & Bar, 2009; Cabanac, 2002), judgment (Clore & Huntsinger, 2007), tasks

involving effort (Critchley et al., 2003), and consciousness more generally (Barrett & Bliss-Moreau, 2009; Craig, 2009; Damasio, 2000; Russell, 2003; Wundt, 1897).

In addition to the salience network, our results also suggest a common role for several other networks during the construction of subjective mental experiences, most notably the default network and the frontoparietal network. The finding that the default network is commonly active during the experience of mental states is consistent with the hypothesis that this network is involved in the process of conceptualization—in which representations of prior experiences are brought to bear to construct representations of the past, the future, or the present moment (for discussion, see Oosterwijk et al., 2012; Lindquist et al., 2012). The common engagement of the frontoparietal network across body states, emotions, and thoughts suggests that all these mental states involve executive control (Seeley et al., 2007; Dosenbach et al., 2008; Vincent et al., 2008). This network may modulate activity in other functional networks to help construct an instance of a mental state. Finally, although our analyses focused on the cortical surface of the brain, we also examined common activation in subcortical areas during emotions, body states, and thoughts. We found common activations within subcortical regions such as the pallidum, putamen, and cerebellum across bodily feelings, emotions, and thoughts. These regions may be part of the limbic network (Yeo et al., 2011) that we hypothesize generates and/or represents somatovisceral changes that are experienced as the core affective tone that is common to every mental state (also see Oosterwijk et al., 2012).

Although the same distributed brain networks were implicated in body feelings, emotions, and thoughts, we also found evidence that different network profiles were associated with each mental state category. First, as we predicted, the salience network was engaged significantly more during body feelings than during thoughts in the "immersion" phase. This

pattern of activation was present across multiple regions of the salience network, including the

dorsal AI, the vlPFC (pars opercularis), and the aMCC. Emotions also demonstrated increased

activation in the salience network compared to thoughts, including in the left vlPFC (pars

opercularis), the right aMCC and the right TPJ. Additionally, subcortical regions hypothesized to

be involved in core affective generation, such as the thalamus, pallidum, and caudate, were more

engaged during body feelings than during thoughts. Together, these results suggest that core

affect, as supported by the salience network, plays a relatively more important role in emotions

and body feelings than in thoughts.

During the "experience" phase of the experiment we found that the salience network was

equally engaged during all mental states. The default network, however, showed stronger

engagement during thoughts than during emotions and bodily states. This result is consistent

with previous findings that show the default network's robust involvement in spontaneous

thought (Andrews-Hanna, Reidler, Huang, & Buckner, 2010), predicting the future (Spreng &

Grady, 2010; Addis et al., 2007) and mental state attribution or theory of mind (Spreng & Grady,

2010; Mitchell, Banaji, & Macrae, 2005). Together, these findings suggest that conceptualization

plays a larger role in mental states in which the representation of prior experiences is used to

guide plans, associations, and reflections about a situation.

Together, these findings demonstrate that body feelings, emotions, and thoughts,

although subjectively distinct, cannot be localized to distinct regions (or even networks) within

the human brain. Instead, body feelings, emotions, and thoughts each involve a relatively

different combination of the same set of distributed brain networks. Recent evidence

demonstrates that even instances of the same superordinate category (e.g., emotion) involve

relatively different combinations of the same set of distributed brain networks. In a neuroimaging

experiment, Wilson-Mendenhall and colleagues (2011) examined which distributed brain circuits engaged when people conceptualized different situations as instances of a discrete emotion (e.g., anger or fear). Based on a constructionist view on the mind, Wilson-Mendenhall and colleagues hypothesized that this distributed circuitry would not be specific to anger or fear, but it would support basic psychological processes such as conceptualization, core affect, and executive control. This study is particularly important because it illustrates how the situation in which an emotion is experienced shapes the way the brain is engaged during that emotion.

Using the scenario immersion method, participants were cued to conceptualize situations describing physical danger (e.g., being lost in the woods) or social evaluation (e.g., being unprepared during a meeting at work) as an instance of an emotion (i.e., fear or anger) or as an instance of a non-emotional mental state (i.e., planning or observing). The results showed that the same emotion was associated with very different brain states across different situations. For example, the brain state representing fear in physical danger situations shared only 47% of the active voxels with the brain state representing fear in social evaluation situations. Furthermore, consistent with the network account proposed in this chapter, both anger and fear demonstrated engagement of regions in the salience network (e.g., posterior insula, midcingulate) in situations where physical harm was anticipated. Social evaluation situations, in contrast, demonstrated activation of the ventromedial prefrontal cortex, which is part of the default network and specifically associated with self-related, evaluative processes (see Amodio & Frith, 2006; Mitchell, Heatherton, & Macrae, 2002; Northoff et al., 2006). Together, these data highlight a basic premise of our constructionists account: A mental state cannot be understood separately from the context in which it is experienced.

To our knowledge, these two neuroimaging studies are the first to test explicitly a constructionist functional architecture of the mind by assessing both similarities and relative differences in distributed brain patterns during the experience of different mental states. The findings are consistent with the reviewed evidence from meta-analyses and analyses of intrinsic connectivity that mind–brain correspondence may be best understood by examining relative differences in the engagement of distributed networks that support basic psychological processes. Moreover, these findings directly call into question the faculty psychology view that different classes of mental states differ categorically at the level of brain organization.

Conclusion

In this chapter, we have presented a constructionist functional framework of mind–brain correspondence, with the basic premise that mental states emerge from the combination of more basic core systems, or psychological "ingredients" that map to the functional states of broadscale brain networks. Despite the fact that the first two decades of neuroimaging used a faculty psychological viewpoint as their guiding framework, the research we reviewed here demonstrates clearly that faculty psychology should be discarded. Instead, the meta-analyses, intrinsic network studies, and individual neuroimaging studies reviewed in this chapter point to a constructionist model of the mind in which not only emotions but also other mental states emerge from the combination of broadscale brain networks that support basic psychological functions.

It is important to note that our constructionist approach does not explain subjectively different mental states out of existence (see also Barrett, 2012), nor does it argue that all subjective experiences look the same in the brain. Take fear as an example. An individual brain state for one instance of fear in a given context is distinguishable from the brain state of, say,

anger, concentration, or curiosity. The point is that the similarities and differences between these brain states are best understood not by focusing on the unique subjective experience that they represent at a given moment in time, but by focusing instead on the interaction between broad, domain-general processes that cause the subjective experience to emerge. Specificity in subjective experience (e.g., a specific feeling of fear when preparing for a job talk vs. a specific feeling of fear when bleeding from a deep finger cut) occurs because each instance of an emotion is tailor made to a given context by a unique situated conceptualization supported by a pattern of brain activity that engages general psychological processes (Barrett, 2012; Wilson-Mendenhall et al., 2011). Specificity is not caused by the activation of a module or dedicated network for fear, however. Although there might be some brain pattern that characterizes all instances of fear (which further research must still discern), we argue that this pattern is a combination of intrinsic networks and not an anatomically prescribed, inheritable network. Thus, our constructionist view accounts for the heterogeneity of mental states by assuming that each mental state is represented by a unique brain state that involves networks supporting general psychological processes such as language, conceptualization, interoception, exteroception, and executive control. Furthermore, we argue that the context in which the mental state occurs may be more informative in guiding the interpretation of the engaged psychological processes than the categorical label of the subjective mental state itself.

The evidence presented in this chapter has important scientific implications. First of all, the presented findings challenge the assumption that subjective experiences (i.e., how we experience our mental states as qualitatively different) reveal in a one-to-one fashion how the brain works (i.e., that different mental states must be associated with functionally specific brain activation). These data instead contribute to a new understanding of how mental states, including

emotions, are realized by the brain. Rather than states that differ in kind from one another, mental states might instead be considered complex "recipes" that reflect the relative weighting of a number of domain-general "ingredients" of the mind.

Second, the data presented in this chapter challenge traditional views on a strict separation of different mental faculties, such as perception, cognition, and emotion (or seeing, feeling, and thinking; see also Barrett, 2009; Barrett & Bar, 2008; Pessoa, 2008; Duncan & Barrett, 2007). In the literature, scientists still refer to cognitive, social, and affective neuroscience as different domains of inquiry. Nevertheless, the networks discussed in this chapter are important not only in emotion but also other domains, such as decisions (Kringelbach & Rolls, 2004), attention (Corbetta & Shulman, 2002; Lenartowicz et al., 2010), memory (Spreng et al., 2009), semantic processing (Binder et al., 2009), mentalizing (Spreng et al., 2009), and consciousness more generally (also see Craig, 2009; Nelson et al., 2010).

In future research, it will be important to model the interaction of the networks hypothesized to support basic psychological processes when examining a person's mental state. For instance, already there is some evidence that is consistent with the idea that brain regions supporting conceptualization (i.e., the default network) combine with brain regions supporting core affect (e.g., aspects of the limbic and salience networks) during the experience of emotion. One recent study found that a correlation between the default network and networks supporting core effect (e.g., thalamus, basal ganglia, insula) significantly predicted participants' ratings of valence as they watched evocative movies in the scanner (Viinikainen et al., 2012). Another recent study found a similar interactive pattern between the default network and aspects of the salience network (e.g., insula, aMCC) when participants mentalized about both the self and others (Lombardo et al., 2009).

We hope that with more incremental research, experimental support for a constructionist view of the mind will contribute to the identification of a set of neural "common denominators" that link a range of findings across psychological domains that appear very different on the surface (e.g., emotions vs. thoughts vs. perceptions). It is often argued that psychology is not useful in the age of the brain; similarly, it is sometimes argued that neuroimaging cannot offer much, beyond being a form of new phrenology. In our constructionist framework, psychology and neuroimaging can be used to inform and constrain one another as we attempt to understand how the brain constructs the mind.

Acknowledgments

Notes

1. The neural reference spaces reported in both Vytal and Hamann (2010) and Kober et al. (2008) were surprisingly similar to those reported by Lindquist et al. (2012), especially given that the Lindquist et al. meta-analysis included a slightly different sample of studies than the others, and that Lindquist et al. (2012) and Kober et al. (2008) used a different method than Vytal and Hamann (2010).

2. Vytal and Hamann (2010) claim to have found evidence of specific patterns for discrete emotions, but upon further inspection, their meta-analytic findings look quite similar to our own. They report clusters with peaks that have relatively greater activity for one emotion than all others, but these peaks are part of clusters that overlap between different emotions. That is, they fail to show the kind of specificity that would be necessary to claim evidence for the anatomical basis of discrete emotions in the brain. It is beyond the scope of this chapter to discuss the methodological differences between the Vytal and Hamann meta-analysis and our own, but for a discussion, see Lindquist et al. (2012).

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Table 5.1. Overview of Seven Intrinsic Networks

Brain regions	Task domains	Psychological description
	"Limbic network" (Yeo et al., 2011)	
Bilateral anterior temporal lobe, medial temporal lobe, subgenual anterior cingulate cortex, medial and lateral orbitofrontal cortex (although Yeo et al.'s network only covers the cortex, we also hypothesize that the basal ganglia, including the caudate, putamen, globus pallidus, and central nucleus of the amygdala will be a part of this network).	• Emotion and affect (Lindquist et al., 2012; Andrews-Hanna et al., 2010) • Autobiographical memory (Spreng & Grady, 2010)	*Core affect generation:* engaging visceromotor control of the body to create core affective feelings of pleasure or displeasure with some degree of arousal.
	"Salience network" (Seeley et al., 2007) or "ventral attention network" (Yeo et al., 2011; Corbetta & Shulman, 2002) or "cingulo-opercular network" (Vincent et al., 2008)	
Bilateral anterior midcingulate cortex (aMCC), anterior insula (AI) and midinsula, frontal operculum, and parts of the pars opercularis and temporoparietal junction.	• Cognitive control (Cole & Schneider, 2007) • Stimulus-driven control of attention (Corbetta & Shulman, 2002) • Set maintenance (Dosenbach et al., 2006) • Maintaining subgoals (Fincham et al., 2002)	*Body-directed attention:* using representations from the body to guide attention and behavior. This ingredient might use changes in the homeostatic state of the body to signal salient events in the environment and regulate behavioral responses.

- Anxiety (Seeley et al., 2007)

- Representation of the body (Craig, 2009)

- Pain (Lamm, Decety & Singer, 2010)

"Default network" (Dosenbach et al., 2008; Vincent et al., 2008; Yeo et al., 2011)

Medial prefrontal cortex, parts of the pars triangularis, retrosplenial area, posterior cingulate cortex/precuneus, medial temporal lobe (hippocampus, entorhinal cortex), bilateral superior temporal sulcus, parts of the anterior temporal lobe (ATL), and angular gyrus.	• Autobiographical memory (Spreng & Grady, 2010) • Prospection (Spreng & Grady, 2010) • Theory of mind (Spreng & Grady, 2010) • Moral reasoning (Greene, Sommerville, Nystrom, Darley & Cohen, 2001) • Context-sensitive visual perception (Bar, 2004) • Spontaneous thought (Andrews-Hanna et al., 2010) • Emotion (Lindquist et al., 2012; Andrews-Hanna et al., 2010) • Semantics, phonology, sentence processing (Binder et al., 2009)	*Conceptualization:* representing prior experiences (i.e., memory or category knowledge) to make meaning of sensations from the body and the world in the moment.

"Frontoparietal network" (Dosenbach et al., 2008; Vincent et al., 2008; Yeo et al., 2011) or "executive control network" (Seeley et al., 2007)

Bilateral dorsolateral prefrontal cortex (dlPFC), inferior parietal lobe, inferior parietal sulcus, and aspects of the middle cingulate cortex (mCC).	• Task-switching (Crone, Wendelken, Donohue, & Bunge, 2006) • Alerting to a stimulus after a cue (Fan et al., 2005) • Planning (Fincham et al., 2002) • Rule-specific processing (Sakai & Passingham,	*Executive attention:* modulating activity in other ingredients to create a unified conscious field during the construction of a mental state (e.g., selecting some conceptual content when meaning is made of sensations and inhibiting other content; selecting some sensations for conscious awareness

2006)

- Working memory (Sakai & Passingham, 2003)

"Dorsal attention network" (Corbetta & Shulman, 2002; Yeo et al., 2011)

Bilateral frontal eye fields, dorsal posterior parietal cortex, fusiform gyrus, area MT+.	• Top-down control of visuospatial attention (Corbetta et al., 2002)	*Visuospatial attention:* modulating activity in an ingredient for processing visual content in particular (e.g., selecting which visual sensations are selected for conscious awareness and inhibiting others).

"Somatomotor network" (Yeo et al., 2011)

Precentral and postcentral gyri (sensorimotor cortex), Heschl's gyrus (primary auditory cortex) cortex, posterior insula.	• Audition (Morosan et al., 2001) • Somatovisceral sensation (Eickhoff et al., 2006)	*Exteroceptive sensory perception:* representing auditory and tactile sensations.

"Visual network" (Yeo et al., 2011)

Occipital lobe	• Vision (Engel et al., 1994)	*Exteroceptive sensory perception:* representing visual sensations.

Note. The table lists the brain regions that are found to comprise each network across studies (column 1), the references that contribute to a functional understanding of each network (column 2), and the psychological *description* that is supported by the network as hypothesized by a constructionist framework (see further in Lindquist & Barrett, 2012).