Commentary

Neuroimaging as a New Tool in the Toolbox of Psychological Science

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ABSTRACT—*During the past quarter century, advances in imaging technology have helped transform scientific fields. As important as the data made available by these new technologies have been, equally important have been the guides provided by existing theories and the converging evidence provided by other methodologies. The field of psychological science is no exception. Neuroimaging is an important new tool in the toolbox of psychological science, but it is most productive when its use is guided by psychological theories and complemented by converging methodologies including (but not limited to) lesion, electrophysiological, computational, and behavioral studies. Based on this approach, the articles in this special issue specify neural mechanisms involved in perception, attention, categorization, memory, recognition, attitudes, social cognition, language, motor coordination, emotional regulation, executive function, decision making, and depression. Understanding the contributions of individual and functionally connected brain regions to these processes benefits psychological theory by suggesting functional representations and processes, constraining these processes, producing means of falsifying hypotheses, and generating new hypotheses. From this work, a view is emerging in which psychological processes represent emergent properties of a widely distributed set of component processes.*

KEYWORDS—*functional magnetic resonance imaging; cognitive processes; social processes; clinical processes; developmental processes*

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New imaging technologies are having a demonstrable impact on the landscape of scientific research. The most expensive imaging instrument, and the most vivid example, is the Hubble Space Telescope. The Hubble telescope was deployed in April 1990 and has undergone three major repairs and upgrades since that time. It has also provided data and images at a resolution Galileo Galilei could not have imagined when, early in the 17th century, he discovered the craters on the moon, sunspots, the rings of Saturn, and the moons of Jupiter by gazing through his first crude telescope. The discoveries made possible by the high-resolution data and images from the Hubble nearly four centuries later include massive black holes at the center of galaxies, the existence of precursors to planetary systems like our own, and a greater quantity and distribution of dark matter than expected. As important as were the data provided by the Hubble Telescope, however, these discoveries were dependent on extant theories and methodologies. The discovery of stellar black holes at the centers of galaxies, for instance, was guided by general relativity theory and supported by research using several converging methodologies (e.g., Dolan, 2001).

Developments in neuroimaging during the past quarter century have increasingly made it possible to investigate the differential involvement of particular brain regions in normal and disordered thought in humans. Previously, studies of the neurophysiological structures and functions associated with *psychological* states and processes were limited primarily to animal models, postmortem examinations, electrophysiological measures, and observations of the occasional unfortunate individual who suffered trauma to or disorders of the brain (e.g., Raichle, 2003). The detailed three-dimensional color images provided by neuroimaging, modeling statistical properties of the working brain, have captured the imagination of the public and the scientific community, shaped funding priorities at federal funding agencies and foundations, and produced a dramatic growth in scientific papers and journals in the area (Cacioppo et al., 2007).

This special issue of *Current Directions in Psychological Science* summarizes recent theoretical advances in various fields of psychological science that are attributable in part to the use of neuroimaging technology—most prominently, functional magnetic resonance imaging (fMRI). Although reading these reviews leaves the impression that neuroimaging is an important new tool in the toolbox of psychological science, one cannot help but also be impressed that neuroimaging—like the Hubble Space Telescope—is most productive scientifically when its use is guided by extant theories and complemented by converging methodologies.

In the typical neuroimaging study, psychological states and processes are manipulated and activation in different brain regions is measured. The logic of this design is best suited for drawing inferences about the differential involvement of particular brain regions in specific psychological operations. For instance, when Poeppel and Monahan (2008, this issue) ask how speech signals are represented and processed in the brain, they are using neuroimaging along with converging methods from psychological science, and guided by the blueprint of competing theoretical accounts for speech perception, to investigate the differential involvement of particular brain regions in psychological states and processes. It is also possible *under certain conditions* to draw reasonable inferences about psychological operations based on regions of brain activation (Cacioppo & Berntson, in press; Cacioppo & Tassinary, 1990; Henson, 2006; Poldrack, 2006; Sarter, Berntson, & Cacioppo, 1996).

Across the articles in this special issue, evidence from lesion studies, animal studies, neuroimaging, single-cell recording, event-related brain potentials, transcranial magnetic stimulation, computational modeling, and behavior is reviewed to investigate the brain regions involved in perception, attention, categorization, memory, recognition, attitudes, social cognition, language, motor coordination, emotional regulation, executive function, decision making, and depression. Together, the evidence converges on the view that psychological states and processes are mediated by a network of distributed, often recursively connected, interacting brain regions, with the different areas making specific, often task-modulated contributions (see Poeppel & Monahan, 2008).

DISTRIBUTED NETWORKS INVOLVED IN COGNITIVE REPRESENTATIONS AND FUNCTION

Humans are visual creatures. The visual properties of scenes drive neurons in the lateral geniculate nucleus of the thalamus, and visual perception has been found to involve a dorsal stream, or "where pathway," and a ventral stream, or "what pathway." The dorsal (where) stream includes the areas designated V1, V2, V5/MT, and the inferior parietal lobule and is associated with motion, representation of object locations, and control of the eyes and arms when visual information is used to guide saccades or reaching. The ventral (what) stream includes the areas V1, V2, V4, and the inferior temporal lobe (areas that include the lateral occipital complex and the fusiform gyrus) and is

associated with form recognition, object representation, face recognition, and long-term memory (Engel, 2008, this issue). Grill-Spector and Sayres (2008, this issue) provide evidence that changes in the size, position, orientation, and other aspects of physical appearance of faces activate the lateral occipital complex; differences in the identity of individuals are related to adaptation responses in the fusiform gyrus; and changes in facial expression and gaze direction involve the superior temporal sulcus.

Different theoretical representations and decompositions of speech perception into processing components are described, and the neural outcomes associated with each of these theoretical representations are reviewed, by Poeppel and Monahan (2008). Here, too, the evidence suggests the involvement of a specialized, interconnected set of neural regions that are widely distributed across the temporal, parietal, and frontal lobes. Specifically, the early spectrotemporal analyses involve bilateral auditory cortices and the superior temporal cortex, and phonological analyses involve the middle and posterior portions of the superior temporal sulcus. The processing streams then appear to divide into a ventral stream—which maps auditory and phonological representations onto lexical conceptual representations and involves the middle temporal gyrus and inferior temporal sulcus—and a dorsal stream—which maps auditory and phonological representations onto articulatory and motor representations and involves the Sylvian parietotemporal area, posterior frontal gyrus, premotor cortex, and anterior insula (Poeppel & Monahan, 2008).

The attentional modulation of perceptual processes is influenced by motivational states and goals as well as by stimulus properties. Visual attentional control can modulate neural activity in the lateral geniculate nucleus and superior colliculus, as well as in the posterior parietal cortex (specifically, the regions of the superior parietal lobule and the lateral intraparietal area within the intraparietal sulcus) and the frontal eye field and supplementary eye field within the prefrontal cortex (Yantis, 2008, this issue). These perceptual and attentional processes contribute to the acquisition of knowledge about the world that is organized categorically. Barsalou (2008, this issue) notes that the dominant theory in cognitive science posits that this knowledge is represented in an abstract, amodal fashion and constitutes semantic memory. He shows in his review, however, that categorical knowledge includes modal representations using the same neural mechanisms involved in perception, affect, and action. In Barsalou's view, the representation of a category involves a neural circuit distributed across the relevant modalities, *all* of which can become activated during conceptual processing. Thus, conceptual processing can be viewed as an embodied rather than purely abstract process.

How does categorical knowledge being represented in this distributed, modal fashion square with the neuroscientific evidence for differences in the localization of short- and long-term memory processes? Nee, Berman, Moore, and Jonides

(2008, this issue) suggest that the evidence supporting the qualitative distinction between short- and long-term storage processes has been misinterpreted, and they suggest that the data instead support a unitary model of memory in which the same regions of the brain that represent perception, action, and affect are involved in both short- and long-term storage processes. That is, short- and long-term memories do not differ in representation but in the activation by attention, which in turn involves a frontal biasing (i.e., maintenance) of representational cortices (e.g., frontal eye fields and intraparietal sulcus for spatial representations; superior temporal sulcus and Sylvian parietotemporal area for phonological and articulatory representations). For instance, damage in the presylvian region produces deficits in short- and long-term memory that depends on phonological material, and the greater prevalence of such material in studies of short- than of long-term storage processes may inadvertently have led to evidence that this region was involved uniquely in short-term memory (Nee et al., 2008). Short- and long-term memory retrieval also activates overlapping regions of the left lateral frontal cortex, whereas the monitoring of retrieved information, whether from short- or long-term memory, is associated with the anterior prefrontal activation (cf. Cabeza, Dulcos, Graham, & Nyberg, 2002).

Neuropsychological research dating back several decades suggested structures in the medial temporal lobe (e.g., the hippocampus) were involved in declarative rather than nondeclarative learning. Unlike the distinction between short- and long-term memory, the distinction between declarative and nondeclarative learning is supported by neuroimaging research. For instance, research by Knowlton and Foerde (2008, this issue) has shown that when performance on a probabilistic classification task is based on declarative memory performance the medial temporal lobe is activated, whereas when performance on the task is based on nondeclarative memory performance the striatum is activated.

Knowlton and Foerde (2008) also review evidence showing that nondeclarative skill learning, at least for simple tasks, is associated with repetition suppression—reductions in the regions of neural activation associated with the initial performances of a task (e.g., the premotor region)—a finding that has been interpreted as indicating a greater efficiency of processing in the neural structures involved in novice performance. Priming-related reductions, on the other hand, are found in perceptual and prefrontal regions, with only the latter associated with behavioral facilitation. Knowlton and Foerde (2008) duly note, however, that activation in the perceptual cortices may appear to be less important in the extant literature in part because of the type of priming paradigms that have been used in fMRI research.

The complexities of social living, such as recognizing individuals and groups, negotiating nontransitive social hierarchies and shifting alliances, using language to communicate and manipulate, and engaging in social exchanges over extended periods and locales, place special demands on the capacities of the human brain. Mitchell (2008, this issue) reviews evidence

that thinking about thinking people (e.g., impression formation, social causality)—in contrast, for instance, to thinking about physical causality—is associated with activation of the medial prefrontal cortex, the right temporo-parietal junction, and the medial parietal region (e.g., the precuneus/posterior cingulate cortex). Mitchell (2008) suggests that the activation of the medial prefrontal cortex appears to be involved whenever people are obliged to consider the psychological characteristics of another person, whereas the temporo-parietal junction appears to be activated when the attentional and perceptual requirements of taking the perspective of another are invoked. The medial parietal region, on the other hand, is activated during the retrieval of episodic memories and self-knowledge, as well as during the viewing of two or more interacting people (e.g., Iacoboni et al., 2004).

The brain has evolved to guide behavior in contextually flexible, coordinated, and adaptive ways, and, as with attention, there are top-down as well as bottom-up influences on the orchestration of motor processes. Oliveira and Ivry (2008, this issue) focus on the top-down influences in their discussion of goals as higher-level action representations that connect sensory and motor processes to guide response selection and motor coordination. They review fMRI studies showing that motor planning and externally guided movements are associated with activity in the posterior superior parietal region and, at least for externally guided movements, in premotor regions; internally generated movements are associated with activity in the basal ganglia, the anterior cingulate cortex, and inferior frontal and parietal cortices; and conflicting action goals and effort are associated with activity in medial frontal areas, including the anterior cingulate cortex and presupplementary motor areas. One suggestion that has emerged from this area of research is that goal representation and action planning are not implemented simply as an abstract code but rather involve embodied processes. Not unlike how Barsalou (2008) invokes modal mechanisms, Rizzolati and Arbib (1998) and Skipper, Nusbaum, and Small (2006) review evidence for the role of embodied representations in categorization and language.

The fundamental idea that the motor system is important for cognition and perception, through prior experience and mirror neurons, has become an important contribution of neuroscience to bolstering theoretical constructs in the psychology of embodied understanding. However, much of the work on the mirror system in cognition and understanding has been carried out with trained nonhuman primates or with adult humans. For any theory of adult function to be viable, it is critical to understand the development of these mechanisms. Diamond and Amso (2008, this issue) review work on the neural substrates underlying cognitive development, including the mirror-neuron system and neonatal imitative behaviors and maternal touch and gene expression. As the authors note, a major contribution of neuroscience to theories of cognitive development is "demonstrating the remarkable role of experience in shaping the mind,

brain, and body" (p. 136). Such cross-cutting work is necessary to begin to link biological development with learning and experience. Moreover, as cognition can no longer be studied in isolation from the social context of its use, this work suggests the importance of understanding development within its social context of parental interaction. Given the importance of social context, then, it is important to go beyond the treatment of specific processes to understand how such processes depend on the goals they are directed at achieving.

To achieve one's goals, one has to be able to represent the likely rewards (and punishments) associated with different decisions, encode the risk or certitude that the reward will be obtained, update these representations, and act on the basis of these representations. O'Doherty and Bossaerts (2008, this issue) review evidence regarding the brain regions associated with each of these components of decision making. Specifically, they report that the encoding of reward expectation is associated with activation of the orbitofrontal cortex, medial prefrontal cortex, amygdala, and ventral striatum; recognizing greater risk or uncertainty associated with obtaining a reward correlates with increased activity in the anterior insula and lateral orbitofrontal regions; updating of reward expectancies is associated with the ventral striatum and orbitofrontal cortex; and selecting one of several responses to obtain the greatest reward involves the striatum, with the ventral striatum more involved in the prediction of reward across the various options and the dorsal striatum more involved in the selection among the alternatives (O'Doherty & Bossaerts, 2008).

The frontal regions have long been thought to be involved in executive functions such as formulating goals and plans; selecting among options to achieve these goals; monitoring the consequences of actions in light of one's goals; and inhibiting, switching and regulating one's behaviors accordingly. Aron (2008, this issue) reviews evidence that the initiation of a motor response proceeds from the planning areas of the frontal cortex to the putamen, globus pallidus, thalamus, primary motor cortex, motor nucleus in the spinal cord, and finally to the muscles. Being able to inhibit a motor response once it has been initiated has obvious adaptive value, and Aron (2008) shows that this inhibition involves the right inferior frontal cortex, which projects to the subthalamic nucleus (a region of the basal ganglia that may act on the globus pallidus to block the motor response). Monitoring for response conflicts, in turn, appears to involve the dorsal anterior cingulate and the adjacent presupplementary motor area, which, in turn, is connected to the right inferior frontal cortex and subthalamic nucleus. Switching also involves the presupplementary motor area and the right inferior frontal cortex (Aron, 2008). This work has led to a model in which "the [presupplementary motor area] may monitor for conflict between an intended response and a countervailing signal . . . Then, when such conflict is detected, the 'brakes' could be put on via the connection between the right [inferior frontal cortex] and the [subthalamic nucleus] region" (Aron, 2008, p. 127).

Emotional regulation is another form of executive function in which activity of the amygdala and insula cortex, which are involved in emotional responding, is modulated by activity in the prefrontal cortex (e.g., BA10, ventromedial prefrontal cortex, dorsolateral prefrontal cortex) and anterior cingulate. Ochsner and Gross (2008, this issue) review evidence that different components of reappraisal processing correspond to different areas of prefrontal activation: Selective attention and working memory components are related to dorsal portions of the prefrontal cortex, language or response inhibition are related to ventral portions of the prefrontal cortex, monitoring or control processes are related to the dorsal anterior cingulate cortex, and reflections on one's emotional state are related to dorsal portions of the medial prefrontal cortex. Although the correspondences proposed by Ochsner and Gross (2008) do not match perfectly those articulated by Aron (2008), the overlapping role for the anterior cingulate is noteworthy in light of the notion that the presupplementary motor area may be especially involved in the monitoring and control of motor conflicts.

The complexities of daily living are simplified in part by the formation of preferences and attitudes, which can serve as behavioral guides and simplify decision making. These attitudes can be explicit or implicit. Stanley, Phelps, and Banaji (2008, this issue) review evidence suggesting that the activation of implicit attitudes toward social groups (e.g., minorities) is associated with increased activity in the amygdala, dorsolateral prefrontal cortex, and anterior cingulate cortex. The cumulative evidence to date suggests that the automatic evaluation of a stimulus (e.g., social category) is associated with amygdala activation, the monitoring for response conflicts (e.g., the extent to which the stimulus elicits competing impulses) is associated with anterior cingulate activation, and the regulation of those impulses is associated with dorsolateral prefrontal activation.

Failures of effective emotional regulation can become costly in personal, social, and economic terms when these failures become systemic. Depression, for instance, has been estimated to cost more than $43 billion per year in the United States (Greenberg, Stiglin, Finkelstein, & Berndt, 1993). Understanding the variation in biological systems that leads to individual differences in neural mechanisms of emotional regulation is critical to understanding how some systemic failures become chronic and debilitating.

Gotlib and Hamilton (2008, this issue) review evidence that depressed individuals show less activity in the dorsolateral prefrontal cortex and greater activation of the amygdala and subgenual anterior cingulate cortex to emotional stimuli than do healthy controls. Parallel findings for basal activity levels in these brain regions are also noted. These findings are consistent with Gotlib and Hamilton's notion that depression is in large part a disorder of emotion regulation in which the normal inhibitory influence of limbic structures by the anterior cingulate and dorsolateral prefrontal cortex is disrupted, although the subgenual anterior cingulate cortex may play an especially critical role in this dysregulation (Gotlib & Hamilton, 2008).

Given the importance of the anterior cingulate and dorsolateral prefrontal cortex in motor control, attention, and emotion, the individual variation in function in these areas that can lead to depression may also explain that disorder's other associated cognitive symptoms.

Indeed, understanding the relationship between biological variation in neural mechanisms and psychological processes is important beyond clinical problems. Kosslyn et al. (2002) and Vogel and Awh (2008, this issue) have argued that, to bridge the gap between psychological phenomena and their underlying biological substrata, such variation should be regarded as important data in its own right. Kosslyn et al. (2002) describe how an idiographic approach can be used to address three types of issues: the nature of the mechanisms that give rise to a specific ability, the role of psychological or biological mediators of environmental challenges, and the existence of variables that have nonadditive effects with other variables. Vogel and Awh (2008) extend this argument in their discussion of three additional ways in which an idiographic approach can contribute to psychological theory: validating neurophysiological measures, demonstrating associations among constructs, and demonstrating dissociations among similar constructs. Thus, an idiographic approach, which complements the more typical nomethetic approach, can be applied in any domain to help elucidate psychological theory.

Together, the theory and data summarized in this special issue of *Current Directions in Psychological Science* highlight the notion that encephalization and the remarkable connectivity in the human brain provide the substrate for the integration of inputs from widely distributed neural regions (only some of which are amenable to current brain-imaging technology) whose activation and organization can be contextually determined. The distributed nature of and substantial overlap among the extant networks calls for a revision in our thinking about basic psychological constructs. The early reliance on introspection as a method of identifying elemental psychological processes led to a recognition of the category error—the intuitively appealing but often erroneous notion that the organization of psychological phenomena maps in a one-to-one fashion onto the organization of underlying neural substrates. Perception, memories, emotions, and beliefs were each once thought to be localized in distinct sites in the brain. The contributions to this special issue clearly indicate that psychological and behavioral concepts do not each map onto clear and identifiable "centers," but rather that each concept is associated with a distributed, interconnected set of neural regions. What appears at one point in time to be a singular theoretical construct (e.g., memory), when examined in conjunction with evidence from the brain (e.g., lesions, neuroimaging), may reveal a more complex and interesting organization at both levels (e.g., declarative vs. procedural memory processes). Conversely, what appeared to be distinct constructs (e.g., short- vs. long-term memory) may need to be reconsidered in light of new neuroscientific evidence. We suspect we are far from seeing the last of such revisions to psychological theories. It is only through these revisions, and corresponding refinements in our understanding and conceptions of the underlying neural functions, that we can reduce the category error and move toward an isomorphism between the psychological and biological domains.

Neuroimaging and work in neuroscience more generally are reshaping the constructs that are being used to build psychological theories. Psychological research during the 20th century resulted in many of the basic psychological elements derived from introspection to be recast as the product of multiple, more specific component processes. As illustrated by the articles in this special issue, many of these component processes involve a network of distributed, often recursively connected, interacting brain regions, with the different areas making specific, often task-modulated contributions. Moreover, a single neural region can often be involved in what have been treated as very different psychological processes. One implication is that what have been considered basic psychological or behavioral processes are being conceptualized as manifestations of computations performed by networks of widely distributed sets of neural regions.

How might these neural components be combined to produce distinct psychological processes? One metaphor is the Lego set, in which the computations performed in localized neural regions are fixed (like distinct Lego pieces), but different pieces and configurations of these building blocks produce different psychological processes. An alternative metaphor is the periodic table in chemistry, in which different neural component processes may have properties and affinities whose function (computation) depends on the network of areas with which they are combined. There is no evidence at present to favor either perspective, but the important point here is that they suggest very different ways of thinking about neural activity and psychological function.

In sum, neuroimaging work is leading to a rethinking of how psychological and neural functions are parcelled. For instance, the close proximity of motor control, emotional appraisal, attention, working memory, and behavioral regulation suggests that these functions may not be as separable as they are currently treated and studied. We may well need a new lexicon of constructs that are neither simply anatomical (e.g., Brodmann area 6 vs. Brodmann area 44) nor psychological (e.g., attention, memory), as we usher in a new era of psychological theory in which what constitutes elemental component processes (functional elements) are tied to specific neural mechanisms (structural elements) and in which the properties of interrelated networks of areas may indeed be more than the sum of the parts.

CONCLUSION

Critics who say neuroimaging is costly and has contributed little if anything to psychological theory sometime appear to expect the images of the working brain to come with labels regarding their cognitive functions. Although an adequate specification of

neurobiology should contribute to our understanding of cognitive architecture and function, our understanding of the relevant neurobiology is influenced strongly by our extant theoretical models regarding cognitive architecture and function (see Hagoort, 2008, this issue). The contributions to this special issue demonstrate that neuroimaging is an important new tool in the toolbox of psychological science, but one that is most productive scientifically when its use is guided by psychological theories and complemented by converging methodologies. This approach, in which theory and converging methods are used hand in hand to expand our understanding of the neural mechanisms involved in cognition and the contributions of individual and functionally connected brain regions to these processes, promises to advance psychological theory by suggesting functional representations and processes, by imposing significant constraints on these processes, and by producing not only new behavioral hypotheses but also new means of falsifying theoretical hypotheses.

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