Functional Neuroimaging and Psychology: What Have You Done for Me Lately?

Joseph M. Moran and Jamil Zaki

Abstract

■ Functional imaging has become a primary tool in the study of human psychology but is not without its detractors. Although cognitive neuroscientists have made great strides in understanding the neural instantiation of countless cognitive processes, commentators have sometimes argued that functional imaging provides little or no utility for psychologists. And indeed, myriad studies over the last quarter century have employed the technique of brain mapping—identifying the neural correlates of various psychological phenomena—in ways that bear minimally on psychological theory. How can brain mapping be made more relevant to behavioral scientists broadly? Here, we describe three trends that increase precisely this relevance: (i) the use of neuroimaging data to adjudicate between competing psychological theories through forward inference, (ii) isolating neural markers of information processing steps to better understand complex tasks and psychological phenomena through probabilistic reverse inference, and (iii) using brain activity to predict subsequent behavior. Critically, these new approaches build on the extensive tradition of brain mapping, suggesting that efforts in this area—although not initially maximally relevant to psychology—can indeed be used in ways that constrain and advance psychological theory. ■

INTRODUCTION

Scientists have measured blood flow in the living human brain for over 50 years (Ingvar & Lassen, 1961). In the last quarter century, however, the use of noninvasive techniques such as PET and (later) fMRI has exploded, and these techniques have emerged as near-ubiquitous methods in the psychologist's toolkit. fMRI and PET have been applied to domains as diverse as lie detection and love in search of the ever-elusive neural correlates of X. But, like Brussels sprouts at Thanksgiving dinner, some have wondered whether functional imaging really does complement the bird or serves solely as an attractive yet unpalatable garnish to the broader enterprise of psychological research. For instance, in a classic commentary on the study of emotion, Lazarus (1984) wrote that "[e]fforts to deal with areas of confusion in psychological theory by reduction to anatomy and physiology usually represent an attempt to clarify obscurities at one level of analysis by reference to obscurities at another." (p. 128). Lazarus' views are shared by many psychologists who often view neuroimaging as only dubiously relevant to their questions of interest. As these techniques reach the age of majority, it is worth taking stock of whether neuroimaging has matured enough to contribute meaningfully to psychology.

This reflection is especially pertinent given the collision of two tides in the general view of neuroimaging. On the one hand, people rate scientific explanations of psychological phenomena as more satisfying when they contain "brain scan" information—even when that information is logically unrelated to the explanation at hand (McCabe & Castel, 2008; Weisberg, Keil, Goodstein, Rawson, & Gray, 2008). On the other hand, members of the scientific community have invoked voodoo (Vul, Harris, Winkielman, & Pashler, 2009) and dead salmon (Bennett, Baird, Miller, & Wolford, 2011) in leveling frequent charges that neuroimaging has not (Coltheart, 2006; Cacioppo et al., 2003) or even cannot (Gul & Pesendorfer, 2008) constrain our understanding of psychological processes. Henson (2005, 2006) eloquently answered several such criticisms by outlining specific ways in which neuroimaging data can be brought to bear on theories at the psychological level of explanation. However, Henson's insights and those of others (e.g., Poldrack, 2006) have too often been ignored by both sides of the imaging hullaballoo: Critics have often failed to recognize some valid applications of neuroimaging, and neuroimaging has often been wielded in a manner ill-befitting its real utility.

The aims of the present article are thus simple. We will argue that the tradition of brain mapping in neuroimaging—although potentially a powerful source of insight for psychologists—has often been used in ways that provide little or no power to constrain psychological theory. Much of the data available from brain mapping studies do little to help psychologists working in classic cognitive domains (such as memory) to inform and advance information processing models. We believe that this observation has led some psychologists to take an overly cynical stance on the ability of imaging to make such contributions. Recent advances in neuroimaging design and analysis techniques

Harvard University

that we describe in this article may render this criticism outdated and as such suggest the emergence of a very exciting time in which complementary contributions may be forged across the disciplines of psychology and cognitive neuroscience. The goal for this article then is to emphasize ways in which neuroimaging has, can, and will be used to contribute knowledge to psychology that is difficult to glean by nonphysiological methods.

Here we will emphasize three such uses of imaging. First, the logic of association and dissociation allows for adjudication between competing psychological theories that make similar behavioral predictions. Second, the vast landscape of data amassed by the brain mapping tradition has allowed for consistent association between activity of a given brain region and likely information processing steps. This structure to function mapping has allowed researchers to draw relatively reliable probabilistic reverse inferences about the neural markers of specific cognitive processes, which can be used to reveal the mechanistic "ingredients" (the set of basic cognitive processes that combine to give rise to a complex psychological phenomenon) that support complex psychological phenomena. Third, neuroimaging has allowed for the investigation of brain–behavior relationships by using the brain as in independent rather than dependent variable, which has bolstered our ability to constrain psychological models with insights gained from neuroimaging.

Before describing these advances in detail, we will take a brief foray into the short, but remarkably extensive history, of neuroimaging research. The aim here is to chart the divergence of two related methods that have had powerful effects on the development of neuroimaging investigations and have helped to resolve intractable questions in psychology.

NEUROIMAGING—DOWN AT THE CROSSROADS

David Ingvar and colleagues' early work on CBF (e.g., Ingvar & Risberg, 1967) was pioneering in that it allowed biologists to measure the regional flow of blood in the brain in response to the performance of cognitive tasks such as reciting a series of digits in reverse (Risberg & Ingvar, 1973). This work was limited in spatial resolution and was too invasive for widespread use in typical populations, as it required injection of a radiotracer into the carotid artery but provided the foundation on which all later developments in neuroimaging stand. With the advent of PET in the 1980s, researchers could map changes in blood flow in a much more precise manner and with a bolus intravenous injection that made the technique simpler to implement and thus more scalable. The first demonstrations of distinct regions of the cortex responding to the presentation of single words (Petersen, Fox, Posner, Mintun, & Raichle, 1988) and to distinct visual stimuli (Fox et al., 1986) represented a crossroad in the history of behavioral science by promising psychologists the

unprecedented power of being able to look directly into the mind's black box and observe the living brain as it went about its business. Importantly, these two early studies (from the same research group) engendered radically different scientific approaches, all while using the same technique and ostensibly asking similar experimental questions. In one case (Petersen), the neuroimaging data were relevant directly to competing cognitive accounts of a psychological phenomenon, whereas in the other case (Fox), the neuroimaging data were relevant at the level of analysis of brain organization but were of no relevance to cognitive theory.

Begetting the first experimental tradition, Petersen et al. (1988) demonstrated that cortical activity discriminates between visually and auditorily presented words. Critically, these data argued directly in favor of one psychological interpretation of the functional organization of language and directly against another. Before this work, the prevailing view in clinical neurology was that words were initially encoded visually and then transformed into an auditory code for semantic and articulatory access (serial coding of linguistic information; Geschwind, 1965). Cognitive models, on the other hand, emphasized the existence of separate modality-specific codes for words presented visually and verbally. Petersen and colleagues showed with neuroimaging data that perception of visually and auditorily presented words activated different modality-specific regions of cortex, but that repetition or semantic processing of visually presented words did not activate the auditory regions suggested by Geschwind's model of transformation into auditory codes, arguing in favor of a more distributed model of word processing (parallel processing of linguistic codes; Coltheart, 1985; Rumelhart & McClelland, 1982).

Such uses of neuroimaging to constrain theory rely on forward inference (Henson, 2006), an approach that, in turn, depends on two complementary forms of logic. The first is the logic of dissociation (a type of reasoning allied with dissociations in neuropsychology; see, e.g., Bechara et al., 1995), which holds that qualitatively distinct patterns of brain activity accompanying different tasks or stimulus types (e.g., words presented visually vs. auditorily) imply psychological dissociation between these phenomena (existence of separable visual/verbal codes). This dissociability, in turn, can render single process models (e.g., of serial conversion between visual and verbal word codes) untenable. The second form of forward inference relies on the complementary logic of association, which holds that overlapping brain activation across two distinct tasks imply that similar cognitive mechanisms support those tasks. For example, both experiencing pain and observing a loved one experiencing pain engage regions in the so-called "pain matrix," including anterior insula, anterior cingulate, and SII (Kross, Berman, Mischel, Smith, & Wager, 2011; Singer et al., 2004). By the logic of association, this neural overlap implies that direct experience and observation of pain may share information processing features. Although the logic of association and dissociation is, of course, not

ironclad (both because neuroimaging is a relatively coarse physiological method and because the same brain region could be involved in multiple processes depending on contextual factors) forward inference allows neuroscientific data to provide converging, irreplaceable evidence about the mechanisms underlying numerous psychological phenomena.

The second research tradition sparked by early neuroimaging work has a more checkered past in psychology. It began with Fox et al.'s (1986) landmark article, which used PET to map the retinal projection topography of human primary visual cortex. Presciently, Fox et al. concluded that "[a]pplications of this strategy for high-resolution brain mapping potentially are quite broad" (p. 808). In so doing, Fox et al. (1986) fostered the research tradition of brain mapping—isolating the neural activity associated with particular stimuli or task demands—that has become extraordinarily commonplace in cognitive neuroscience. Many modern applications of this tradition make direct connection with longstanding theory in neurophysiology and produce rapid advances in our understanding of brain organization, as is the case with high-resolution retinotopic mapping studies (Logothetis, 2008). In addition, since Fox et al.'s early finding, brain mapping has been used to identify the neural correlates of such higher visual phenomena as the representation of faces (Parvizi et al., 2012; Kanwisher, McDermott, & Chun, 1997), bodies (Downing, Jiang, Shuman, & Kanwisher, 2001), and places (Epstein & Kanwisher, 1998), as well as countless nonvisual phenomena such as affective experience (Phillips et al., 1997) and theory of mind (Zaki, in press; Mitchell, 2009; Saxe, Carey, & Kanwisher, 2004; Saxe & Kanwisher, 2003).

Although it has been enormously popular, two major factors have curtailed psychologists' enthusiasm for brain mapping. First, the rise of multivoxel pattern analysis and other multivariate imaging techniques (Norman, Polyn, Detre, & Haxby, 2006) has called into question the basic tractability of simple one-to-one structure to function mappings in neuroscience. For example, multivoxel pattern analysis has revealed that the cluster of fusiform gyrus once attributed solely to perceiving faces (Kanwisher et al., 1997) may respond to other stimulus classes (e.g., places) as well (Hanson & Halchenko, 2008).

A second and more problematic issue is that, even if scientists can state unequivocally that a single brain region (e.g., visual area MT) responds to only one class of stimuli (e.g., motion; Tootell et al., 1995), this knowledge may not add anything of interest to psychological theory. The notion that the brain houses cognition surprises no one, and for many psychologists, knowing exactly which part of the brain instantiates a psychological process is of little use. For example, even if we could localize romantic love to the ACC (Bartels & Zeki, 2004), what does that tell us about love? Such a finding may tell us something about the ACC, but at Marr's (1982) computational and algorithmic levels, it tells us next to nothing about how the mind of a human represents love. That is, results from brain mapping often fail to connect in meaningful ways with psychological theory.

Here, we will argue that multiple advances in neuroimaging now provide such a connection. These novel techniques can further allow scientists to repurpose of the wealth of brain mapping data toward a clear goal: using the results from neuroimaging to refine thinking about human psychology.

WHAT HAVE YOU DONE FOR ME LATELY? PUTTING BRAIN MAPPING DATA TO WORK

Critically, expanding the contribution of neuroimaging to psychology requires scientists to repurpose the foundation of knowledge built by brain mapping research in novel ways. Just as learning the guitar requires the development and automation of a physical mapping between finger placement, strings, and sound produced, developing a semantic network of knowledge in neuroimaging has required the careful and repeated association of functions with structures. Now the challenge for the field has been to develop past the basic C chord shape and use this vast knowledge network as a basis for the inventive improvisation that is possible only once the fundamentals are sound. We believe that the following theoretical approaches provide just such a means, and allow neuroimaging to fulfill its promise as a technique truly complementary to psychological investigation, in at least two ways. The rest of the article will expand upon these advances.

PROBABILISTIC REVERSE INFERENCE

Among the primary complaints leveled against brain mapping is that it can support inaccurate or misleading reverse inference. That is, given that a particular brain region responds to a certain type of psychological phenomenon, researchers might—and often do—assume that engagement of that region in other settings implies that those settings include similar psychological ingredients. This is problematic because many brain regions likely support a slew of computations, as opposed to a single psychological mechanism. As such, assumptions about cognitive processes based on brain activity boil down to a researcher's highly subjective decisions about how to label a given locus of brain activity. For example, if a researcher documents activation in the medial-temporal lobe when a participant sees a word, does this mean that the participant is (i) encoding that word or (ii) thinking about a physical place that the word might conjure up for them? Both of these processes have been related to the medial-temporal lobe, and it is unclear, a priori, how to interpret this activity. At its worst, reverse inference has led to meaningless popular press assertions that—for example—voters feel "conflicted" about a political candidate based on activity in their ACC (Miller, 2008; Iacoboni et al., 2007) or that consumers love their iPhones based on activity in anterior insula (Lindstrom, 2011).

That said, a new tradition is carving out areas in which reverse inference can be both credible and useful. Specifically, researchers are now employing "brute force" data-informatic techniques that combine results from countless brain mapping studies with Bayesian inference to derive the actual probability that—given activity in a particular brain region—the study that observed this activation included a given psychological phenomenon (Poldrack, 2011; Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011; Yarkoni, Poldrack, Van Essen, & Wager, 2010). Such an approach can be executed both within and across data sets.

Reverse Inference within Data Sets

A number of pioneering studies in the last few years have used patterns of neural activation to draw accurate inferences about what participants are experiencing (e.g., which of a set of images a participant is viewing; see Kay, Naselaris, Prenger, & Gallant, 2008). This form of reverse inference not only demonstrates the power of brain activity to predict individual subjective states; more broadly, it suggests that scientists can leverage neuroimaging data to gather novel information about the "building blocks" of psychological tasks. Consider a recent study by Poldrack, Halchenko, and Hanson (2009), in which researchers used brain activity from a set of participants performing numerous tasks (e.g., risk taking, response inhibition, semantic judgments) to predict—based on neuroimaging data alone—which of a number of tasks new participants were completing. Beyond classifying these tasks with an impressive degree of accuracy, this analysis revealed which patterns of brain activity predicted the performance of each task and identified which common neural networks (e.g., dorsomedial thalamus and striatum) accurately predicted multiple tasks. Finally, this allowed Poldrack et al. to map these neural networks onto behavioral features of each task, and begin to build a "cognitive ontology" of psychological ingredients that might bind tasks together at the level of the brain (Damoiseaux et al., 2006). Such a cognitive ontology could codify findings from neuroimaging in a way that facilitates their application to psychology by, for example, allowing psychologists to generate new hypotheses regarding the cognitive processes involved in tasks that had previously been analyzed from the information processing perspective. This network-level analysis can provide new insights—directly from the function of the brain–about the common processes that characterize large numbers of cognitive and psychological phenomena. Because such a network-level analysis requires the assumption that regions interacting in networks are performing the same or similar computations, it is important to note that major advances in imaging analysis over the last 10 years or so have allowed us as a field to map out these networks intrinsically (at rest) and during task performance and in comparison with different developmental age groups (Dosenbach et al., 2010) and even different species (Vincent et al., 2007). One of the major findings from the functional connectivity literature is the remarkably powerful stability of involvement of given regions in given functional networks (Yeo et al., 2011). To the degree that one imagines that regions interact in a similar way when they form part of stable networks, we can presumably be more confident that the kinds of computations they engage in will be similar.

Reverse Inference across Data Sets

Probabilistic reverse inference can also be performed across data sets, for example, using meta-analytic techniques (Lamm, Decety, & Singer, 2011; Wager, Jonides, & Reading, 2004). In one particularly powerful example of this approach, Yarkoni and colleagues (www.neurosynth.org) amassed neuroimaging data from thousands of published neuroimaging articles and matched this activity to commonly used words in each manuscript. This technique allows for a formal characterization of how likely it is—given activation of a particular neural structure—that an article is assessing a particular psychological construct. First, articles are combed for how often they mention particular phrases of interest and are then divided into sets based on whether or not those phrases appear at high frequency (e.g., one mention of "self-referential" for every 1000 words). Then, activations reported in each article are extracted and tagged for having been reported (or not) with those keywords. Using this analysis engine, one can determine, for example, that 87% of articles reporting activation in the posterior cingulate cortex also included "self referential processing" at high frequency. Although this information is, in isolation, less than useful, it begins to allow us to weed out alternative cognitive explanations for the presence of activation in a given brain region. Because we know that 87% of posterior cingulate cortex articles also include the frequently used term "self referential processing," we can assume a relatively high level of confidence that self-referencing is one of the cognitive mechanisms at play in our own experiment that observed posterior cingulate activation. If "emotion," for example, is observed in only 4% of such articles, then it becomes disingenuous of us to argue that our posterior cingulate activation is reflecting emotional processing. This kind of quantification allows for much more rigorous application of reverse inference as researchers are no longer free to cherry pick examples from the literature where "brain region X has been shown in paper Y that examined cognitive process Z." The ultimate utility of this approach is in improving the quality, reliability, and utility of neuroimaging data, and further, these quantification values can only improve as more and more data are added to such databases. In turn, this allows much greater confidence in the results emerging from neuroimaging and thus much greater confidence in the relative strengths of structure-function mappings observed by cognitive neuroscientists. Although admittedly biased toward scientists' choices about how to describe their work (Poldrack, 2011), this approach offers a number of qualitative improvements over prior forms of

reverse inference. Not only does it allow for estimations of how strongly linked particular brain regions and psychological processes are, but it also allows for the estimation of base rates related to each brain region. For example, regions with high base rates of activation (e.g., the anterior insula, which is engaged across a significant minority of tasks) necessarily provide less power to predict participants' psychological states than those with low base rates of engagement. Thus, the use of large meta-analytic data sets allows researchers to use neuroimaging data in new ways (to perform reverse inference) and also to understand when imaging data will be most (and least) useful in drawing these inferences.

Summary

The development of methods for probabilistic reverse inference provides neuroscientists with deeply generative new tools for informing psychological theory. Critically, the meta-analytic techniques described here are wholly dependent on the exhaustive tradition of brain mapping. That is, without thousands of studies focused on localizing particular psychological tasks and experiences in the brain, scientists would have no foundation on which to model the power of brain activity to predict psychological experiences. This points out an intriguing twist in the relationship between neuroscience and psychology: Although brain mapping is often used in ways that do not directly inform psychological theory, it is this same approach that is now opening the door to a deeper understanding of how brain activity can indeed be used to constrain and build such theories.

THE BRAIN AS PREDICTOR

Another powerful method for constraining psychological theory using neuroimaging comprises flipping the brain's typical role: from that of a dependent variable to that of an independent variable (cf. Berkman & Lieberman, 2011). This broad approach has been used in many ingenious ways to provide at least two qualitative advancements to the role of neuroimaging in psychology. First, it refines our understanding of the functional role of brain activity as relevant to psychological phenomena. Second, it refines investigation of highly pertinent psychological phenomena (such as the experience of conscious will) whose mechanisms have remained underspecified using previously available methods. Although true causation requires random assignment of observations to different levels of an independent variable, we feel that each of the fMRI predictions detailed below have strong theoretical grounding and provide us with information that goes well beyond the observation that brain region X is associated with cognitive process Y. We first discuss results in the domain of decision-making, broadly construed and then outline a technical advance that allows direct use of the brain as an independent factor, real-time fMRI.

Decision-making

People often act in ways that contradict norms of rationality (Kahneman, 2003), and further fail to understand the sources of their choices and attitudes (Nisbett & Wilson, 1977; Festinger & Carlsmith, 1959). Although many psychologists and economists have explored the sources of irrationality (Wilson, Wheatley, Meyers, Gilbert, & Axsom, 2000; Tversky & Kahneman, 1974, 1981), using brain activity to predict subsequent decisions can provide converging evidence about the mechanisms that likely support both rational and irrational choices.

A growing body of work in neuroscientific research is now answering this call. For example, people often change their attitudes for reasons unbeknownst to them, and yet neuroscientists have been able use brain activity to predict later attitude change. In one instance of this effect, individuals who claim to equally prefer two items (e.g., two posters)—but are forced to choose between them—later claim to like the chosen item more than the nonchosen one (Brehm, 1956). A recent study found that this postchoice shift in preference can be predicted by activity in the ventral striatum (Sharot, De Martino, & Dolan, 2009), an area broadly involved in the computation of value (Rangel, Camerer, & Montague, 2008). This new insight from neuroimaging (that changes in attitude can be predicted before they occur and rely on changes in brain regions that signal value) stands in contrast to the prevailing views from cognitive dissonance theory— that we change our attitude postchoice because it is inconsistent with our behavior (Festinger, 1962), or from self-perception theory (Bem, 1967), that we infer our attitude from our behavior (e.g., "I must really like poster A, because that's the one I chose"). This particular observation represents well the use of a novel prediction approach that is entirely dependent upon yet goes beyond the tradition of brain mapping. Finally, individuals' preferences are often altered by others' opinions or persuasive messages (Latane, 1981; Asch, 1955). Recent work has reliably predicted such socially induced shifts in preference using brain activity in the ventral striatum (Zaki, Schirmer, & Mitchell, 2011; Klucharev, Hytonen, Rijpkema, Smidts, & Fernandez, 2009) as well as medial prefrontal cortical regions often associated with considering the minds of others (Falk, Berkman, Mann, Harrison, & Lieberman, 2010).

Brain activity can also predict interpersonal choices, such as those to altruistically help others. Historically, psychologists and philosophers have debated the mechanisms underlying altruism: Some theorists argue that individuals are instinctively selfish, but curtail these impulses to help others out of a sense of obligation or a strategic search for the benefits (e.g., reciprocity or reputation) that altruism can produce (DeWall, Baumeister, Gailliot, & Maner, 2008; Camerer & Fehr, 2006; Nowak, Page, & Sigmund, 2000). Others argue that altruism requires no such top–down control, but instead provides individuals with an intrinsic hedonic experience that prompts generous action

(de Waal, 2008; Andreoni, 1990). Neuroimaging data provide an important complementary source of evidence in this domain. This is because neuroimaging has produced reliable markers of both top–down control over prepotent responses (prominently in the anterior cingulate and lateral pFC; Botvinick, Braver, Barch, Carter, & Cohen, 2001) and the experience of reward and value-based decision-making (prominently in mesolimbic dopaminergic targets such as ventral striatum and ventromedial pFC; Rushworth, Noonan, Boorman, Walton, & Behrens, 2011; Knutson, Taylor, Kaufman, Peterson, & Glover, 2005). As such, brain activity in either of these systems before altruistic choices provides important supportive evidence for a control- or value-based view of altruism.

Recently, neuroimaging studies have demonstrated that neural markers of both of these processes can predict altruism, in a context-dependent fashion. In some cases, prosocial and cooperative behavior tracks with activity in regions in lateral pFC associated with control (Steinbeis, Bernhardt, & Singer, 2012; Spitzer, Fischbacher, Herrnberger, Gron, & Fehr, 2007), whereas other research demonstrates that activity in dopaminergic targets predicts prosociality (Zaki & Ochsner, 2012; Zaki & Mitchell, 2011; Hare, Camerer, Knoepfle, & Rangel, 2010; Harbaugh, Mayr, & Burghart, 2007) in a manner tightly linked to individuals' levels of prosocial choices both inside (Zaki, Lopez, & Mitchell, 2013) and outside the laboratory (Morelli, Rameson, & Lieberman, 2012). This suggests a dual-process model in which altruism can be driven by either value or control, in a context-dependent fashion. Critically, because these different patterns of brain activity underlie functionally similar (i.e., prosocial) choices, neuroimaging here affords an important complement to behavioral approaches to the study of prosociality.

Conscious Will

We have summarized multiple ways in which brain activation can predict later decisions. Libet and colleagues' early EEG experiments (Libet, Gleason, Wright, & Pearl, 1983) set the stage for later fMRI investigations of the controversial psychological concept of conscious will. Libet's work showed that readiness potentials can predict the onset of a self-guided decision up to a second before the behavior was initiated. In a fascinating fMRI experiment that cuts to the heart of research at the confluence of philosophy, psychology, and neuroscience, Soon and colleagues (Soon, Brass, Heinze, & Haynes, 2008) were able to use neuroimaging in a surprisingly novel manner—to reveal the outcome of a person's freely made decision several seconds before the participant acted upon that decision. In this task, participants viewed a stream of single letters (presented for 500 msec each) and during that stream were at liberty to decide when they were going to make a button press. Participants made their response and then indicated during the presentation of which letter (and hence at what time) they had made their decision.

Results revealed that activations in the medial pFC and medial parietal cortices predicted a participant's given response between 7 and 10 sec before the participant indicated that they had made their choice. These results, in concert with other work in neuroimaging that reveals a role of for these regions in self-relevance (e.g., Moran, Macrae, Heatherton, Wyland, & Kelley, 2006) provide us with curious information about the experience of conscious will that should spur development of theory in psychology.

Real-time fMRI

Scientists' understanding of brain–behavior relationships can be further advanced through a relatively recent innovation in neuroimaging, the use of real-time fMRI (Hinds et al., 2011; Park, Park, & Kim, 2009; deCharms et al., 2004). In many cases, this approach can provide even stronger evidence about the causal links between brain activity and experience. For instance, Yoo and colleagues (Yoo et al., 2012) monitored activation in the parahippocampal cortex (PHC) in real time, a region important for the encoding of visual scenes. Rather than presenting information about the activation to participants as others had done previously, Yoo and colleagues defined states of PHC activation as either "good" or "bad" for subsequent encoding and conditionalized their trials on this basis. When moment-to-moment PHC activation was low (i.e., "good" preparedness for encoding) or high ("bad" preparedness for encoding), the experimenters presented novel scenes to participants and revealed that later recognition memory performance was improved when scenes were presented immediately after the identification of "good" PHC brain states. This method is intimately predicated on prior brain mapping studies indicating PHC's involvement in memory formation for scenes, yet answers the charge that neuroimaging data cannot be used to imply that particular brain states cause particular cognitive changes in a subtle and satisfying manner.

Summary

A few things are worth noting about the brain as predictor approach. The lion's share of research employing this approach has been published in the last 5 years. Yet, for its short tenure, this approach has been used to predict behaviors across a number of varied domains, spanning choices made seconds to weeks after brain activity is recorded. More importantly, this tradition—although useful simply for its ability to clarify the functional role of brain activity—achieves its maximal utility when piggybacking on the tradition of brain mapping. In conjunction, these two approaches allow researchers to use neuroimaging not only to confirm psychological predictions but also to create new ones. This toolbox of techniques for imaging researchers can produce a better direct mapping between what we have discovered with behavioral methods over many years of research and what we have

discovered with neuroimaging methods over the recent past. The ability to use brain states to predict decisions and to improve memory are just two of many such exciting developments that are wholly dependent on the development of a technique that had been initially maligned as nothing more than phrenology in glorious Technicolor. We must first ask ourselves whether these innovations were foreseeable when those first murky images of the human brain at work began to swim into view and, if not, whether similarly exciting developments neuroimaging may hold in the next 20 years are, at present, equally opaque.

Conclusion

The path of developments in the industry of neuro-imaging exemplifies those in any economic industry. Early development of an exciting new technology (e.g., the home computer by Atari, Apple, and others) leads to a rapid expansion in the marketplace (e.g., the IBM-compatible PC), fueled by ever-decreasing barriers to entry and innovation on all sides (e.g., vast improvements in transistor technology and cheapening permanent storage). After this initial flush period of development, a tipping point occurs at which the market is unable to sustain the existence of so many suppliers of a once-rare-but-now-generic product. The market experiences a shakedown, during which suppliers who are unable to innovate disappear (e.g., Compaq), and innovative new technologies (the laptop, tablet computing) begin to dominate, precipitating the beginning of a new cycle of boom followed by shakedown. We believe that neuroimaging is at the precipice of its first shakedown and that this shakedown will necessarily entail the retooling of our ideas away from more traditional technologies (brain mapping studies) to newer, leaner, and more subtle "technologies," such as the brain as predictor approach, forward inference, and the causal application of fMRI, among others we have not had space to mention here.

In summary, whereas some of the earlier criticisms of neuroimaging are valid, we feel that they were largely based on an incomplete perception of the field, a field that, for reasons we have described here, is much more dynamic than some have presupposed and may more accurately be considered the pumpkin pie of psychology's Thanksgiving dinner: iconic, inviting, and containing something for us all to enjoy.

REFERENCES

Andreoni, J. (1990). Impure altruism and donations to public goods: A theory of warm-glow giving. *The Economic Journal, 100,* 464–477.

Asch, S. (1955). Opinions and social pressure. *Scientific American, 193,* 31–35.

Bartels, A., & Zeki, S. (2004). The neural correlates of maternal and romantic love. *Neuroimage, 21,* 1155–1166.

Bechara, A., Tranel, D., Damasio, H., Adolphs, R., Rockland, C., & Damasio, A. R. (1995). Double dissociation of conditioning and declarative knowledge relative to the amygdala and hippocampus in humans. *Science, 269,* 1115–1118.

Bem, D. J. (1967). Self-perception—An alternative interpretation of cognitive dissonance phenomena. *Psychological Review, 74,* 183–200.

Bennett, C. M., Baird, A. A., Miller, M. B., & Wolford, G. L. (2011). Neural correlates of interspecies perspective taking in the post-mortem atlantic salmon: An argument for proper multiple comparisons correction. *Journal of Serendipitous and Unexpected Results, 1,* 1–5.

Berkman, E. T., & Lieberman, M. D. (2011). What's outside the black box?: The status of behavioral outcomes in neuroscience research. *Psychological Inquiry, 22,* 100–107.

Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review, 108,* 624–652.

Brehm, J. (1956). Post-decision changes in the desirability of choice alternatives. *Journal of Abnormal & Social Psychology, 52,* 384–389.

Cacioppo, J. T., Berntson, G. G., Lorig, T. S., Norris, C. J., Rickett, E., & Nusbaum, H. (2003). Just because you're imaging the brain doesn't mean you can stop using your head: A primer and set of first principles. *Journal of Personality and Social Psychology, 85,* 650–661.

Camerer, C. F., & Fehr, E. (2006). When does "economic man" dominate social behavior? *Science, 311,* 47–52.

Coltheart, M. (1985). *Attention and performance XI* (Vol. 1988). Hilldale, NJ: Erlbaum.

Coltheart, M. (2006). What has functional neuroimaging told us about the mind (so far)? *Cortex; A Journal Devoted to the Study of the Nervous System and Behavior, 42,* 323.

Damoiseaux, J. S., Rombouts, S. A., Barkhof, F., Scheltens, P., Stam, C. J., Smith, S. M., et al. (2006). Consistent resting-state networks across healthy subjects. *Proceedings of the National Academy of Sciences, U.S.A., 103,* 13848–13853.

de Waal, F. B. (2008). Putting the altruism back into altruism: The evolution of empathy. *Annual Review of Psychology, 59,* 279–300.

deCharms, R. C., Christoff, K., Glover, G. H., Pauly, J. M., Whitfield, S., & Gabrieli, J. D. (2004). Learned regulation of spatially localized brain activation using real-time fMRI. *Neuroimage, 21,* 436–443.

DeWall, C. N., Baumeister, R. F., Gailliot, M. T., & Maner, J. K. (2008). Depletion makes the heart grow less helpful: Helping as a function of self-regulatory energy and genetic relatedness. *Personality and Social Psychology Bulletin, 34,* 1653–1662.

Dosenbach, N. U. F., Nardos, B., Cohen, A. L., Fair, D. A., Power, J. D., Church, J. A., et al. (2010). Prediction of individual brain maturity using fMRI. *Science, 329,* 1358–1361.

Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science, 293,* 2470–2473.

Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature, 392,* 598–601.

Falk, E. B., Berkman, E. T., Mann, T., Harrison, B., & Lieberman, M. D. (2010). Predicting persuasion-induced behavior change from the brain. *Journal of Neuroscience, 30,* 8421–8424.

Festinger, L. (1962). Cognitive dissonance. *Scientific American, 207,* 93–102.

Festinger, L., & Carlsmith, J. M. (1959). Cognitive consequences of forced compliance. *Journal of Abnormal Psychology, 58,* 203–210.

Fox, P. T., Mintun, M. A., Raichle, M. E., Miezin, F. M., Allman, J. M., & Van Essen, D. C. (1986). Mapping human visual cortex with positron emission tomography. *Nature, 323,* 806–809.

Geschwind, N. (1965). Disconnexion syndromes in animals and man. Part 1. *Brain, 88,* 237–294.

Gul, F., & Pesendorfer, W. (2008). The case for mindless economics. In A. Caplin & A. Shotter (Eds.), *The foundations of positive and normative economics* (pp. 3–42). Oxford, UK: Oxford University Press.

Hanson, S. J., & Halchenko, Y. O. (2008). Brain reading using full brain support vector machines for object recognition: There is no "face" identification area. *Neural Computation, 20,* 486–503.

Harbaugh, W. T., Mayr, U., & Burghart, D. R. (2007). Neural responses to taxation and voluntary giving reveal motives for charitable donations. *Science, 316,* 1622–1625.

Hare, T. A., Camerer, C. F., Knoepfle, D. T., & Rangel, A. (2010). Value computations in ventral medial prefrontal cortex during charitable decision making incorporate input from regions involved in social cognition. *Journal of Neuroscience, 30,* 583–590.

Henson, R. (2005). What can functional neuroimaging tell the experimental psychologist? *Quarterly Journal of Experimental Psychology A, 58,* 193–233.

Henson, R. (2006). Forward inference using functional neuroimaging: Dissociations versus associations. *Trends in Cognitive Sciences, 10,* 64–69.

Hinds, O., Ghosh, S., Thompson, T. W., Yoo, J. J., Whitfield-Gabrieli, S., Triantafyllou, C., et al. (2011). Computing moment-to-moment BOLD activation for real-time neurofeedback. *Neuroimage, 54,* 361–368.

Iacoboni, M., Freedman, J., Kaplan, J., Jamieson, K. H., Freedman, T., Knapp, B., et al. (2007). This is your brain on politics. *New York Times, 11,* 1–2.

Ingvar, D. H., & Lassen, N. A. (1961). Quantitative determination of regional cerebral blood-flow in man. *Lancet, 2,* 806–807.

Ingvar, D. H., & Risberg, J. A. (1967). Increase of regional cerebral blood flow during mental effort in normals and in patients with focal brain disorders. *Experimental Brain Research, 3,* 195–211.

Kahneman, D. (2003). A perspective on judgment and choice: Mapping bounded rationality. *American Psychologistl, 58,* 697–720.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience, 17,* 4302–4311.

Kay, K. N., Naselaris, T., Prenger, R. J., & Gallant, J. L. (2008). Identifying natural images from human brain activity. *Nature, 452,* 352–355.

Klucharev, V., Hytonen, K., Rijpkema, M., Smidts, A., & Fernandez, G. (2009). Reinforcement learning signal predicts social conformity. *Neuron, 61,* 140–151.

Knutson, B., Taylor, J., Kaufman, M., Peterson, R., & Glover, G. (2005). Distributed neural representation of expected value. *Journal of Neuroscience, 25,* 4806–4812.

Kross, E., Berman, M. G., Mischel, W., Smith, E. E., & Wager, T. D. (2011). Social rejection shares somatosensory representations with physical pain. *Proceedings of the National Academy of Sciences, U.S.A., 108,* 6270–6275.

Lamm, C., Decety, J., & Singer, T. (2011). Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. *Neuroimage, 54,* 2492–2502.

Latane, B. (1981). The psychology of social impact. *American Psychologist, 36,* 343–356.

Lazarus, R. S. (1984). On the primacy of cognition. *American Psychologist, 39,* 124–129.

Libet, B., Gleason, C. A., Wright, E. W., & Pearl, D. K. (1983). Time of conscious intention to act in relation to onset of cerebral-activity (readiness-potential)—The unconscious initiation of a freely voluntary act. *Brain, 106,* 623–642.

Lindstrom, M. (2011). You love your iPhone. Literally. *New York Times,* p. A21.

Logothetis, N. K. (2008). What we can do and what we cannot do with fMRI. *Nature, 453,* 869–878.

Marr, D. (1982). Vision: A computational investigation into the human representation and processing of visual information. Henry Holt and Co. Inc., New York, NY.

McCabe, D. P., & Castel, A. D. (2008). Seeing is believing: The effect of brain images on judgments of scientific reasoning. *Cognition, 107,* 343–352.

Miller, G. (2008). Neuroimaging. Growing pains for fMRI. *Science (New York, NY), 320,* 1412.

Mitchell, J. P. (2009). Inferences about mental states. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, 364,* 1309–1316.

Moran, J. M., Macrae, C. N., Heatherton, T. F., Wyland, C. L., & Kelley, W. M. (2006). Neuroanatomical evidence for distinct cognitive and affective components of self. *Journal of Cognitive Neuroscience, 18,* 1586–1594.

Morelli, S. A., Rameson, L. T., & Lieberman, M. D. (2012). The neural components of empathy: Predicting daily prosocial behavior. *Social Cognitive and Affective Neuroscience.* doi:10.1093/scan/nss088.

Nisbett, R., & Wilson, T. (1977). Telling more than we can know: Verbal reports on mental processes. *Psychological Review, 84,* 231–259.

Norman, K. A., Polyn, S. M., Detre, G. J., & Haxby, J. V. (2006). Beyond mind-reading: Multi-voxel pattern analysis of fMRI data. *Trends in Cognitive Sciences, 10,* 424–430.

Nowak, M. A., Page, K. M., & Sigmund, K. (2000). Fairness versus reason in the ultimatum game. *Science, 289,* 1773–1775.

Park, H. J., Park, B., & Kim, D. J. (2009). Real-time functional MRI for patient monitoring during a language task. *Conference IEEE Engineering in Medicine and Biology Society, 2009,* 5389–5392.

Parvizi, J., Jacques, C., Foster, B. L., Withoft, N., Rangarajan, V., Weiner, K. S., et al. (2012). Electrical stimulation of human fusiform face-selective regions distorts face perception. *The Journal of Neuroscience, 32,* 14915–14920.

Petersen, S. E., Fox, P. T., Posner, M. I., Mintun, M., & Raichle, M. E. (1988). Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature, 331,* 585–589.

Phillips, M. L., Young, A. W., Senior, C., Brammer, M., Andrew, C., Calder, A. J., et al. (1997). A specific neural substrate for perceiving facial expressions of disgust. *Nature, 389,* 495–498.

Poldrack, R. A. (2006). Can cognitive processes be inferred from neuroimaging data? *Trends in Cognitive Sciences, 10,* 59–63.

Poldrack, R. A. (2011). Inferring mental states from neuroimaging data: From reverse inference to large-scale decoding. *Neuron, 72,* 692–697.

Poldrack, R. A., Halchenko, Y. O., & Hanson, S. J. (2009). Decoding the large-scale structure of brain function by classifying mental states across individuals. *Psychological Science, 20,* 1364.

Rangel, A., Camerer, C., & Montague, P. R. (2008). A framework for studying the neurobiology of value-based decision making. *Nature Reviews Neuroscience, 9,* 545–556.

Risberg, J. A., & Ingvar, D. H. (1973). Patterns of activation in the grey matter of the dominant hemisphere during memorizing and reasoning. A study of regional cerebral blood flow changes during psychological testing in a group of neurologically normal patients. *Brain: A Journal of Neurology, 96,* 737–756.

Rumelhart, D. E., & McClelland, J. L. (1982). An interactive activation model of context effects in letter perception: Part 2. The contextual enhancement effect and some tests and extensions of the model. *Psychological Review, 89,* 60–94.

Rushworth, M. F. S., Noonan, M. A. P., Boorman, E. D., Walton, M. E., & Behrens, T. E. (2011). Frontal cortex and reward-guided learning and decision-making. *Neuron, 70,* 1054–1069.

Saxe, R., Carey, S., & Kanwisher, N. (2004). Understanding other minds: Linking developmental psychology and functional neuroimaging. *Annual Review of Psychology, 55,* 87–124.

Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people. The role of the temporo-parietal junction in "theory of mind". *Neuroimage, 19,* 1835–1842.

Sharot, T., De Martino, B., & Dolan, R. J. (2009). How choice reveals and shapes expected hedonic outcome. *Journal of Neuroscience, 29,* 3760–3765.

Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R. J., & Frith, C. D. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science, 303,* 1157–1162.

Soon, C. S., Brass, M., Heinze, H. J., & Haynes, J. D. (2008). Unconscious determinants of free decisions in the human brain. *Nature Neuroscience, 11,* 543–545.

Spitzer, M., Fischbacher, U., Herrnberger, B., Gron, G., & Fehr, E. (2007). The neural signature of social norm compliance. *Neuron, 56,* 185–196.

Steinbeis, N., Bernhardt, B., & Singer, T. (2012). Impulse control and underlying functions of the left DLpFC mediate age-related and age-independent individual differences in strategic social behavior. *Neuron, 73,* 1040–1051.

Tootell, R. B., Reppas, J. B., Dale, A. M., Look, R. B., Sereno, M. I., Malach, R., et al. (1995). Visual motion aftereffect in human cortical area MT revealed by functional magnetic resonance imaging. *Nature, 375,* 139–141.

Tversky, A., & Kahneman, D. (1974). Judgment under uncertainty: Heuristics and biases. *Science, 185,* 1124–1131.

Tversky, A., & Kahneman, D. (1981). The framing of decisions and the psychology of choice. *Science, 211,* 453–458.

Vincent, J., Patel, G., Fox, M., Snyder, A. Z., Baker, J., Van Essen, D., et al. (2007). Intrinsic functional architecture in the anaesthetized monkey brain. *Nature, 447,* 83–86.

Vul, E., Harris, C., Winkielman, P., & Pashler, H. (2009). Puzzlingly high correlations in fMRI studies of emotion, personality, and social cognition. *Perspectives on Psychological Science, 4,* 274–290.

Wager, T. D., Jonides, J., & Reading, S. (2004). Neuroimaging studies of shifting attention: A meta-analysis. *Neuroimage, 22,* 1679–1693.

Weisberg, D. S., Keil, F. C., Goodstein, J., Rawson, E., & Gray, J. R. (2008). The seductive allure of neuroscience explanations. *Journal of Cognitive Neuroscience, 20,* 470–477.

Wilson, T. D., Wheatley, T., Meyers, J. M., Gilbert, D. T., & Axsom, D. (2000). Focalism: A source of durability bias in affective forecasting. *Journal of Personality and Social Psychology, 78,* 821–836.

Yarkoni, T., Poldrack, R. A., Nichols, T. E., Van Essen, D. C., & Wager, T. D. (2011). Large-scale automated synthesis of human functional neuroimaging data. *Nature Methods, 8,* 665–670.

Yarkoni, T., Poldrack, R. A., Van Essen, D. C., & Wager, T. D. (2010). Cognitive neuroscience 2.0: Building a cumulative science of human brain function. *Trends in Cognitive Sciences, 14,* 489–496.

Yeo, B. T. T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., et al. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *Journal of Neurophysiology, 106,* 1125–1165.

Yoo, J. J., Hinds, O., Ofen, N., Thompson, T. W., Whitfield-Gabrieli, S., Triantafyllou, C., et al. (2012). When the brain is prepared to learn: Enhancing human learning using real-time fMRI. *Neuroimage, 59,* 846–852.

Zaki, J. (in press). Cue integration: A common framework for physical perception and social cognition. *Perspectives on Psychological Science*.

Zaki, J., Lopez, G., & Mitchell, J. (2013). Person-invariant value: Orbitofrontal activity tracks revealed social preferences. *Social Cognitive and Affective Neuroscience*. doi:10.1093/scan/nst005.

Zaki, J., & Mitchell, J. (2011). Equitable decision making is associated with neural markers of subjective value. *Proceedings of the National Academy of Sciences, U.S.A., 108,* 19761–19766.

Zaki, J., & Ochsner, K. (2012). The neuroscience of empathy: Progress, pitfalls, and promise. *Nature Neuroscience, 15,* 675–680.

Zaki, J., Schirmer, J., & Mitchell, J. (2011). Social influence modulates the neural computation of value. *Psychological Science, 22,* 894–900.