

## LOSING OUR BRAINLESS MINDS: HOW NEUROIMAGING INFORMS COGNITION

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### INTRODUCTION

Coltheart (2006, this issue) is drawn to the analogy of the brain as hardware and psychological processes as software. This view relates to Marr's (1982) important distinction between different levels of analysis, and in particular to his distinction between the algorithm and how it is implemented. Coltheart (2006, this issue) thinks that neuroimaging only tells us about implementation. More specifically, Coltheart (2006, this issue) suggests that neuroimaging provides information about the localization of psychological functions but tells us little or nothing about the functions themselves. Coltheart's (2006, this issue) doubts are further fueled by his review of the literature, where he finds "that no functional neuroimaging research to date has yielded data that can be used to distinguish between competing psychological theories". If we cannot find a counterexample to this claim, he suggests we reconsider our belief that neuroimaging can tell us about cognition.

We will respond to Coltheart's (2006, this issue) challenge with concrete examples from functional neuroimaging studies. First, however, we will consider the plausibility of his claim from a theoretical perspective.

Blood oxygenation level dependent (BOLD) signals measured with functional magnetic resonance imaging (fMRI) in the living human brain provide an indirect but reliable measure of neuronal activity under different task conditions. The correspondence between BOLD and more direct measures of neural activity is now well established: while single unit recordings primarily register the neuronal output of an area, BOLD signals reflect the time-integrated sum of the excitatory and inhibitory inputs and local processing within an area (Logothetis et al., 2001). Since BOLD is clearly complementary to other neural measures, we may begin by considering Coltheart's (2006, this issue) challenge as reflecting

a broader pessimism about the relevance of studying neural processes for understanding cognition. Later, we will consider the question of whether specific difficulties arise for fMRI.

### THE HARDWARE AND THE SOFTWARE

Psychological processes and the neural structures or signals that implement them are different sorts of things. It does not follow that they should be studied independently of each other. Cognitive processes mediate the transformation of information from stimulus to response. Psychology tests hypotheses about these processes by carefully controlling the input to the cognitive apparatus and observing subtle changes in the output, via behavioral measures such as accuracy and speed of response. Yet between stimulus and response, information undergoes a number of transformations across multiple areas and pathways. Reconstructing these transformations may not always be feasible just from looking at the input and the output. Physiological measures are important because they offer a peek inside the system at intermediate representations along the chain of information processing. There is increasing evidence that cognitive processes rely on recursive processing, oscillations, and synchrony mechanisms that clearly influence the algorithmic level, and that are largely impervious to behavioral analysis. The role of these intermediate representations in the production of behavior can be examined by relating variability in those representations, as indexed by neural activity, to variation in performance measures. Work establishing a link between activity of middle temporal lobe neurons and performance on a motion discrimination task represents a classic example (Britten et al., 1992).

Furthermore, the analysis of neural data, especially across species (e.g., human and non-human primates) affords an evolutionary perspective that is invaluable for understanding the human mind. It is our opinion that high-level cognitive mechanisms are likely 'patched up' heirs of lower-level sensory-motor mechanisms. That is,

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a plausible progression for the evolution of higher cognitive functions involves building upon preexisting mechanisms, which evolved for a more basic purpose, and that were maintained by evolution because of their success in solving specific computational problems. For example, the discovery of mirror neurons in monkeys and humans, recruited both during the performance and perception of purposeful actions, provides a simple mechanism to explain high-level cognitive functions such as action understanding and imitation learning (Rizzolatti and Craighero, 2004). Knowledge of how basic processes are implemented can therefore provide important clues into the nature of higher cognitive processes – causing us to chunk the cognitive apparatus into components that cannot be discerned by looking at behavior alone.

Next, let us consider the question of whether neuroimaging is a particularly disadvantaged child in the family of methods for measuring neural activity – a claim that would buttress Coltheart's (2006, this issue) argument. Neuroimaging, like electrophysiology, provides a view of the software running on the hardware (*not* the hardware alone). The two methods are complementary, but the differences in temporal and spatial resolution yield different affordances. Single cell recordings provide a privileged view of how information is coded in the brain. Electrophysiological data therefore relate well to the algorithmic level of analysis, because understanding an algorithm involves understanding the representations it works on, and how it transforms those representations (Marr, 1982). Positron emission tomography (PET) and fMRI, on the other hand, are most immediately suited for determining which parts of the brain are preferentially engaged by specific tasks. It is important to acknowledge that this view does not provide information that is *directly* suggestive about the algorithms used. As Coltheart (2006, this issue) picks up on, many neuroimaging studies have employed a simple logic: subjects are scanned while they perform (at least) two tasks, investigators assume a particular task analysis which identifies a particular psychological process as differentially engaged between the tasks, and the investigators conclude that this function can be localized to particular brain areas. Yet it is important to realize that this "localization of function" methodology only represents the initial discovery phase of investigation. Although neuroimaging researchers have had little choice other than to assume a plausible analysis of the tasks they use; the reality is that, more than fifty years since the cognitive revolution, behavioral psychology has not been able to decide upon even a *crude initial description* of the cognitive processes involved in many simple tasks. Far from being parasitic on psychology, neuroimaging promises to help with this problem. Our example

of inefficient search (see below) demonstrates how the direction of scientific inference can rapidly reverse, so that knowledge about brain activation informs task analysis, rather than *vice-versa*. In addition, recent work demonstrates that fMRI, just like electrophysiology, can be used to address how information is coded in the brain. For instance, it has been shown that one parietal attention area contains a map of the contra-lateral visual field (Serenio et al., 2001), and this map is updated following changes in gaze direction (Medendorp et al., 2003; Merriam et al., 2003). These results strongly suggest that a specific human parietal area uses retinotopic and eye movement signals to encode stimulus position in a gaze-centered frame of reference, as opposed to other possible schemes. In addition, examining brain activity on a trial-by-trial basis, it has been possible to relate behavioral variability to variability in neural signals (Ress et al., 2000; Pessoa and Padmala, 2005; Sapir et al., 2005) and quantify their contribution to behavioral performance. Thus neuroimaging methods are developing that do directly inform the algorithmic level of analysis, and can also determine which intermediate representations are linked to specific behaviors.

#### THE REAL CHALLENGE

Taking these points into consideration, we find it hard to see Coltheart's (2006, this issue) challenge as a compelling test of *whether* neuroimaging can tell us about the mind. Nonetheless, it is useful to consider *how* neuroimaging can tell us about the mind. Further, as Coltheart (2006, this issue) has stressed, it is instructive to look beyond theoretical perspectives, and examine actual empirical grounds. Our first example is brief but illustrates an important point that Coltheart (2006, this issue) appears to have overlooked: neuroimaging data need not "distinguish between competing psychological theories" in order to tell us about cognition. Our second example is more substantive and directly answers to Coltheart's (2006, this issue) challenge; the most important lesson to take away from this example is that "localization of function" and investigations of cognition are not distinct enterprises. Our final and concluding point is that as our knowledge of the brain increases, so will the role of neuroimaging as a tool to study cognition.

#### EXOGENOUS RE-ORIENTING

Cognitive psychology has traditionally made a division between top-down "endogenous" orienting and bottom-up "exogenous" orienting. However, recent neuroimaging work has suggested a novel division within exogenous orienting (for review,

see Corbetta and Shulman, 2002). Neuroimaging evidence indicates that the same neural network mediates orienting of attention to anticipated goal-relevant stimulus information or to salient task-irrelevant sensory stimuli (dorsal fronto-parietal network), whereas a distinct set of areas mediates the reorienting of attention to unexpected or low frequency events (ventral fronto-parietal network) (Kincade et al., 2005). This model has been recently supported by lesion data in patients with spatial neglect (Husain and Rorden, 2003). The implication that separate sets of areas underlie these processes provides an important constraint on theories of attentional control. Thus even neuroimaging studies of localization can make an important contribution through generating strong novel hypotheses about cognitive function, rather than distinguishing between pre-existing theories.

#### INEFFICIENT SEARCH

Our second example answers exactly to Coltheart's (2006, this issue) challenge of using neuroimaging data to "distinguish between competing psychological theories". Some search displays promote "efficient search" in which reaction time is largely independent of set size (a 'flat' search function) whereas other displays promote 'inefficient search' in which reaction time is proportional to set size (a 'sloped' search function). Targets defined by a single feature, such as color, are usually associated with efficient search. Targets defined by the conjunction of two features, such as color and form, are usually associated with inefficient search. In the early 1990's, two competing theories had been proposed, both of which could account for the sloped search function seen in inefficient search. It is worth noting that, even after 25 years of behavioral research on visual search, these theories reflected uncertainty concerning the most basic characterization of the system.

$T_a$ : inefficient visual search uses a parallel search mechanism (Duncan and Humphreys, 1989).

$T_b$ : inefficient visual search uses a serial search mechanism (Treisman and Gelade, 1980).

In parallel search, all items in the search array are processed simultaneously, and the process of searching does not involve any shifts in the location of attention. In serial search, there are multiple shifts of spatial attention to discrete locations until the target is found. According to  $T_a$ , both efficient and inefficient search involve parallel search mechanisms. According to  $T_b$ , efficient search involves a parallel search mechanism, whereas inefficient search involves a serial search mechanism. Corbetta et al. (1995) designed a neuroimaging experiment with the explicit purpose of adjudicating between these theories. The logic of this experiment relied on previous work (Corbetta

et al., 1993) localizing the process of discrete covert attention shifts to a region in posterior parietal cortex. Assuming a consistent structure to function mapping (Henson, 2005), activity in posterior parietal cortex can be used to index the process of shifts in spatial attention.  $T_b$  predicts greater activity during inefficient search relative to efficient search, because inefficient search involves multiple shifts in spatial attention whereas efficient search does not. In contrast,  $T_a$  predicts equal levels of activity in the two conditions, because neither involves shifts in attention. Corbetta et al. (1995) found greater posterior parietal cortex activity during inefficient than during efficient search. They concluded that the neuroimaging data supported  $T_b$ , the serial mechanism of inefficient search.

Did this experiment definitively resolve the question of serial *versus* parallel mechanisms in inefficient search? It did not, because later experiments generated uncertainty about the specificity of the structure to function mapping, i.e. which processes are implemented by posterior parietal cortex. For example, Wojciulik and Kanwisher (1999) provided evidence that posterior parietal cortex plays a more general role in attentional selection rather than a role specific to spatial attention shifts. Later work, however, has supported Corbetta et al.'s (1995) original conclusion. Nobre et al. (2003) ruled out one possible confound, by showing that feature conjunction alone does not activate posterior parietal cortex. Müller et al. (2003) provided supporting evidence, reporting that posterior parietal cortex activity increases parametrically with set size during inefficient search. Other supporting evidence comes from Ashbridge et al. (1997), who found that inactivation of posterior parietal cortex with transcranial magnetic stimulation (TMS) only impairs search for conjunction but not feature targets.

The important point to note is that while the Corbetta et al. (1995) study did not definitively resolve the debate, it altered it in a very significant way. Specifically, it altered it so that work on localization of function directly impacts theorizing about cognitive processes. It is now the case that virtually all accounts of visual search, including parallel accounts (e.g., Deco et al., 2002), both acknowledge and address posterior parietal cortex involvement (for reviews, see Chelazzi, 1999; Shipp, 2004). The issue of what processes are involved in inefficient search now hinges, at least in part, on what functions can be attributed to posterior parietal cortex.

#### BEYOND LOCALIZATION TO FUNCTION

Current efforts to map out brain mechanisms of cognition make heavy use of psychological

theories, for the simple reason that these are the only theories available at the moment. Yet there is little doubt that these theories can be improved upon, and there are strong reasons to expect that sophisticated, accurate models of cognitive mechanisms will increasingly come to depend on the interplay between behavioral and neural constraints. We have shown how neuroimaging work is already beginning to evolve from the simple “localization of function” logic, which relies on pre-existing psychology theory, to studies that even while still relying on localization, are helping to generate novel hypotheses about cognitive architecture, and adjudicate between pre-existing cognitive theories. Furthermore as we learn to use fMRI in new ways, we will get more insight into *how* information is coded in the brain and how these representations contribute to behavior. It is easy to predict that neural data, including neuroimaging, will show unexpected and counterintuitive collusions or dissociations between known processes, as well as identify novel operations of the mind. Coltheart (2006, this issue) points out that, so far, neuroimaging has cost a lot and told us little about cognition. We doubt this will be the story in another twenty years. Neuroimaging demands a heavy initial investment. It also offers a very large pay-off. We are confident the brain will add a lot to the mind.

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