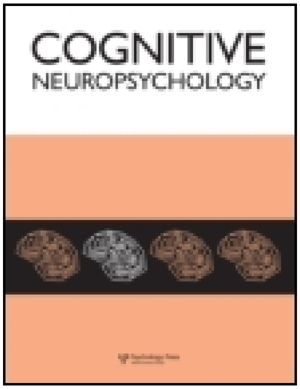

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The specialization of function: Cognitive and neural perspectives

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The specialization of function: Cognitive and neural perspectives

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A unifying theme that cuts across all research areas and techniques in the cognitive and brain sciences is whether there is specialization of function at levels of processing that are "abstracted away" from sensory inputs and motor outputs. Any theory that articulates claims about specialization of function in the mind/brain confronts the following types of interrelated questions, each of which carries with it certain theoretical commitments. What methods are appropriate for decomposing complex cognitive and neural processes into their constituent parts? How do cognitive processes map onto neural processes, and at what resolution are they related? What types of conclusions can be drawn about the structure of mind from dissociations observed at the neural level, and vice versa? The contributions that form this Special Issue of *Cognitive Neuropsychology* represent recent reflections on these and other issues from leading researchers in different areas of the cognitive and brain sciences.

Keywords: Modularity; Additive factors; Brain function; Cognition; Neuropsychology; Functional magnetic resonance imaging.

Functional specialization is a property of biological systems generally. Specialization of function in the human brain is most clear at the periphery of the system at the levels of primary sensory and motor systems. Neuroscientific, psychophysical, and cognitive neuropsychological research over the last half century has demonstrated the existence of cortical maps in primary input and output systems that are organized topographically. Topographic organization—for instance, of eccentricity preferences in early visual cortex—indicates a high degree of specialization of function in the cortical representation of a psychophysical continuum, such as spatial location with respect to the fovea. However, beyond the primary input and output systems there is little agreement as to whether there is specialization of function and, if so, over what cognitive dimensions that specialization should be understood to operate. Perhaps one of the unifying themes that cuts across all research areas and techniques in the cognitive and brain sciences is whether there is specialization of function at levels of processing that are "abstracted away" from sensory inputs and motor outputs.

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The contributions that are collected together within this Special Issue of *Cognitive Neuropsychology* represent recent reflections on this issue from leading researchers in different areas of the cognitive and brain sciences.

Cognitive neuropsychology—the method of revealing the organization of the mind from patterns of spared and impaired performance in brain-damaged individuals—has played a central role in the development of claims about the specialization of function in the human brain for well over a century (e.g., since the contributions of Broca and Wernicke). This method is based on the supposition that it is possible to dissociate different components of cognition through damage to the brain, which has led to the interesting consideration of whether the mere fact that the method works implies certain properties about functional specialization in the human brain (e.g., Caramazza, 1992; Coltheart, 1989; Dunn & Kirsner, 2003; Farah & McClelland, 1992; Rapp, 2001; Shallice, 1988). More recently, with the widespread use of functional neuroimaging techniques such as functional magnetic resonance imaging (fMRI), there has been renewed interest in the mapping of cognitive processes onto neural events and substrates (e.g., Coltheart, 2006; Henson, 2006; Poldrack, 2006; Posner, 2003; Uttal, 2011). But even setting aside brain organization, research into the organization of cognitive processes has fuelled intense debates about whether specialized representations should be posited, or whether the empirical phenomena can be explained without assuming specialization of representational content. Connectionist modelling has made a particularly important contribution to these debates, as it can offer existence proofs of why specialized content need not be assumed in order to observe a particular empirical result (McClelland, Rumelhart, et al., 1986; Rumelhart, McClelland, et al., 1986).

The cognitive revolution was founded on the methodological commitment that an adequate explanation of behaviour must make reference to cognitive processes, and that it is possible to understand the structure and content of the mind through experiments that tease apart complex processes into their component parts. Saul Sternberg's contributions to cognitive psychology, from his now classic 1969 theoretical article (Sternberg, 1969a) through to his most recent contribution on this issue (Sternberg, 2011), are some of the most enduring contributions that have been made to the science of the mind. Motivated in part by the early work of F. C. Donders (Donders, 1868), Sternberg's classic studies (Sternberg, 1966, 1969b) introduced the "additive factors approach". In his initial studies, he systematically varied memory load and measured its effect on speed and accuracy of recall in order to assess the cumulative effects of information-processing stages. Subjects were given a list of *N* numerals to memorize and were then asked whether a test numeral had appeared in the list. Sternberg showed that each additional item in the initial memory set added about 30 to 40 milliseconds to search time, indicating that subjects were engaging in a serial rather than a parallel search. In addition, he showed that the time to respond at test increased linearly with the total size of the memory set, indicating that subjects engage in an exhaustive search, rather than a self-terminating search. Those systematic experimental manipulations provided evidence for cumulative effects of component stages of information processing. More broadly, the introduction of additive factors logic provided a toolbox with which to decompose complex series of cognitive processes into their elementary operations and then to study the content and dynamics of each operation or stage.

We are now at a point where it is possible to direct the insights from many different methods toward a single question of how the mind works—using behavioural performance in normal subjects or individuals with brain damage, neural activation as measured with fMRI, the effects on cognition and neural function of transcranial magnetic stimulation (TMS), neurophysiological recording and stimulation studies in both nonhuman primates and humans, electroencephalography (EEG), magnetoencephalography (MEG), optical imaging, and more. We have the tools to measure and probe the human mind at almost all levels of analysis. However, the strength of our science will not depend on the tools, but on how they are used to develop new ideas and resolve existing issues. This Special Issue of *Cognitive Neuropsychology* is a step in that direction. An element common to all of the papers in this volume, and which distinguishes this group of articles, is the careful scrutiny applied to the role of functional specialization in developing a theory of how the mind/brain works.

The many meanings of "modularity"

Modularity, across the many uses of the term, can be understood as a special case of specialization of function. Hypotheses about cognitive and brain function gain traction when embedded within, or contrasted against, a coherent theoretical framework of modularity. However, there are a number of meanings that have been given to the theoretical term "modularity". In some cases, the different uses of the term "modularity" have led to dichotomies in the cognitive science literature that disappear when the meanings of the word are ironed out. For that reason, we believe it is useful to attempt to (nonexhaustively) lay out some of the more common deployments of the term; this exposition is meant to be purely descriptive and to distinguish different theoretical constructs of modularity. At the broadest level, different notions of modularity can be separated according to whether they are based on a methodological criterion or on properties that a system/process must possess in order to be modular.

1. For Sternberg (2011), a process is modular if it is separately modifiable; in this usage of the term, a module corresponds to a "stage" of processing. Thus, modularity is defined according to a methodological or epistemological criterion. Of course, if a process is observed to be separately modifiable, then within the framework of additive factors logic, certain features of its processing may be inferred. But, for Sternberg (2011), processes that might be hypothesized to have those same processing features, but which could not be demonstrated to be separately modifiable, would not be referred to as modular.

2. An alternative is to define modularity in terms of the properties or characteristics that a process must have in order to be modular. The best known articulation of this view is that developed by Fodor in his monograph "Modularity of Mind" (Fodor, 1983). For Fodor, modules possess some combination, or all, of a set of properties that include information encapsulation, shallow outputs, dedicated neural machinery, a characteristic developmental profile, and being fast, automatic, innate, and domain specific. Of these properties, information encapsulation is, in Fodor's words, "the essence" of modularity. On the basis of that constellation of properties that characterize (putative) modular processes, Fodor hedged (presciently) that modular processes were most likely to be observed at the periphery of the system, in the input and output systems. This is because peripheral processes can operate without access to global information, and so encapsulation would not be a hindrance to their processing (as it would be for more central processes).

Coltheart (2011) provides a direct comparison between what counts as a modular process for Sternberg and what counts as a modular process for Fodor (1983). In many ways, there is very little in common between Fodorian modules and Sternbergean modules, except, perhaps, that both types of modules are domain specific—that is, specialized in their content.

3. Researchers interested in the origins of cognitive and brain processes have tended to emphasize the joint criteria of domain specificity and innateness as defining of the modularity of a process (Cosmides & Tooby, 1994; Pinker, 1997). This research tradition has not emphasized the role of information encapsulation in modularity. Because information encapsulation is not considered a critical "criterion" for modularity of cognitive processes, evolutionary and developmental approaches

have postulated modular processes at all levels of processing. That approach has sparked an interesting discussion of how much of the mind is and is not candidate territory for modular processes (Carruthers, 2005; Fodor, 2000, 2005; Marcus, 2006; Pinker, 1997, 2005a, 2005b; Rabaglia, Marcus, & Lane, 2011). D'Souza and Karmiloff-Smith (2011) argue that those more promiscuous modular theories are challenged by evidence showing deep interactions among all levels of cognitive processes during development.

4. A similar emphasis on domain specificity is advanced within the still narrower construal of modularity by Coltheart, who argues that a "cognitive system is modular when and only when it is domain-specific" (Coltheart, 1999, p. 115; quoted in Coltheart, 2011). This notion of modularity could be considered quite close to Sternbergean modules, as Sternberg (2011) argues that separate modifiability is likely to be implied by domain specificity. However, the important point is that for Sternberg, the modularity of a process is warranted only when it is demonstrated to be separately modifiable; processes that are domain specific but not, for whatever reason, separately modifiable would count as modules for Coltheart but not for Sternberg.

5. A more relaxed construal of modularity has been articulated with respect to patterns of brain activation observed in functional neuroimaging. In the context of neuroimaging work, for instance, Op de Beeck and colleagues (Op de Beeck, Haushofer, & Kanwisher, 2008) have argued that *brain regions* are modular if there is "clustering of selectivity in discrete regions, with clear selectivity discontinuities at the boundaries of these regions" (Op de Beeck et al., 2008, p. 124). Under this approach of defining modularity (i.e., in terms of discontinuities in neural preferences), care must be exercised before concluding that the underlying cognitive processes are also "modular". For instance, if participants are shown different types of stimuli, and one type leads to neural specificity, then it is comfortable to conclude that the underlying cognitive processes are specialized for that type of stimulus. But, as many researchers have noted (see, e.g., Coltheart, 2006, and associated commentaries), this is not enough—it is necessary to dissect out exactly which aspects of the stimulus (and task) the region is responding to and, at that level, design new experiments to establish specificity in the region for that particular stimulus/task component. And even then, issues arise about the way in which cognitive processes (or types) map onto neural processes (or types; see Friston & Price, 2011, and discussion below). The relationship between neural specificity and specificity of the underlying cognitive processes is far from straightforward and is one of the themes that runs throughout the papers of this Special Issue.

6. Another approach for understanding modularity is to abandon "information content" as the primary benchmark of modularity and instead evaluate the modularity of processes in terms of the dynamics of information processing. Within this framework, so-called "modular" processes are counterposed to interactive processes (for cogent discussion on this point, see Coltheart, 2011). In other words, processes are modular if they do not leak or spread activation to other processes before they complete their processing. This deployment of the term "modularity" is prevalent, for instance, in theories of language processing (Levelt, 1999). Pulvermüller contrasts modularity with embodied views of cognition, in stating that "cortical functions might be served by distributed interactive functional systems [i.e., embodied cognition] rather than local encapsulated modules" (Pulvermüller, 2005, p. 576). This version of modularity is somewhat derivative of Sternbergian modularity, in that certain aspects of the dynamics of information exchange are precluded if the processes are modular.

Summary

A number of different meanings, all well defined in their respective contexts, have been given to the term "modularity" (for an overview, see Barrett & Kurzban, 2006). The goal, of course, is not to conclude whether a process is modular for its own sake, but to understand substantive issues such as the dynamics of that process, the nature of its computations, its scope of input and output, the other processes with which it interfaces, its neural implementation, and so on. For instance, if a process were found to be domain specific but not innate (e.g., printed word recognition; Dehaene & Cohen, 2011), then this would raise important questions about how cognitive and neural processes can become tuned in a highly specialized way to a completely learned category (see Plaut & Behrmann, 2011, for a computational model that explores this issue).

Moreover, the degree to which neural reorganization can result in cognitive recovery after impairment to purported modules needs to be reconciled with strong claims of modularity, domain specificity, and innateness. This issue is potentially even more complex when understanding the developmental trajectory of cognitive and neural organization. D'Souza and Karmiloff-Smith (2011) argue that specialization of function in the adult brain represents the "consolidated end state of a developmental process", and so caution must exercised when using adult organization as a model for studying development. These considerations emphasize that an understanding of the origins of (putative) modules can reveal critical aspects of their functional properties as well as their functional interactions within broader cognitive and neural systems (Gallistel, 1993; Hauser, Chomsky, & Fitch, 2002; Karmiloff-Smith, 1992).

Modularity at the cognitive and neural levels

One of the most important issues that runs throughout the cognitive and brain sciences is how cognitive processes relate to brain processes. When a purely psychological theory (a theory that makes no reference to the brain) identifies a specialized cognitive process, should we "expect" there to be a dedicated brain region for that process? What should the grain of our search in the brain be for that process—cellular through to systems level? Might some well-defined cognitive processes not map one-to-one to brain processes? Perhaps even more difficult is to consider the reverse direction of inference: If a particular brain region is observed to respond to well-defined inputs and to be connected to other regions that also have well-defined stimulus preferences, then what types of inferences are sanctioned about the underlying cognitive processes?

In some ways, the entire enterprise of cognitive neuropsychology validates the idea that modification of the brain can lead to separate modifiability of cognitive processes; a core component of this method is the observation that a cognitive process has been separately modified in a given individual. However, this straightforward paradigm assumption does not carry over into functional neuroimaging. For functional neuroimaging, separate modifiability of neural processes/regions does not ipso facto constitute evidence for separate modifiability of cognitive processes.

Poldrack (2006) and Henson (2006) distinguished two types of inference: reverse inference (Poldrack, 2006) and forward inference (Henson, 2006). Reverse inference is reasoning from some pattern of brain activation to the claim that a given cognitive process is engaged, which Poldrack (2006) formalizes within a framework of Bayesian inference. The strength of reverse inference, as described by Poldrack, increases with the selectivity of the neural response to the putative cognitive process and the strength of prior evidence that the putative cognitive process engages that region (see Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011). Forward inference, as defined by Henson (2006), is a way of distinguishing among two cognitive theories that differ in that one theory postulates a cognitive process involved in one experimental condition (A) but not in another condition (B), while the other theory does not postulate a difference in cognitive processes between the two conditions. If the pattern of brain activation differs between the two conditions, then that would constitute, according to forward inference, positive evidence for the theory that states that an additional cognitive process is involved in Condition A. Henson (2011) further considers the nature of the inferences that one might derive when reasoning from observed neural effects to the structure and organization of cognitive processes.

On the other side of this issue is the problem of ascribing highly specific functions to neural processes using functional neuroimaging. As Friston and Price (2011) discuss, the fact that brain regions are shown to be dissociable with functional neuroimaging, and thus have the property of separate modifiability, does not imply one way or the other whether those regions are necessary and/or sufficient for the (putative) underlying cognitive process. There are multiple reasons why. One is that it is very difficult, if not impossible, to study a "part of the brain" in isolation from the network of regions within which that region is embedded (for discussion, see also Rabaglia et al., 2011). A second reason is that there is degeneracy (Price & Friston, 2002) in neural networks (e.g., Edelman, 1978; for discussion and full references see Price & Friston). Quoting from Price and Friston's repositioning of Edelman's definition, degeneracy is "the ability of elements that are structurally different to perform the same function or yield the same output".

At first pass, it would seem to be the case that lesion evidence can ground inferences about the necessity of a given region for a given cognitive process, while functional neuroimaging data can ground inferences about the sufficiency of a given region for a given cognitive process. However, Price and Friston (2002) articulate a strong form of an argument against this, in maintaining that lesion evidence alone cannot ground inferences about necessity. The reason why is that brain lesions may compromise not only the processes that were subserved by the damaged tissue but also processes that are subserved by functionally connected regions (Price, Warburton, Moore, Frackowiak, & Friston, 2001). Price, Friston, and colleagues (Friston & Price, 2011; Price et al., 2001) refer to this property of brain lesions as "dynamic diaschisis". Previous work by those authors (Price et al., 2001) provides an example of dynamic diaschisis in that patients with lesions to left frontal cortex and expressive but not receptive language impairments show reduced neural responses to printed words in temporal regions that are known to be functionally coupled with the damaged frontal regions. However, this raises the question of whether the fact that lesions induce effects of dynamic diaschisis should reduce confidence in inferences about the necessity of a lesioned area for a given cognitive function that is observed to be impaired. For instance, even though it is the case that neural responses in the temporal lobe are "yoked" in critical ways to processing in the frontal cortex, it may still be the case that the integrity of those frontal regions is necessary for the normal operation of some of the cognitive processes involved in reading. What is clear, however, is that the simple model of "lesions provide a window into which parts of the brain are necessary for which aspects of cognition" will not work, and that these issues must be worked out empirically for each pattern of cognitive/neural dysfunction.

A potentially even more complicated situation arises, according to D'Souza and Karmiloff-Smith (2011), for understanding developmental cognitive impairments. Those authors argue that developmental cognitive impairments may not represent selective impairment to a specialized (read: "modular") process, but rather cascading effects of perturbations early in development that prevent specialization of function from developing. How such "derailed modularization" might affect, through dynamic diaschisis, processing within a broader network of regions represents an important issue for future cognitive neuroscientific research.

In order to understand the significance of dynamic diaschisis, we need a deeper understanding of the relationship between the dynamics of information flow among levels of processing within a cognitive model and interregional connectivity in the brain. This is particularly important because the additive factors method applies to stage models, and different types of (postulated) information exchange among functionally distinct systems (cascaded activation, interactivity) preclude the use of the additive factors approach for dissociating different levels of processing. Turning this around, an important issue is whether neural evidence of interactivity among regions/processes can be counted as evidence against a theory that holds that the different regions subserve distinct stages of processing, where "stage" is understood in the Sternbergean sense. Coltheart (2011) points out that in order for neural evidence of interactivity among regions to count as evidence against a stage model of processing, "one would have to demonstrate that [the function of those] . . . pathways in cortex . . . is to deliver the type of feedback that [the] model denies". This level of correspondence between neural data and cognitive models represents an important direction for future research.

Rabaglia et al. (2011) also address the degree to which configurations of neural activation can be used to support or reject claims of modularity. They demonstrate that shared neural resources among cognitively distinct tasks can give rise to the well-replicated observation that variation across different tasks is highly correlated within individuals. In other words, even for tasks that would putatively depend on dissociable (read: "modular") systems, such as mathematical versus verbal reasoning, individuals who tend to be good on one task also tend to be good on another task. The authors argue through meta-analytic and computational simulation approaches that constellations of neural overlap vary among combinations of distinct tasks (i.e., there is no common pattern in the overlap of all tasks), and a single domain-general cognitive parameter need not be postulated in order to account for substantial explained variance across different tasks. The authors argue that even if components of a network of regions are shared between two different tasks, that finding may not be problematic for claims of domain specificity or modularity, as different computations may depend on different aspects of a broad network.

The cognitive neuropsychological approach, together with functional neuroimaging methods, offers a vehicle with which to understand not only the brain regions that are involved, but whether their role is sufficient, necessary, or both for executing a given operation. As Friston and Price (2011) emphasize, conducting functional neuroimaging in brain-damaged individuals offers the opportunity to test hypotheses about whether intact abilities in brain-damaged individuals are supported by latent brain networks that are not typically "online" in the normal system because there are other redundant networks that typically carry out the process. As the authors emphasize, a complete treatment of modularity and its role in understanding the brain basis of cognitive processes must account for functional activation in both healthy and damaged brains, as well as behaviour in both healthy and brain-damaged individuals.

This Special Issue of *Cognitive Neuropsychology*

Cognitive Neuropsychology is an excellent venue to host the collective contribution made by the papers gathered together in this volume. The journal has, over the last several decades, come to be aligned with a brand of cognitive research that emphasizes the study of cognition through an analysis of patterns of performance under conditions of brain damage. Under the new leadership of the journal starting in 2010, the journal has broadened its aims to include new methods, while at the same time remaining faithful to the central goal of articulating detailed cognitive theories. The articles collected together within this volume advance our understanding of the roles of modularity and functional specialization in deriving inferences about the structure of the mind from behaviour in normal and brain-damaged individuals, functional neuroimaging, computational modelling, development, and the study of individual differences.

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