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Review

Understanding brain networks and brain organization

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Abstract

What is the relationship between brain and behavior? The answer to this question necessitates characterizing the mapping between structure and function. The aim of this paper is to discuss broad issues surrounding the link between structure and function in the brain that will motivate a network perspective to understanding this question. However, as others in the past, I argue that a network perspective should supplant the common strategy of understanding the brain in terms of individual regions. Whereas this perspective is needed for a fuller characterization of the mind-brain, it should not be viewed as panacea. For one, the challenges posed by the many-to-many mapping between regions and functions is not dissolved by the network perspective. Although the problem is ameliorated, one should *not* anticipate a *one*-to-*one* mapping when the network approach is adopted. Furthermore, decomposition of the brain network in terms of meaningful clusters of regions, such as the ones generated by community-finding algorithms, does not by itself reveal "true" subnetworks. Given the hierarchical and multi-relational relationship between regions, multiple decompositions will offer different "slices" of a broader landscape of networks within the brain. Finally, I described how the function of brain regions can be characterized in a multidimensional manner via the idea of diversity profiles. The concept can also be used to describe the way different brain regions participate in networks.

Keywords: Brain; Networks; Function; Structure

1. From areas to networks

Much has been written about the issue of localizability of mental processes, a problem that is at the core of neuroscience as a scientific discipline. Even a cursory look at the field reveals a continual swing of the pendulum between holistic and modular explanations (for an excellent account, see Shallice's book [1]).

The simplest way to conceptualize the relationship between a brain area and behavior is to assume a one-to-one mapping between an area and its function. For example, the primary visual cortex is linked to visual perception, or a set of more basic visual functions, such as "edge detection". Such an exercise becomes considerably less straightforward for more central areas (that is, farther from the sensory periphery), but we can imagine extending it throughout the brain. The end product of such a strategy would be a list of area–function pairs: $L = \{(A_1, F_1), (A_2, F_2), \ldots, (A_n, F_n)\}$. Brain areas might then be labeled as "perceptual", "motor", "cognitive", "emotional", "motivational", and so on, based on their purported functions and how they are envisioned to shape

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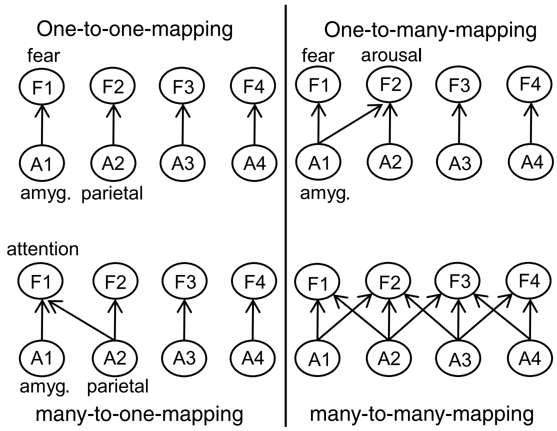

Fig. 1. Structure-function mapping in the brain. A central argument of the paper is that because the mapping from structure to function is *many*-to-*many*, understanding the instantiation of functions by the brain necessitates sophisticated frameworks whose basic elements are networks, not regions. Abbreviations: A1, ..., A4: areas 1 to 4; amyg: amygdala; F1, ..., F4: functions 1 to 4; Reproduced with permission [2].

behavior. For instance, we could describe the amygdala as emotional given its contributions to fear conditioning, and the dorsal-medial PFC as cognitive given its role in the processing of response conflict [2].

Disregarding for now the thorny issue of what precisely is meant by “area” and “function”, it is readily apparent that brain regions participate in many functions, and that many functions are carried out by many regions (Fig. 1). For instance, the dorsal-medial PFC is important for a diverse range of cognitive operations, as well as for emotional processing. This region thus provides an example of an area involved in many functions, namely an instance of a one-to-*many* mapping. Conversely, both frontal and parietal regions participate in attentional and executive processes, illustrating the situation of multiple regions carrying out a related function, an instance of a *many*-to-one mapping.

More generally, the mapping between structure and function is both *pluripotent* (one-to-many) and *degenerate* (many-to-one). Pluripotentiality means that the same structural configuration can perform multiple functions. Degeneracy refers to the ability of structurally different elements to perform the same function or yield the same output [3] – or to be able to complete a task. Notably, degeneracy should be distinguished from *redundancy*, which occurs when structurally identical elements perform the same function (as in “back-up” engineering systems). To the extent that pluripotentiality and degeneracy are accepted concerning the mind-brain,[1] the combination of the two indicates that there are no “necessary and sufficient” brain systems. In particular, the existence of two or more degenerate systems that do *not* overlap precludes the existence of a single necessary area for a given function [7].

In the above discussion, I bypassed the difficult question of what constitutes a brain region and, even more challengingly, what constitutes a function. Clearly, structure-function relationships can be defined at multiple levels, from the precise (for instance, primary visual cortex is concerned with edge detection) to the abstract (for instance, primary visual cortex is concerned with visual perception), and structure-function relationships will depend on the specific level that is targeted. Some authors have suggested that, at some levels of description, a brain region does *not* have more than one function. For instance, the left posterior fusiform gyrus in temporal cortex, which has been implicated in the processing of word forms, animal structures, and so on, can be described by a single, more abstract label of “sensori-motor integration” [8]. Price and Friston suggest that whether a region can have more than one function depends on the level of the relationship, such that at a sufficiently abstract level, a region will have a single function – though note that for this notion to be useful, the abstractness has to be relatively limited, and not simply a vague description such as “cognitive function”. Although the search for better conceptualizations of a region’s functions is valuable, I propose below that the region level is *inadequate* to describe how brain structure is linked to mental function. More forcefully, understanding the structure-function mapping at the level of brain regions is unproductive because regions are not a meaningful *unit* in this regard.

[1] See Pessoa [4] for examples concerning emotion and cognition; Cisek [5] for examples concerning perception and action; and Schultz [6] for discussion related to dopamine function.

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