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Understanding emotion with brain networks

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Abstract

Emotional processing appears to be interlocked with perception, cognition, motivation, and action. These interactions are supported by the brain's large-scale non-modular anatomical and functional architectures. An important component of this organization involves characterizing the brain in terms of networks. Two aspects of brain networks are discussed: brain networks should be considered as inherently overlapping (not disjoint) and dynamic (not static). Recent work on multivariate pattern analysis shows that affective dimensions can be detected in the activity of distributed neural systems that span cortical and subcortical regions. More broadly, the paper considers how we should think of causation in complex systems like the brain, so as to inform the relationship between emotion and other mental aspects, such as cognition.

Introduction

Why does emotion matter for cognition? Research in the past two decades has described how emotion interacts and is integrated with cognition [1]. Supporting these interactions are the brain's non-modular anatomical and functional architectures [2–4]. Signal distribution and integration are the norm, allowing the confluence of information related to perception, cognition, emotion, motivation, and action. Thus, emotion is interlocked with all these mental domains via internetwork communication.

To better understand how brain networks inform the understanding of the interactions between emotion and cognition, we need to refine how they are conceptualized [5–7]. Here, two aspects of brain networks will be discussed: brain networks should be considered as 1) inherently overlapping, as well as 2) highly dynamic and context-sensitive. This discussion leads to the question of how emotions are represented in the brain. Even more broadly, the paper considers how we should think of causation in complex systems like the brain, so as to inform the relationship between emotion and other mental aspects, such as cognition.

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From regions to networks: What's right and what's wrong with networks

Neuroscience has been always interested in circuits. Yet, the last 15 years have witnessed vigorous progress in neuroscience and network science analysis methods alike, with networks described at multiple levels, from micro (neuronal) to meso (pathways) to macro (whole-brain) levels [8]. In most instances, understanding structure-function mappings at the level of brain regions may be less productive because regions are not a meaningful computational *unit* in this regard [6]. Networks of brain regions collectively support complex behaviors. Thus, *the network itself is the unit*, not the brain region. Processes that support behavior are implemented by the interaction of multiple areas, which are dynamically recruited into multi-region coalitions.

Networks are overlapping, not disjoint

One of the goals of network analysis of brain data is to partition brain regions into clusters or "communities" that consist of regions that communicate more strongly (or that behave more alike) within the community than across it [9]. Most analyses describe networks in terms of disjoint sets, such that each brain region belongs to a single cluster of regions. But this assumes that brain areas compute a fairly well defined and specific function [6]. An alternative is to conceptualize networks as containing *overlapping* regions [10–13], such that specific areas belong to several intersecting networks [14]. In this manner, the processes carried out by an area will depend on its network affiliation (that is, the regions it clusters with) at a given time. What determines a region's affiliation? An hypothesis is that the functional/behavioral *context* plays a pivotal role [15]. For example, region A will be part of network N_1 during a certain context C_1 but will be part of network N_2 during another context C_2.

These ideas resonate with the "flexible hub theory" [16], where some regions are suggested to flexibly shift their functional connectivity (that is, the degree to which signals from two regions co-vary in time) patterns as a function of task demands. To further understand potential network overlap, in a recent investigation of functional MRI (fMRI) data, we determined during rest and task conditions the distribution of "membership values," that is, the extent to which each region participated across multiple networks ([17], see also [18]). Regions of the task-negative (or "default") network, for example, participated in multiple networks simultaneously. Distributed participation was even more evident in a community of frontal and parietal regions important for attention and executive control, consistent with their multifunctional roles [19]. Overall, it is suggested that overlapping networks implement context-dependent computations that bring about behavioral flexibility.

Functional MRI is currently limited in its ability to inform the organization of brain networks at finer spatial resolutions. Such level is informed by recent neurotechniques that have precise control of cellular- and pathway-level activation and silencing, including optogenetics. A current debate is whether, within a structure, neuronal populations linked to appetitive and/or aversive processing are anatomically intermingled or segregated (for intermingled examples, see [20,21]; for segregated examples, see [22,23]). This literature is particularly relevant to inform the question of circuit/network overlap.

At least three scenarios are relevant. First, segregated populations within a region may be involved in interactions with separate regions (Figure 1A). In this case, we can refer to sub-regions of a larger anatomical region, which contains distinct populations of cells. In fact, in terms of networks, this situation could be described as involving disjoint and not overlapping networks. However, in some contexts, it is possible that the sub-regions involved, when combined, form noteworthy functional units, so the description in terms of overlapping networks may still be informative. Second, intermingled neuronal populations may exist, each of which is connected with different regions (Figure 1B). In this case, the neuronal sub-populations would be expected to exhibit different functional properties. Third, the same neurons may affiliate with different regions as a function of context (Figure 1C). For instance, neurons in a nucleus of the amygdala may affiliate with accumbens neurons in one context but with BNST neurons in a different one. In cellular-level studies, this possibility has not received as much attention yet. However, examples of how neurons or neuronal populations multiplex signals are well documented [24,25]. In such situations, multiple signals may be combined and transmitted even through a single “communication channel,” and even at the same time.

Networks are dynamic, not static

Brain networks are not static but evolve temporally. Functional connections vary as a function of context, and are altered by cognitive, emotional, and motivational variables (see [1]). Therefore, network organization must be understood dynamically [26–29]. Indeed, the growth of methods to describe time-varying functional connectivity has begun to yield novel characterizations of how network organization evolves [30–32].

An example of changes to network organization is illustrated by a study in which participants performed a cognitive task during reward vs. no-reward conditions [33]. When a cue at the beginning of the trial signaled the possibility of reward, the functional connections between cortical regions important for cognitive processing and subcortical regions involved in reward processing increased systematically (Figure 2). In particular, the functional connections of the nucleus accumbens increased with all but one of the regions engaged by the task.

More generally, there are two important ways in which brain networks are dynamic. First, we can consider how specific networks evolve across time (Figure 3A–B). At the spatiotemporal resolution of fMRI, we and others have started to characterize how emotion influences the temporal unfolding of large-scale network organization [34–37]. In a recent study [36], periods of “anxious anticipation” were associated with transient and sustained changes to the salience, executive, and task-negative networks in the human brain. Notably, how the bed nucleus of the stria terminalis and the amygdala participated in network communication (as quantified by the measure of centrality) was altered during anxious states.

Second, networks do not comprise fixed collections of regions. Networks are suggested to be dynamic coalitions of brain regions that form and dissolve to meet specific computational needs [6]. Accordingly, network descriptions need to specify how groupings of regions evolve temporally (Figure 3C–D). This poses several challenges, as the very notion of a network as a coherent unit is challenged. For instance, at what point does a coalition of regions become something other than, say, the salience network? Conceptualizing networks as inherently overlapping, as described previously, helps to mitigate this problem. For example, each node can be considered to be a member of multiple networks with a specific probability-like “membership value” [17], which fluctuates across time.

How are emotions represented in the brain?

Findings from pattern analyses of neuroimaging data show that affective dimensions and emotion categories can be detected in the activity of distributed neural systems that span cortical and subcortical regions. Indeed, attempts to classify brain states from distributed patterns of fMRI activation to predict these attributes have yielded high levels of specificity [38]. Some results indicate that emotion categories are not contained within any one region or system, but are represented as configurations across multiple brain networks [38]; for debate about emotion categories, see [39].

Interestingly, in one study [40], predictive patterns spanned multiple cortical and subcortical systems, with no single system being necessary or sufficient for predicting affective experience. Furthermore, predictive patterns were not reducible to activity in traditional “emotion-related” regions (e.g., amygdala) or resting-state networks (e.g., task-negative network).

When investigating the representation of emotions in the brain with fMRI, the spatial resolution of the technique must be considered, and the results interpreted with some caution. Although multi-voxel (distributed) representations have been proposed to be more sensitive spatially, consideration of Figure 1 highlights the fact that the issue is not simple, particularly when heterogeneous subcortical structures are involved. For instance, if the voxel size is larger than the tissue in Figure 1A, the subpopulations will be averaged or unsystematically linked to voxel placement; the situation is more problematic in Figure 1B, of course. Critically, Figure 1C highlights a scenario where the problem would exist *regardless* of the spatial resolution, and even cellular-level resolution would not solve it. This is because a region’s function will depend on the pattern of signal co-variation across regions.

This last case illustrates how the study of the brain basis of emotion benefits from studying functional relationships between regions. This could be done, for example, by employing machine learning to investigate patterns of functional connectivity ([41], see also [42]). In one study, we proposed combining functional connectivity with “functional fingerprint” analysis ([43], see also [44]). We used a meta-analytic approach to analyze the functional profiles of brain regions that exhibited co-activation with insular subdivisions (dorsal anterior, ventral anterior, and posterior insula). Functional profiles were determined based on interrogating fMRI study databases in terms of multiple task “domains” such as emotion, memory, attention, and action. The results suggested that all insular subdivisions are functionally diverse and that characterizations of the insula should move beyond cognition-emotion-interoception partitions.

I have proposed that the representation of emotion in the brain can be understood in terms of *functionally integrated systems* that involve large-scale cortical-subcortical networks that are sensitive to bodily signals [45]. The high degree of signal distribution and integration in the brain provides a nexus for the intermixing of information related to perception, cognition, emotion, motivation, and action. Importantly, as described above, the functional architecture consists of multiple overlapping networks that are dynamic and context-sensitive. Thus, how a given brain region affiliates with a specific network shifts as a function of task demands and brain state. Whereas the proposal of functionally integrated systems is consistent with multivariate and machine learning analyses of fMRI data indicating that emotional states are highly distributed, the model also predicts that brain "signatures" of affective dimensions are highly context-dependent, and may not generalize well across tasks and conditions.

How to think of causation in complex systems like the brain?

When we consider how emotion is represented in the brain and interacts with cognition, as in other areas of neuroscience, we tend to reason according to a *billiard ball* causal model (at least implicitly). In this model, force applied to a ball (external stimulus activating a region) leads to its movement until it hits the target ball (activation of an anatomically connected region) (Figure 4A). But this mode of thinking, which has been very productive in the history of science, is too impoverished when complex systems are considered [see 46]. When systems are not isolable, understanding the interrelatedness between "sub-systems" means that we should consider interactions between systems and integration of signals as the central elements to be unraveled.

Whereas thinking of causation in complex systems is challenging, we can consider the situation illustrated in Figure 4B. When the initial force is applied to the yellow ball and it hits the target ball, the goal is to understand the evolution of the *system* of coupled elements as they interact with one another across time. In a related vein, an important goal for mind-brain scientists should be to understand the interactions between emotion and perception/cognition.

At the broadest level, the present discussion speaks to how we should study systems as complex as minds and brains. As advocated elsewhere [e.g. 47,48], the focus should not be on parts but on *processes*, which must be understood not solely in terms of their putative constituent elements but in terms of interactions and temporal evolution. In the brain, we will be often interested in describing the joint state of a set of regions, and how this joint state evolves through time. Consider the set of activity strengths for a set of brain regions: $x_1, x_2, \cdots, x_n$. The vector $\boldsymbol{x}$ describes the current state of the system and $\boldsymbol{x}(t)$ describes its trajectory across time. At a particular time, the state of a set of regions can be represented as a point in multidimensional state space in which each axis represents a region's activity. Therefore, the evolution of the system can be described as a spatio-temporal trajectory ([49], for an example involving cell recordings, see [50]).

In this view, we can advance our understanding of the emotional brain by studying and characterizing spatio-temporal trajectories (that is, how the joint activity across multiple brain regions evolves across time) of distributed systems believed to be central to emotional functions. And given the large-scale, overlapping, and dynamic nature of brain networks, emotion matters not only for closely associated motivational processes, but for perception, action, and cognition.

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Highlights

- Interactions between emotion and cognition rely on large-scale distributed networks
- Brain networks are composed of overlapping regions (not disjoint sets of regions)
- Brain networks are dynamic, not static
- Understanding interactions requires characterizing causation in complex systems

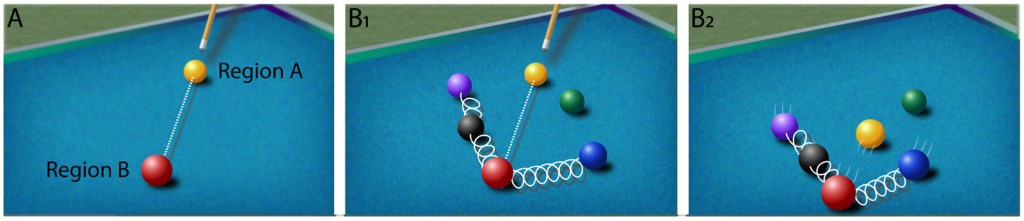

Figure 1.

Overlapping networks and neuronal populations. Blue and green circles represent brain regions of (relatively) separate networks. The orange circle indicates a region that is functionally linked to both networks. The small circles in A–C indicate neurons. (A) Segregated populations within a region are involved in interactions with separate brain regions/networks. (B) Intermixed neuronal populations within a region are involved in interactions with separate brain regions/networks. (C) The same population of neurons within a region is functionally connected with different brain regions/networks.

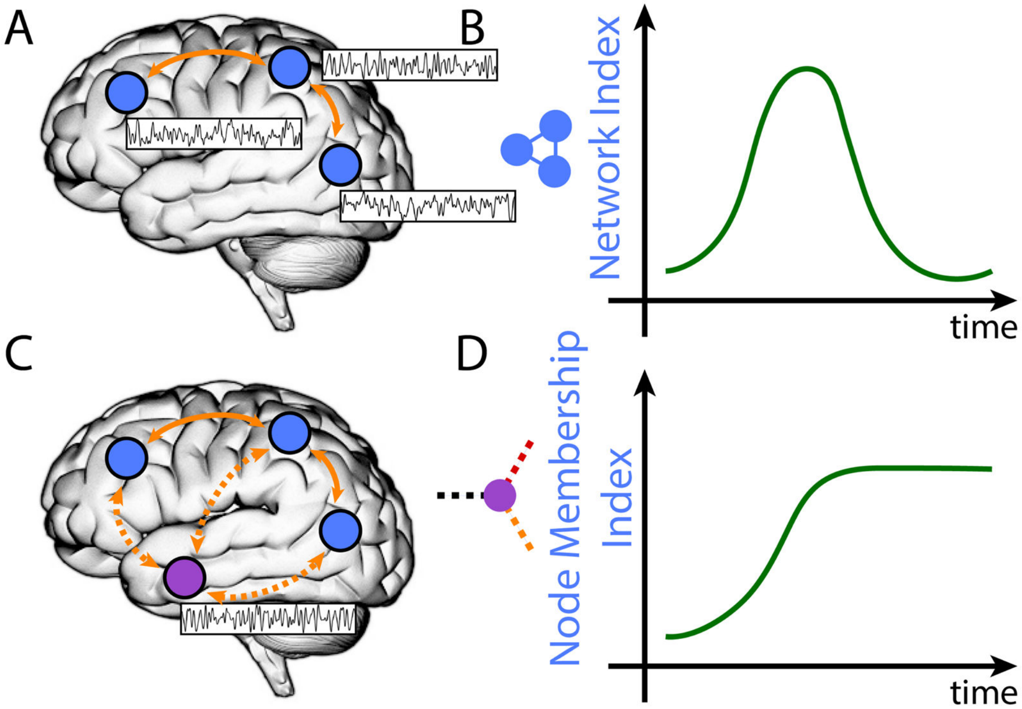

Figure 2.

Widespread changes in functional connectivity during cognitive-motivational interaction. (A) Representation of two communities during the control condition (no reward). Nodes indicate community organization (red: subcortical community; teal: cortical community) and edges indicate functional connections (purple: between-community edges). (B) Changes in reward vs. control connectivity between the two communities are shown. Reproduced with permission from Kinnison, Padmala, Choi, and Pessoa (2012).

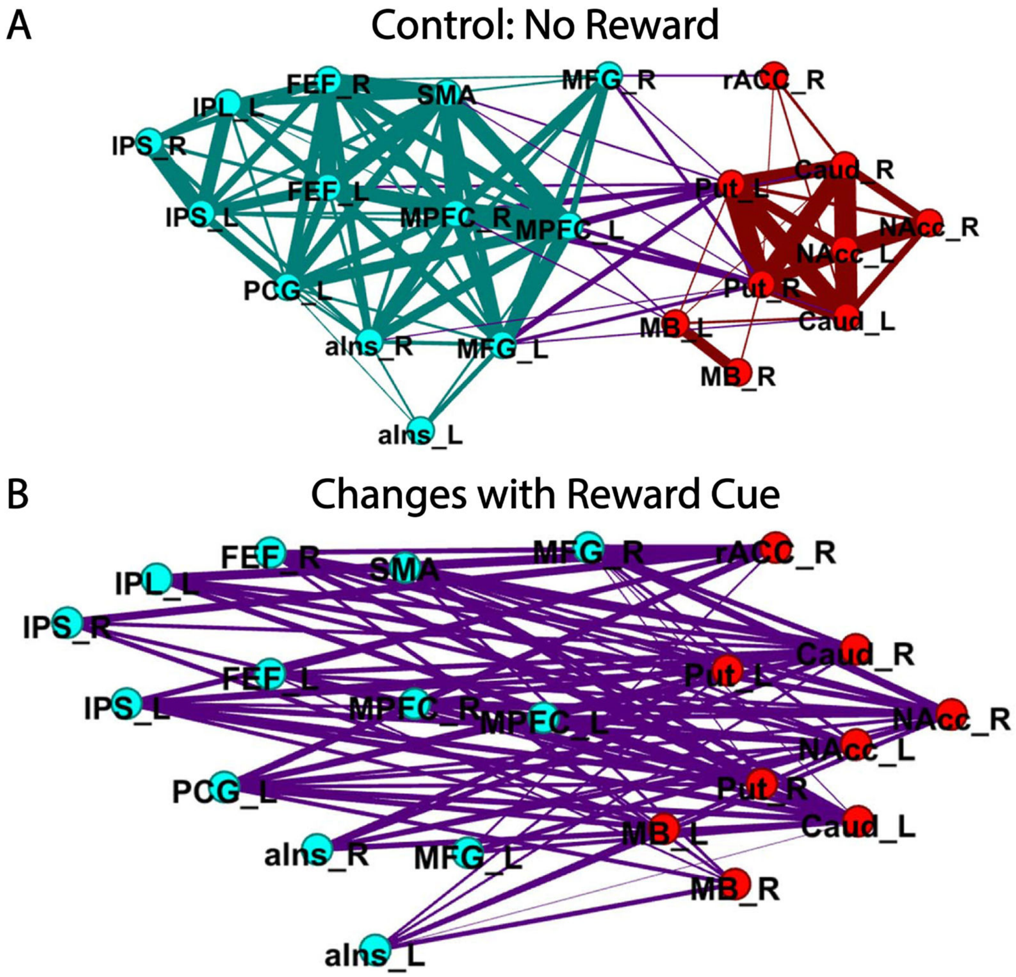

Figure 3.

Brain networks are dynamic. (A–B) Specific network properties (“network index”) evolve across time. (C–D) A region’s grouping with multiple networks evolves across time as indicated by the “membership index” (inset: white region and its functional connections to multiple networks). The region indicated in white increases its coupling with one of the networks and stays coupled with it for the remainder of the time.

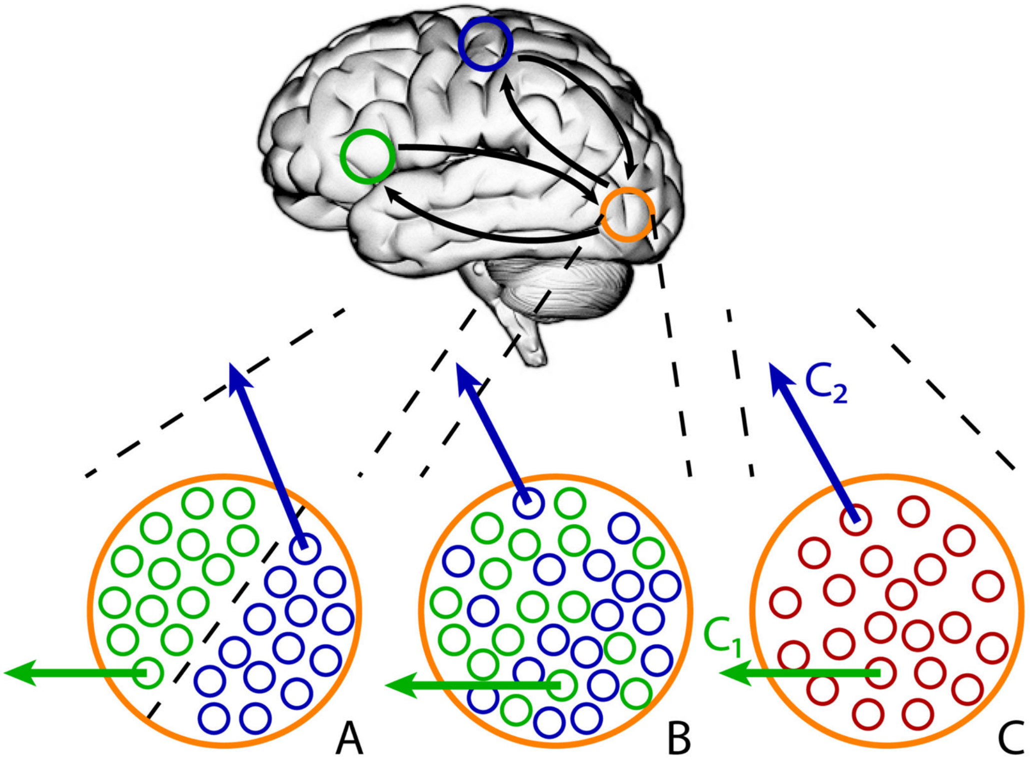

Figure 4.

Causation in complex systems. (A) Simple billiard ball model of causation applied to the interactions between brain regions. (B) Some of the balls are connected by springs to suggest that they are coupled. When the yellow ball eventually hits the red one (B1), not only is the red ball affected but all of the ones coupled with it (B2). Thus, the overall goal of explanation is to understand the evolution of the coupled system as it evolves temporally (B2).