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Dissociable changes in functional network topology underlie early category learning and development of automaticity

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ABSTRACT

Recent work has shown that multimodal association areas—including frontal, temporal, and parietal cortex—are focal points of functional network reconfiguration during human learning and performance of cognitive tasks. On the other hand, neurocomputational theories of category learning suggest that the basal ganglia and related subcortical structures are focal points of functional network reconfiguration during early learning of some categorization tasks but become less so with the development of automatic categorization performance. Using a combination of network science and multilevel regression, we explore how changes in the connectivity of small brain regions can predict behavioral changes during training in a visual categorization task. We find that initial category learning, as indexed by changes in accuracy, is predicted by increasingly efficient integrative processing in subcortical areas, with higher functional specialization, more efficient integration across modules, but a lower cost in terms of redundancy of information processing. The development of automaticity, as indexed by changes in the speed of correct responses, was predicted by lower clustering (particularly in subcortical areas), higher strength (highest in cortical areas), and higher betweenness centrality. By combining neurocomputational theories and network scientific methods, these results synthesize the dissociative roles of multimodal association areas and subcortical structures in the development of automaticity during category learning.

Introduction

Network science provides a set of robust tools that are increasingly used to describe and understand neural systems (Bullmore and Sporns, 2009; Sporns, 2014). Neurons or brain regions are represented as network nodes, and structural or functional connections between regions are represented as network edges. Recent studies demonstrate that the topology of functional brain networks can reconfigure quickly as the result of learning (Bassett et al., 2013b; Bassett et al., 2011, Bassett et al., 2015) and task engagement (Bassett et al., 2006; Ekman et al., 2012; Fornito et al., 2012; Kitzbichler et al., 2011). In several cases, this reconfiguration leads to more integrated and less segregated processing (Cole et al., 2014; Ekman et al., 2012; Kitzbichler et al., 2011) and involves strong reconfiguration in some nodes, while global network properties can remain relatively stable (Bassett et al., 2006; Moussa et al., 2011; Rzucidlo et al., 2013; Braun et al., 2015). In particular, nodes in multimodal association areas—within frontal, temporal, and parietal cortex—flexibly change their community affiliation during learning (Bassett et al., 2013b; Bassett et al., 2011, Bassett et al., 2015), their connectivity pattern during rule application and preparatory attention (Cole et al., 2013; Ekman et al., 2012), and the cost-efficiency of their connectivity during accurate performance of working memory tasks (Bassett et al., 2009; Braun et al., 2015).

Despite these results, it is unlikely that connectivity changes in cortical association areas underlie functional network reconfigurations across all tasks. For example, connectivity changes and integrative processing in the basal ganglia are likely to be of utmost importance during initial learning of some categorization tasks (Ashby and Ennis, 2006). A body of behavioral and neurobiological evidence suggests that the brain areas associated with categorization are organized in relatively separate category learning systems and that different categorization tasks engage the systems differently (Ashby and Maddox, 2005; Nomura and Reber, 2008; Poldrack and Foerde, 2008; for a formalization of this multiple-systems hypothesis in a neurocomputational model, COVIS, see: Ashby et al., 1998; Ashby, Paul, & Maddox, 2011). Rule-based tasks, in which the optimal strategy is easy to verbalize and can be learned through a logical reasoning process, recruit a declarative-learning system that is based on explicit reasoning and hypothesis

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testing. Learning in this system is implemented in a network of areas including prefrontal cortex, basal ganglia, and hippocampus. Many of the previous studies reporting network reconfiguration during learning and task performance are similar to rule-based tasks in that they seem to rely heavily on executive function (e.g., Bassett et al., 2011; Braun et al., 2015; Cole et al., 2013; Ekman et al., 2012). This might explain why connectivity changes in cortical association areas accompanied network reconfigurations in such studies.

On the other hand, learning of information-integration categorization tasks does not require executive function. Information-integration tasks require the integration of information from two or more stimulus components at a pre-decisional stage, and they recruit a procedural-learning system implemented in the circuitry of the basal ganglia (caudate, putamen, pallidum, and related thalamic nuclei). Thus, it is likely that changes in connectivity in the basal ganglia and related subcortical structures underlie network reconfiguration during learning of information-integration categorization tasks.

Even so, Ashby et al. (2007) proposed that in contrast to early learning, automatic categorization is mediated entirely within cortex and that the development of automaticity is associated with a gradual transfer of control from the basal ganglia to cortical–cortical projections from the relevant sensory areas directly to the premotor areas that initiate the behavior (see also, Ashby et al., 2010; Helie et al., 2015). Some neuroimaging results support this view of how automaticity develops (DeGutis and D'Esposito, 2009; Waldschmidt and Ashby, 2011).

During the acquisition of virtually all skills, improvements in accuracy asymptote long before improvements in response time (e.g., Crossman, 1959; Helie et al., 2010). Numerical simulation studies show that the relatively fast changes in accuracy that occur during early skill acquisition are likely to reflect learning-related changes in the basal ganglia and related subcortical areas, whereas the slower changes in the speed of correct responding likely reflect the switch to cortically controlled automatic performance (Ashby et al., 2007). This dissociation in behavioral measures can be used to study whether and how changes in functional networks are related to different stages of category learning. We can expect changes in the connectivity of subcortical areas—instead of cortical association areas—to predict initial category learning best. Furthermore, this central role of the basal ganglia should be more apparent in the prediction of accuracy than in the prediction of response times.

Here we explore these predictions using a combination of network science and multilevel regression (Gelman and Hill, 2007). We study how changes in the connectivity of brain regions can predict behavioral changes during extensive training in a task known to foster procedural category learning (Ashby et al., 2003). Our analysis approach is illustrated in Fig. 1. The red broken-line boxes represent points where data entered the analysis. Structural images were used to define 742 small clusters of voxels that were used as units for subsequent analyses (i.e., network nodes). Only nodes localized in a number of regions of interest (ROI) were included in the analysis. These ROIs were chosen based on neurocomputational theory and previous research on the neural correlates of category learning (see Soto et al., 2013). Thus, the analyses focus specifically on the brain network thought to be involved in category learning.

Functional scans from each block of training were preprocessed and the average BOLD signal was computed from each cluster of voxels defining an individual node. Functional connectivity matrices were built by computing the wavelet correlation between average BOLD signals and then thresholding these correlations. The functional connectivity matrices were then used to compute a number of graph measures (for a summary description of each measure, see Table 1) for each node of the network, providing a characterization of the node's topological role in the functional network at a particular point during categorization training (that is, during each block).

Changes in network measures across training were used in regression analyses to predict corresponding changes in accuracy and response times. Based in our hypotheses, we expected that measures computed from subcortical nodes, instead of nodes located in cortical association areas, would predict initial category learning best, and that the importance of subcortical areas would be more apparent in the prediction of accuracy than in the prediction of response times.

Finally, regression coefficients were analyzed further to explore the specific relation between each predictor measure and behavior.

Materials and methods

Experimental procedures

Participants

Ten healthy undergraduate students from the University of California, Santa Barbara (6 males, 4 females), voluntarily participated in this study in exchange for course credit or a monetary compensation. This is a small but sufficient sample size (Snijders and Bosker, 2012) that has been shown to provide unbiased estimates of regression coefficients in multilevel regression (Bell et al., 2014; Maas and Hox, 2005; see discussion in the supplementary material). All participants gave their written informed consent to participate in the study. The institutional review board of the University of California, Santa Barbara, approved all procedures in the study.

Standard univariate and multivariate analyses of the imaging data acquired on this sample have been previously reported (Soto et al., 2013; Waldschmidt and Ashby, 2011). We excluded one person from the full sample of eleven participants due to incomplete data.

Behavioral task

The stimuli were circular sine-wave gratings of constant contrast and size (see example in Fig. 3A) that varied in orientation from 20° to 110° and in frequency from 0.25 to 3.58 cycles per stimulus width. Fig. 3B shows the category structure used to train participants; each dot in the figure represents a different stimulus and the dotted line represents the boundary separating the two categories. Previous research suggests that this task is mastered through procedural learning (e.g., Ashby et al., 2003; Maddox et al., 2004). During each trial, participants were presented with one of these stimuli and had to identify the category to which the stimulus belonged by pressing a button; this was followed by feedback indicating the accuracy of the response. Stimuli were presented and responses were recorded using MATLAB augmented with the Psychophysics Toolbox (Brainard, 1997), running on a Macintosh computer. For a more detailed description of the stimuli and apparatus, see Helie et al. (2010).

The experiment consisted of 23 sessions of training in the categorization task, four of which were conducted in the MRI scanner. The training sessions were carried out over 23 consecutive workdays, one session per day. The scanning sessions were sessions 2, 4, 10, and 20, and each consisted of 6 blocks of 80 stimuli, for a total of 480 stimuli per session. Participants selected their responses through response boxes, where the button box in their left hand was correct for the category at the top-left of the bound in Fig. 2B, and the button box in their right hand was correct for the category at the bottom-right of the bound in Fig. 2B. Feedback was displayed for 2 s and consisted of a green check mark for correct responses or a red "X" mark for incorrect responses. If it took more than 2 s for the participant to respond, a black dot was displayed indicating that the response was too slow. Half of the trials included the presentation of a cross-hair before the stimulus presentation.

The 19 sessions of categorization training outside the scanner were similar to the scanner session but carried out on a Macintosh computer. For a more detailed description of these sessions, see Helie et al. (2010).

Neuroimaging

A rapid event-related fMRI procedure was used. Images were obtained using a 3T Siemens TIM Trio MRI scanner at the University of California, Santa Barbara Brain Imaging Center. The scanner was equipped