BRAIN RESEARCH 1075 (2006) 133–141

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BRAIN RESEARCH

Research Report

An event-related fMRI study of the neural networks underlying repetition suppression and reaction time priming in implicit visual memory

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ARTICLE INFO

Article history:
Accepted 23 November 2005
Available online 14 February 2006

Keywords:
Covariance analysis
Functional imaging
Neural network
Visual recognition memory

ABSTRACT

Unfamiliar line drawings were presented to subjects three times during BOLD fMRI scanning. A set of brain areas was detected in which the effect of stimulus repetition on the evoked fMRI response depended on whether or not the drawing could be conceived as a coherent three-dimensional structure. Differential repetition effects were found in the neural response to drawings of both structurally possible and impossible objects. This differential effect of repetition was related to the amount of reaction time priming on the concurrent task involving decisions about three-dimensional structure in the possible but not in the impossible objects. These results point to different neurophysiological processing mechanisms for structurally possible and impossible images and demonstrate neural plasticity that predicts behavioral priming for structurally possible images.

1. Introduction

In a PET activation study of implicit and explicit memory, Schacter et al. (1995) found object-dependent activation effects. In particular, they observed increased CBF in the area of the left temporal and fusiform gyri when subjects made possible/impossible object decisions on previously encoded possible but not impossible objects. No such trends were observed for new objects. This finding was used as support for the role of a Structural Description System (SDS) that computes three-dimensional structural descriptions of visual events. As impossible objects lack a globally coherent three-dimensional geometry, the SDS is unable to successfully compute a singular three-dimensional representation of an impossible object.

While highly compelling, this study fails to address two fundamental concerns. First, it was done using PET imaging in a blocked design. Although attributable to the conditions of state-of-the-art neuroimaging at the time, this is a serious methodological flaw that in and of itself justifies repeating the experiment. Furthermore, as a blocked design, all trials within

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doi:10.1016/j.brainres.2005.11.102

a given block have primarily the same set of experimental conditions (e.g., possible, encoded). Blocked designs in memory experiments are thus very undesirable since they do not establish a rigorously controlled randomized task structure and thus cannot guarantee the elimination of confounding influences that could enable the subjects to by-pass the actual object decision itself (and thus respond, after the first few trials, simply on the basis of the block structure and not stimulus type). Second, there was no behavioral priming effect on the possible/impossible object decision for the impossible objects. This makes it difficult to establish that the observed specificity of the neural activations is due to object type per se and not due to whether other object or task factors may have reduced priming specifically for the impossible objects.

Any investigation of the neural networks underlying cognitive activity must consider the nature of the neural signals involved. It has been proposed that neural response, and by extension hemodynamic repetition suppression (Desimone, 1996; Wiggs and Martin, 1998), are at the basis of perceptual priming mechanisms. Suppression as well as latency reduction of neural responses (as measured by EEG) is thought to occur with the lowering of the perceptual threshold for stimulus identification after repeated exposures (Wiggs and Martin, 1998), which does not require any explicit recollection of having seen the object before.

Despite the evidence linking repetition suppression to perceptual priming across a variety of object decision and identification tasks, the assertion of a linkage between the two phenomena has recently come under criticism in a series of articles (Henson and Rugg, 2003; Henson et al., 2002; Eger et al., 2004) that bring up important questions. Henson and Rugg (2003) systematically scrutinize all of the steps in the link between repetition suppression and perceptual priming formulated in Wiggs and Martin (1998). This link partially relies on implicit assumptions about (1) the mapping between neural activity and hemodynamic response, (2) the mapping between hemodynamic response and behavior, and (3) the mapping between neural activity and behavior.

With regard to the mapping between neural activity and hemodynamic response, Henson and Rugg argue that the generic phenomenon of neural response suppression observed in animals when exposed to repeated stimuli (Brown and Xiang, 1998) might happen too fast to be compatible with the peak and latency reductions observed in human ERP and fMRI studies. Rather, the integrative nature of signal modalities in human neuroimaging studies of higher cognition might reflect modulation by, and interaction with, other brain areas. For example, repetition effects commonly found in the lateral occipital complex (Grill-Spector et al., 1999) might not be directly attributable to response suppression of neurons residing at that brain location. Further, Henson and Rugg note in light of residual uncertainty in the biophysical relationship between neural activity and hemodynamic response (Logothetis et al., 2001) that even if there was a direct link between neural and hemodynamic responses at particular brain locations, the sign of the relationship would not be unequivocally clear. We have tried to accommodate these concerns and chosen a multivariate approach in our data analysis; this approach pays attention to interactions between brain areas and changes in activation across stimulus repetitions of both signs.

Henson and Rugg (2003) note further that the presumed relationship between hemodynamic/neural response suppression and perceptual learning can show dissociation in certain circumstances: for instance, repetition effects are usually not found in early sensory or motor regions (Schacter and Buckner, 1998) although it is equally plausible for these regions to be modulated by attention or reaction time as the more commonly found lateral occipital complex. Additionally, as shown in a recent report (Dobbins et al., 2004), the type of perceptual learning influences whether response suppression is present. In the cited report, priming was found with concomitant cortical deactivations across repeated presentations for a fixed relational object-size judgment ("bigger/smaller than a shoebox"). However, switching the relational size judgment to its logical complement ("bigger"→"smaller") between repetitions abolishes most priming behavior and cortical de-activation, hinting at the learning of the stimulus–response association, rather than a true facilitation of object-related knowledge. Other studies have also found that hemodynamic response suppression requires that objects are attended to (Eger et al., 2004), challenging the automaticity of neural response suppression for repeated exposures to visual stimuli which was also suggested by Wiggs and Martin (1998).

In the current study, we set out to probe the link between priming and repetition effects in a modified trial-based version of the possible/impossible object decision (PI-OD) task (Schacter and Cooper, 1993, 1995) using event-related fMRI. Using efMRI and a modified trial-based PI-OD paradigm resolves the two concerns stemming from the original Schacter and Cooper PET findings. By contrast to the trial-based paradigm, the PI-OD task has typically been implemented as a block-mediated priming paradigm consisting of an initial structural encoding phase, where subjects view both types of objects without explicit awareness of the structural possibility attribute, followed by the object decision test block. In the object decision block, subjects indicate whether intermixed encoded and new possible and impossible stimuli are indeed "impossible" or "possible" in structure. Sample possible and impossible objects are shown in Fig. 1.

This design has revealed priming effects for possible, but not for impossible objects, and involved the left inferior temporal gyrus (Schacter et al., 1995). Our trial-mediated

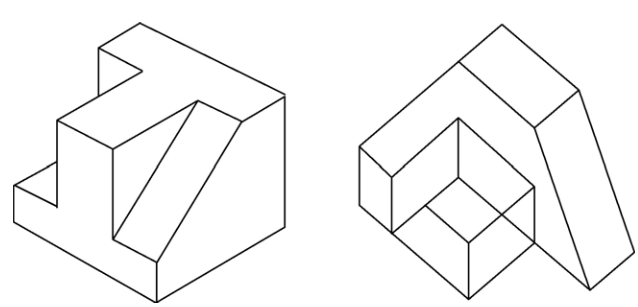

Fig. 1 – Examples of possible (*P*) and impossible (*I*) objects used in the object decision task. Left: *P*-object; right: *I*-object.