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Non-holistic coding of objects in lateral occipital complex with and without attention

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ABSTRACT

A fundamental issue in visual cognition is whether high-level visual areas code objects in a part-based or a view-based (holistic) format. Previous behavioral and neuroimaging studies that examined the viewpoint invariance of object recognition have yielded ambiguous results, providing evidence for either type of representational format. A critical factor distinguishing the two formats could be the availability of attentional resources, as a number of priming studies have found greater viewpoint invariance for attended compared to unattended objects. It has therefore been suggested that the activation of part-based representations requires attention, whereas the activation of holistic representations occurs automatically irrespective of attention. Using functional magnetic resonance imaging in combination with a novel multivariate pattern analysis approach, the present study probed the format of object representations in human lateral occipital complex and its dependence on attention. We presented human participants with intact and half-split versions of objects that were either attended or unattended. Cross-classifying between intact and split objects, we found that the object-related information coded in activation patterns of intact objects is fully preserved in the patterns of split objects and vice versa. Importantly, the generalization between intact and split objects did not depend on attention. We conclude that lateral occipital complex codes objects in a non-holistic format, both in the presence and absence of attention.

Introduction

A hallmark of human object perception is the recognition of objects despite variations in their exact appearance. In line with this characteristic, object representations in high-level visual brain areas have been found to generalize across changes in size, position or orientation (Eger et al., 2008; Grill-Spector et al., 1999). Yet, the specific representational code realizing such invariant representations is still largely unknown. In particular, one central question is whether an object is coded as a collection of *parts* (Biederman, 1987; Hummel and Biederman, 1992; Marr and Nishihara, 1978) or in a *view-based* format (Edelman and Bülthoff, 1992; Poggio and Edelman, 1990; Tarr and Pinker, 1989).

Part-based models propose that objects are encoded in terms of their constituent parts, the representations of which are independent of each other and dynamically bound together. Neurons that are tuned to a particular object part could therefore respond to the object part appearing in different configurations or views, allowing for robust object recognition across various manipulations, such as translation across the visual field, size changes and left–right reflection (Biederman, 1987; Hummel and Biederman, 1992; Hummel, 2001). By contrast, view-based models propose that objects are recognized by matching the incoming sensory information to stored views (Edelman and Bülthoff, 1992; Poggio and Edelman, 1990; Tarr and Pinker, 1989). View-based representations are holistic, as the parts of an object are not represented independent of each other and have fixed relative positions (static binding). Under a view-based scheme neurons respond most strongly if objects are presented in learned views or configurations. Nevertheless, recognition of objects in varying views is thought possible by storing many views of an object (Bülthoff and Edelman, 1992; Olshausen et al., 1993; Poggio and Edelman, 1990; Tarr and Gauthier, 1998; Tarr, 1995; Ullman, 1998), interpolating across these views (Logothetis et al., 1994; Poggio and Edelman, 1990; Ullman, 1989) or by a distributed neural representation across view-tuned neurons (Perrett et al., 1998).

Behavioral evidence on the format of object representations is equivocal, supporting both view-based (Edelman and Bülthoff, 1992;

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Murray, 1999; Tarr and Pinker, 1989) and part-based representations (Biederman and Cooper, 1991; Biederman and Gerhardstein, 1993). Neuroimaging research, too, has sought to establish which format of representation underlies object recognition. Studies using functional magnetic resonance imaging (fMRI) show that blood oxygen level-dependent (BOLD) signals in various ventral visual stream regions, such as in lateral occipital and inferior temporal cortices, tend to decrease when an object is shown repeatedly, and found that this repetition suppression (Grill-Spector et al., 2006) is greatest when the repeated view of an object is identical to the original orientation, but decreases with the amount of view change (Andresen et al., 2009; Ewbank et al., 2005; Gauthier et al., 2002). However, in support for part-based representations, other fMRI studies have shown that the ventral stream is largely insensitive to the deletion of local image features or changes in image format (grayscale image vs. line drawing), as long as the individual object parts are present (Hayworth and Biederman, 2006; Kourtzi and Kanwisher, 2000).

Importantly, the representational format might be dependent on the absence or presence of attention. Attended visual objects exhibit robust repetition-priming effects even when their mirror-reflected (Stankiewicz et al., 1998) or half-split (Thoma and Henson, 2011; Thoma et al., 2004) versions are presented as prime stimuli, suggesting a part-based representation. However, when the same prime objects are unattended, visual priming is still found for objects presented in the same view, but completely abolished after view changes (see Thoma and Davidoff, 2007, for a brief review). Hummel (2001) therefore proposed a hybrid model, in which part-based representations are established with attention, whereas view-based representations are automatically activated irrespective of attention.

Inspired by these previous studies and theoretical considerations, the present fMRI study examined the representational format of objects in high-level visual cortex and its dependence on attention. Objects were presented in either an intact or a split configuration (Fig. 1B) and were either attended or unattended. The half-split manipulation, while preserving the constituent object parts, distorted the holistic image in a way that cannot be recovered by the aligning processes of view-based models (Hayward et al., 2010; Thoma et al., 2004). To prevent verbalization of the attended object as a confounding factor, we used a non-semantic attention task, in which participants detected brightness changes on either the object (attended condition) or a contralaterally presented noise stimulus (unattended condition). We reasoned that only if objects are coded as part-based, non-holistic representations, should activation patterns of split objects be informative about those of intact objects. Moreover, if attention was necessary for part-based representations, this configural invariance of object representations should only be observed for attended, but not for unattended objects.

To this end, we used a novel multivariate approach, in which we trained a support vector machine classifier to discriminate between activation patterns of intact objects and tested its predictive capacity for activation patterns of split objects and vice versa. The rationale was that successful generalization between activation patterns of intact and split objects is indicative of a non-holistic format of object representations. Our multivariate approach represents an important advance compared with previous repetition suppression studies, because of mounting evidence that high-level visual areas code objects in a distributed fashion across multiple neuronal populations (Haxby et al., 2001; Rice et al., 2014). In particular, different configurations of an object might activate identical neuronal populations and the difference between configurations only emerges at the pattern level as a distinct weighting of each population. Multivariate methods are able to pick up on these object- or view-specific multivoxel fingerprints, whereas repetition suppression—as a univariate technique—misses out on such pattern-related information. We focused our analyses on the LOC, given a large body of evidence supporting its pivotal role in object processing (Grill-Spector et al., 1998; Malach et al., 1995) and object recognition (Grill-Spector et al., 2000).

Materials and methods

Participants

Eighteen healthy participants (11 female, mean age ± SEM, 23.4 ± 0.8 years) participated in the experiment for payment after giving written informed consent. The study was conducted according to the declaration of Helsinki and approved by the local ethics committee.

Experimental design

The experimental design comprised the factors configuration (intact, split) and attention (attended, unattended) as factors of interest, as well as object (camera, watering can, chair) and side of presentation (left, right) as factors of no interest. Within each of eight experimental runs, an object appeared in four trials in each attention conditions (in two trials per side of presentation). The order of presentation was randomized across the 48 trials of each run.

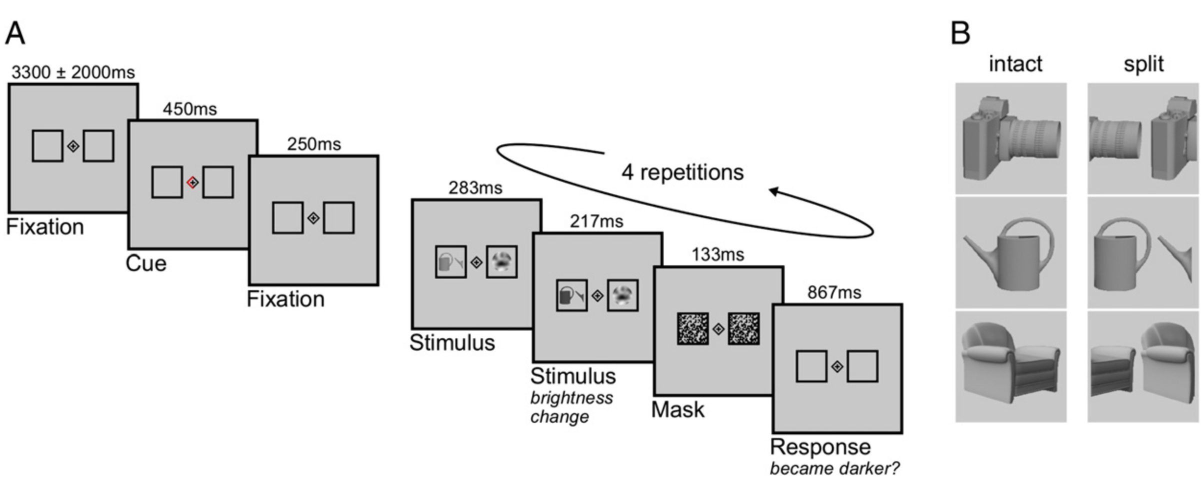

Fig. 1. Experimental procedures and stimuli. A. In each trial a cue indicated the side to which attention should be directed. Subsequently, four repetitions of the stimulus–response phase appeared, during each of which participants had to detect a decrease in brightness of either the object (attended condition) or the noise stimulus (unattended condition). B. The stimulus set consisted of three objects in an intact and half-split configuration.