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Research report

An interplay of fusiform gyrus and hippocampus enables prototype- and exemplar-based category learning

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HIGHLIGHTS

- Different brain structures for prototype- and exemplar-based category learning has been proposed.
- Exemplar based category learning is associated with fusiform gyrus activation.
- Exception learning is associated with hippocampus activation.
- Coupling between Hippocampus and fusiform gyrus activation showed a time displaced course for categorization of Prototypes and Exceptions.

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ABSTRACT

The aim of the present study was to examine the contributions of different brain structures to prototype- and exemplar-based category learning using functional magnetic resonance imaging (fMRI). Twenty-eight subjects performed a categorization task in which they had to assign prototypes and exceptions to two different families. This test procedure usually produces different learning curves for prototype and exception stimuli. Our behavioral data replicated these previous findings by showing an initially superior performance for prototypes and typical stimuli and a switch from a prototype-based to an exemplar-based categorization for exceptions in the later learning phases. Since performance varied, we divided participants into learners and non-learners. Analysis of the functional imaging data revealed that the interaction of group (learners vs. non-learners) and block (Block 5 vs. Block 1) yielded an activation of the left fusiform gyrus for the processing of prototypes, and an activation of the right hippocampus for exceptions after learning the categories. Thus, successful prototype- and exemplar-based category learning is associated with activations of complementary neural substrates that constitute object-based processes of the ventral visual stream and their interaction with unique-cue representations, possibly based on sparse coding within the hippocampus.

1. Introduction

Every day we are confronted with a bewildering variety of objects. Since we are unable to learn about each object separately, we deal with them at the category level. Categorization is the ability to generalize various stimuli into a single class, to extrapolate the categorical knowledge to new members of the stimulus classes, and to discriminate between different classes [1]. The ability to categorize effectively reduces information load and enables us to cope with the constantly changing environment [2]. Grouping similar objects reduces computational demands and enables an organism to use its resources for other purposes [3].

Research focusing on category learning has put forward various differing computational models in order to explain categorization processes for a review, see Ashby et al. [1]. Some of them are exemplar-based and thus assume storage of individual instances of one category and subsequent generalization when being faced with a new stimulus of the same category [4,5]. When being faced with a novel stimulus, its belonging to a certain category is determined by a comparison to previously encountered stimuli. One example would be a neurologist who tries to determine whether or not he sees a brain tumor on an MR image. If it would be similar to pre-

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viously encountered and memorized MR images of brain tumors, he would classify it accordingly. On the contrary, prototype-based models are developed from an abstracting of the central tendencies of stimuli from one category [3]. The neurologist from the previous example would not rely on the memorization of every single tumor image, but instead he would have condensed the previous images into a summary representation to which he then would compare new MR images. Furthermore, there are hybrid models like the cluster-based SUSTAIN model [6]. SUSTAIN explains category learning by initially assuming a very simple category structure that is represented by a single cluster that codes features and four categories. Surprising events, e.g. stimuli that do not fit in the representation of the initial cluster, recruit additional clusters, finally resulting in a set of competitive cluster each representing one category [6]. Another example of a hybrid model is RULEX, the rule-plus-exception-model [7], which assumes a stochastic process in which people can classify objects by forming simple rules with the addition of occasional exceptions. Importantly, different subjects form different simple rules and memorize different exceptions to those rules [7]. The main difference between the two aforementioned models is that RULEX can explain categorization based on two mutually exclusive categories, while SUSTAIN is intended to be a more general learning model [6].

These models try to explain category learning on a cognitive level [8] but make no strong predictions about neural substrates. More recent developments in cognitive neurosciences have tried to identify the neural basis of categorization processes, for example by using functional imaging or by performing comparative studies of humans and animals [2]. Various structures of the brain have been shown to participate in different forms of categorization learning, including visual association areas, the medial temporal lobe (MTL), the prefrontal cortex, and the basal ganglia, with the contribution of these structures depending on the experimental paradigm that is employed [1]. Furthermore, based on this widespread involvement of neural structures, it has been pointed out that it is improbable for categorization to be based on a single neural system, and that it requires the interaction of multiple brain structures and their plastic capabilities [9]. This view is also supported by convergent findings from neuroimaging studies that are not easily explainable by single-system approaches [10].

There has been a growing trend of integration in the two main categorization research fields, computational modeling and cognitive neuroscience, especially supported by the employment of neuroimaging studies. One example is the usage of computational models as the basis for the analysis of fMRI data [11].

Nevertheless, the neural basis of two of the most prominent category learning types, prototype- and exemplar-based learning, is yet unclear. The former might in part be mediated by the fusiform gyrus, as has been shown in a previous categorization study [12], where the activation of the fusiform gyrus changed after learning the membership to a category. Similarly, Pernet et al. [13] yielded evidence for fusiform gyrus activation in letter categorization. It has further been shown, that activation of the so called fusiform face area within the fusiform gyrus could reflect visual expertise [14,15], a process that is also involved in categorization learning.

On the other hand, exemplar-based learning could be processed by the MTL, since the explicit memorization of individual stimuli would require the involvement of memory systems that are tuned to sparse coding properties [16]. It has been shown previously that the activation of single neurons in the hippocampus can be linked to category-specific visual responses [16–18] and that cell firing within the hippocampus correlates with categorization performance [19]. Studies using formal modelling with SUSTAIN could also show an involvement of the MTL in a rule-plus-exception category learning task [11], emphasizing the role of the MTL in the mastering of exceptions to a category rule. The role of the hippocampus in stimulus generalization, representation and categorization has also been highlighted in a recent review [20], describing it as part of a network involving the basal ganglia and the prefrontal cortex and comparing its function to decision making processes.

A comparative study investigating the stages of category learning in humans and pigeons [21] successfully modeled prototype- and exemplar-based strategies over the course of an extended learning phase, showing that both species change their initial prototype-based strategies in order to correctly categorize stimuli that represent exceptions from the general similarity. With this, they also replicated previous studies investigating the time course of category learning [3,22,23]. Unfortunately, there was no investigation of the underlying neural basis for these strategies.

The present study aimed to investigate the neural correlates for prototype- and exemplar-based categorization strategies, in order to contribute to the question if both learning types are part of the same neural process or two individual and distinct processes, as well as to investigate the change of neural activation over the time course of the experiment. For this, we employed the same behavioral paradigm as Cook and Smith [21], in which participants had to categorize unfamiliar abstract stimuli into two groups by means of direct feedback after every trial. The categories consisted of a prototype, five typical stimuli and an exception (which shared more features with the opposing prototype).

Based on previous findings, we expected differential activation patterns for prototypes and typical stimuli on the one hand (prototype-based learning, mediated by the fusiform gyrus) and for exceptions on the other hand (exemplar-based learning, mediated by the hippocampus). Behaviorally, the learning of exceptions should be diminished in the beginning and should progressively increase over the course of the experiment, when participants realize that their prototype-based learning strategy does not work for the exceptions.

2. Material and methods

2.1. Participants

Twenty-eight right-handed and neurologically healthy subjects (12 male and 16 female subjects; mean age: 24.61 years; range: 20–30) participated in the experiment, reimbursed with research credit needed for their studies of psychology, or alternatively with 15€. All subjects gave informed written consent after a detailed explanation of the procedure. The study received ethical approval by the local Ethics Committee of the Medical Faculty of the Ruhr University Bochum, which conforms to the Declaration of Helsinki.

2.2. Stimuli and task

The experiment took place inside of an MRI scanner and was performed using Presentation® software and MRI video goggles with a resolution of 800 × 600 pixels, registering the responses with an MRI-suitable keypad. Participants had to perform a visual categorization task, which was adapted from Cook and Smith [21]. In this task, circular stimuli (400 × 400 pixels) with six binary color dimensions had to be categorized into one of two stimulus "families", with the participants having no prior knowledge about the stimuli or categories. The stimuli were similar in their structure but differed in the color combinations. Each category consisted of one prototype, five typical stimuli that shared five colors with the prototype, and one exception that shared five colors with the prototype of the other category (see Fig. 1). This design prevented the usage of a prototype-based strategy for the exceptions, since this strategy would lead to an incorrect categorization.