between single cell loading, targeted filling of a few cells, and staining of complete populations using bulk loading. The use of all these techniques—alone or in combination—will provide important steps toward the functional characterization of local neural circuits in the brain. Moreover, the simple application to living animals might facilitate novel imaging approaches for optical recordings of neural activity in awake, freely behaving animals.

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In the Eye of the Beholder: Visual Experience and Categories in the Human Brain

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How does experience change representations of visual objects in the brain? Do cortical object representations reflect category membership? In this issue of *Neuron*, Jiang et al. show that category training leads to sharpening of neural responses in high-level visual cortex; in contrast, category boundaries may be represented only in prefrontal cortex.

In 350 BC, Aristotle asked: "What is there"? His answer is given in the title of his book: *Categories*. Ever since, philosophers and scientists have asked how we carve the world into distinct categories.

Two millennia later, neuroscientists have begun to tackle this question with methods Aristotle could not have dreamt of. Using single-cell recording and functional magnetic resonance imaging (fMRI), they can ask: what are the neural mechanisms that underlie categorization, and visual perception in general? The first steps in answering this question were made when, in the 1950s, David Hubel and Torsten Wiesel began to elucidate the response properties of single neurons in early visual cortical areas. Later, scientists shifted their focus to more high-level visual areas, such as inferotemporal cortex, where Bruce et al. (1981) discovered single neurons that respond selectively to complex object categories like faces and hands. Most recently, researchers have tackled the central question of how cortical object representations arise in the first place and specifically how they may be shaped by experience (Op de Beeck et al., 2006; Baker et al., 2002).

In this issue of *Neuron*, Jiang et al. (2007) report a study in which they combine the old question about the nature of categories with the contemporary neuroscientists' question about the origin of cortical object representations. Inspired by previous electrophysiological studies in monkeys (Freedman et al., 2001), they ask: what are the neural mechanisms that underlie the formation of visual categories through experience? Specifically, does training sharpen neural object representations? Further, is neural sensitivity higher to differences between stimuli belonging to different categories compared to stimuli belonging to the same category?

In the new study, human participants were trained for an average of 5 hr to discriminate between two types of cars. The cars came from a morphed two-dimensional stimulus continuum, and the category boundary was assigned arbitrarily, such that one stimulus dimension was relevant for the categorization task (an approach similar to that of Freedman et al., 2001). Participants were presented with three stimuli sequentially, and had to guess which of the latter two belonged to the same category as the first one, and were given immediate feedback about their performance. The participants accurately learned the two categories, and their classification performance showed a sharp transition at the category boundary.

To assess neural changes associated with visual experience of the car stimuli, the participants' brains were scanned using fMRI before and after training. The authors used an fMRI adaptation paradigm; this technique is based on the fact that if neural activity in a given brain region is reduced for the repeated presentation of the same stimulus compared to presentation of two different stimuli, then that region must be sensitive to the difference between those two stimuli. Adaptation can thus be used as a measure of neural sensitivity or ''tuning.'' Jiang et al. presented pairs of stimuli from their car set (in contrast to training, where stimuli were presented three at a time). The two stimuli on each trial were either the same or different, and the stimuli on ''different'' trials could belong to the same or different trained categories.

First, the authors focused their analysis on the lateral occipital area (LO), an object-selective human brain region which may correspond approximately to monkey inferotemporal cortex. Before category training, this region was not sensitive to stimulus differences: the response magnitude to ''different'' stimulus pairs was no larger than that for ''same'' pairs. However, after training, right LO showed a higher response to ''different'' compared to ''same'' stimulus pairs. Crucially, the participants performed a ''position-change'' task during fMRI scanning, which was unrelated to the categorization task on which they were trained, thus ruling out potential task confounds. Thus, the authors demonstrate for the first time with fMRI in humans that visual experience with particular stimuli for several days can lead to increased neural sensitivity for these stimuli in object-selective brain regions, as measured by adaptation. A putative underlying mechanism for this finding is the sharpening of tuning of object-selective neurons through visual experience (Baker et al., 2002); however, the indirect nature of the fMRI BOLD signal requires that such interpretations be stated with care.

Second, Jiang et al. asked whether a neural correlate of categorical perception could be found in LO: is the fMRI signal higher on ''different'' trials when the two stimuli belong to different categories compared to when they belong to the same category? This effect would indicate categorical object representations, such that the neural representations of stimuli belonging to the same category are more similar than those of stimuli belonging to different categories. Critically, the stimulus pairs under comparison were equidistant in the stimulus space and matched for physical similarity, thus avoiding low-level confounds. Interestingly, Jiang et al. found no effect of category membership in LO: the responses on ''different'' trials after training were no higher when the two stimuli came from opposite sides of the category boundary than when they did not. Thus, although object representations in LO are refined by visual experience, this study found no evidence for a representation of learned category structure in LO.

To further investigate effects of category membership, the authors conducted an additional fMRI experiment in which participants were asked to categorize the car stimuli during scanning, in contrast to the first experiment where the task had been independent of category membership. With this manipulation, Jiang et al. did obtain a category membership effect: neural activity in right lateral prefrontal cortex (rLPFC) was higher for stimulus pairs that belonged to different categories than for equidistant pairs belonging to the same category. The authors conclude that this region is likely to contain category-selective neurons.

Taken together, these results lend weight to a model of perceptual learning according to which visual experience sharpens neuronal tuning of object representations in inferotemporal cortex, in a manner that is independent of category membership and task; in contrast, cells in prefrontal cortex are tuned to the category membership of the stimuli (Miller and Cohen, 2001). Furthermore, the study confirms and extends previous studies on the neural basis of visual experience and categorization in both monkeys (Freedman et al., 2001) and humans (Op de Beeck et al., 2006). Specifically, this is the first fMRI study showing a sharpening of ''tuning'' in object-selective brain regions through visual experience.

At the same time, the study poses questions for future research. First, Jiang et al. find no evidence of a categorical effect in high-level visual cortex. However, the human object-selective region lateral occipital complex (LOC) usually falls into two components: a posterior and lateral portion, LO, which Jiang et al. studied; and a more anterior and medial portion, pFs. The latter is commonly thought to contain higher-level object representations than LO (Grill-Spector et al., 2001), but could not be investigated by Jiang et al. because it could not be localized reliably in some participants. The question arises whether this region might have shown the category-specific effect that was not obtained in LO; this would indicate that visual categories might be represented perceptually in high-level visual cortex rather than only in the frontal lobe. The possibility that pFs might show a categorical effect is plausible given that other authors (Rotshtein et al., 2005) *have* found evidence for categorical representations in the fusiform face area (FFA), which borders on pFs.

Second, it is not entirely surprising that Jiang et al. did not find a categorical effect in high-level visual cortex when one considers that they find no *behavioral* evidence for categorical perception: perceptual discriminability of stimuli on opposite sides of the category boundary after training was not elevated compared to stimuli on the same side of the boundary. This finding contradicts results from earlier psychophysical categorization studies (Goldstone, 1994) which do find improved performance across the category boundary after training. Future research will need to address this discrepancy. One possibility is that the car stimuli used by Jiang et al. had strong pre-existing representations that could not be sufficiently altered by category training to give rise to such a category effect. It is possible that the lack of a categorical effect in high-level visual cortex can be explained by the lack of a behavioral effect, and one might hypothesize that behavioral paradigms which lead to such an effect would reveal a neural categorical effect in LOC.

Third, the category-specific effect in prefrontal cortex was only found when participants were engaged in a categorization task. This design confounds the relevant stimulus conditions with task performance: higher activity on ''between-category'' than ''within-category'' trials could potentially reflect general target detection as opposed to categorization per se. Jiang et al. argue against this alternative account by showing that the magnitude of the category effect in prefrontal cortex correlates with accuracy in performing the classification task across participants. Although this finding lends some weight to the account that prefrontal cortex is in fact involved in categorization per se, a remaining caveat is that incorrect trials were not excluded from this analysis, so the correlation across subjects could also reflect general target detection.

Fourth, in Jiang et al.'s study, categories were determined by the experimenters: an arbitrary category boundary was assigned along one of the two physical stimulus dimensions, and participants were taught the location of this boundary with feedback. Thus, this study addresses the effect of supervised learning on category formation. In everyday life, this situation can be likened to a parent teaching a child the difference between a cat and a dog. A second form of category learning, in contrast, is unsupervised and stimulus driven. For instance, phonemes are auditory categories that are not taught, but nevertheless show a categorical perception effect: two sounds belonging to the same phoneme category are perceived as more similar than sounds belonging to different phoneme categories, even if physical similarities are equated (Liberman et al., 1957). A remaining question, therefore, is whether common or distinct neural mechanisms underlie these two forms of category learning. Specifically, one might conjecture that unsupervised category learning is unlikely to be mediated by prefrontal cortex, as seems to be the case for supervised category learning; instead, this form of learning might involve category-specific changes in visual areas.

A further question in this context is which behavioral mechanisms drive unsupervised category learning and how they differ from those at work in the paradigm of Jiang et al. One possibility is that observers in unsupervised paradigms form categories by exploiting statistical regularities of the visual environment (Fiser and Aslin, 2002). For instance, it has been shown both in the auditory (Maye et al., 2002) and low-level visual domain (Rosenthal et al., 2001) that stimuli with high relative frequency of occurrence become category prototypes, whereas low-frequency stimuli form category boundaries. However, questions remain: does this effect also hold for complex, object-like visual stimuli? If so, how does frequency of occurrence interact with physical stimulus attributes, and does this type of unsupervised learning require active categorization or merely visual exposure to the frequency spectrum (Turk-Browne et al., 2005)? Finally, do the representations established through unsupervised learning differ from those arising after supervised learning?

The nature and origin of categories has been debated since the times of Aristotle, and the role of experience in shaping cortical object representations is engaging modern neuroscientists. The creative experiments by Jiang et al. provide new insight into these questions. Most importantly, Jiang et al. show that experience shapes cortical object representations: training on visual stimuli can increase neural sensitivity in object-selective brain regions. The exact mechanisms underlying these changes remain to be elucidated; but Jiang et al. have made an important step in the right direction.

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