Neural mechanisms of visual categorization: Insights from neurophysiology

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Abstract

How does the brain recognize the meaning of sensory stimuli? Through experience, we easily learn to group stimuli into meaningful categories such as “chair”, “table” and “vehicle”. Although much is known about how the brain processes and encodes basic visual features (e.g. color, orientation, and motion direction), much less is known about how the brain learns and represents the behavioral relevance, or category, of stimuli. This article will review a number of recent experiments which suggest that neuronal activity in primate prefrontal, temporal and parietal cortical areas likely plays significant, though complementary, roles in visual categorization and category learning.

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1. Introduction

Of course, we are not born with a built-in neural responses that closely follow changes in visual feature properties. However, visual feature processing is often gradual and involves something beyond the sort of neuronal encoding that is typically associated with sensory stimuli. Because of this, neuronal encoding of categories must solve a number of extremely complex problems including processing basic features of sensory stimuli, determining the meaning of those stimuli, and generating behaviors that lead us to successfully and efficiently achieve our immediate and long-term goals. Remarkably, the brain routinely solves each of these problems with relative ease, though neuroscientists are only just beginning to understand some of the neural machinery underlying these processes. This article will focus on one aspect of this process: understanding how visual feature representations are transformed into more abstract signals which reflect the behavioral relevance, or meaning, of stimuli.

Our experience of the world around us is not an accurate reflection of its physical features. Instead, we often group sensory stimuli according to their category membership or behavioral meaning. This process of dividing stimuli into classes according to their functional relevance is a critical stage of both perceptual and cognitive processing because it provides meaning to our sensory experiences. For example, recognizing that a new item is a “television” instantaneously imparts a great deal of information about its features and functions. The ability to group stimuli into categories is one of the foundations of complex behavior. Without it, we would be unable to rapidly distill a new situation or event down to its fundamental essence, making it almost impossible to quickly decide how to respond.

Decades of studies have revealed a great deal about how the brain processes basic visual features such as color, orientation, and motion direction. However, less is known about how the brain learns and encodes the category membership of visual stimuli. Categories frequently contain items that vary greatly in their physical similarity to one-other, but which have similar functions or meanings (e.g. “fruit”). Furthermore, categories (especially lower-level perceptual categories) are often separated from one-another by sharp “category boundaries” (Barsalou, 1992; Ashby and Maddox, 2005), such that physically similar items may be perceived as distinct if they belong to different categories (e.g., the phonemes “ba” and “pa”). Because of this, neuronal encoding of categories must involve something beyond the sort of neuronal encoding observed for basic visual features: gradual changes in neural responses that closely follow changes in visual feature properties. Of course, we are not born with a built-in library of higher level, more abstract, categories like cars, computers, and cameras. Instead, we develop our own mental lexicon of categories and concepts through learning and experience.

This article will summarize the results from a number of recent studies that have given new insights into how the brain learns and represents abstract visual categories. We will primarily focus on neurophysiological recording studies in monkeys trained to perform visual categorization tasks. These studies have revealed that the activity of single neurons, particularly those in the prefrontal and posterior parietal cortices (PPCs), can encode the category membership, or meaning, of visual stimuli that the monkeys had learned to group into arbitrary categories. In contrast, neuronal activity in the inferior temporal and middle temporal (MT) areas seemed more involved in visual feature processing, and did not carry explicit signals about the category membership of stimuli.

2. Behavioral evidence for categorization throughout the animal kingdom

Categorization is not an ability that is unique to humans. Instead, perceptual categorization and category-based behaviors are evident across a broad range of animal species, from relatively simple creatures like insects to primates. For example, a clever study by Wytknethn et al. (1996) demonstrated that crickets categorize the sound frequency spectrum into two distinct groups. It turns out that there are two types of sounds that are particularly important for crickets: mating calls (around 4-5 kHz) and echolocation signals (25-80 kHz) from predatory bats. Naturally, crickets try to maximize their chance of locating a mate and minimize their chance of being eaten by a bat. This study revealed that crickets treat the frequency spectrum categorically, with a category boundary near 16 kHz; they will approach tones with frequencies less than 16 kHz and turn away from frequencies over 16 kHz, with sharp discrimination right around the 16 kHz boundary. This innate categorization behavior allows crickets to simply and effectively improve their chances for reproduction and survival.

Birds, and particularly pigeons, also show an impressive capacity for categorization, particularly for visual stimuli. Decades of laboratory experiments have shown that pigeons can learn, through operant conditioning, to indicate (by pecking a lever in a Skinner box) whether a visual image contains stimuli from a particular category. For example, they can learn to report whether images contain items such as trees (Herrnstein et al., 1976; Herrnstein, 1979), people (Herrnstein and Loveland, 1964), animals (Roberts and Mazmanian, 1988), or even man-made objects (Verhave, 1966). In some cases, pigeons’ categorization abilities can even generalize to novel images that they had not seen during training (Herrnstein and Loveland, 1964), suggesting a more abstract and flexible strategy than simply memorizing each visual image and its
required behavioral response during training. Not surprisingly, the flexibility and generality of categorization abilities in pigeons is limited. For example, pigeons have difficulty in learning and utilizing more abstract categories or rules such as “same” and “different” (Wright et al., 1983; Edwards et al., 1983; for a more detailed review, see Cook, 2001).

The increasingly flexible behavior of more advanced animals such as monkeys and humans must depend on more sophisticated abilities to learn and recognize more advanced categories and concepts. In addition, complex animals have a remarkable ability to learn new categories and to generalize that knowledge to new situations. In humans, most categories, such as “table”, “vehicle” and “telephone”, are learned and can be continually expanded and refined through additional learning and experience. Likewise, the wide behavioral repertoire of non-human primates suggests that they also can more easily learn and utilize more complex categories and rules. In fact, this has been demonstrated by a number of laboratory studies showing that monkeys can learn complex categories such as animal versus non-animal (Roberts and Mazmanian, 1988), food versus non-food (Fabre-Thorpe et al., 1998), tree versus non-tree, fish versus non-fish (Vogels, 1999), ordinal numbers (Orlov et al., 2000) and also more abstract categories such as “same” and “different” (Premack, 1983; Wallis et al., 2001).

3. Brain mechanisms underlying visual categorization

How does the brain learn and represent visual categories? In order to move towards a satisfying answer to this question, we must first determine which brain areas are most likely to play a role in representing the category membership of visual stimuli. One possibility is that information about the category, or meaning, of stimuli might be encoded in brain areas involved in processing basic visual features. For example, visual shape categories might be encoded by neurons in ventral stream visual areas (e.g., areas V4 and the inferior temporal cortex (ITC)) that are known to play an important role in visual form processing and object recognition. Alternatively, neuronal representations in shape processing areas might instead show a more faithful representation of stimulus features. In that case, more abstract category signals might be evident in downstream brain areas, such as the prefrontal cortex (PFC) and medial temporal lobe (MTL), which are directly interconnected with sensory areas but typically not thought to be centrally involved in basic sensory processing. In a series of studies, we tested these hypotheses by directly comparing neuronal activity in the PFC and ITC in monkeys trained to perform a shape-categorization task. These experiments revealed that many PFC neurons encoded stimuli according to their category membership, while ITC neurons showed weaker category effects and seemed more involved in visual feature processing.

3.1. Prefrontal cortex

An extensive body of evidence suggests that the PFC is involved in guiding and controlling complex goal-directed behaviors in both humans and non-human mammals. For example, numerous neuropsychological studies of patients with frontal lobe damage and neurophysiological investigations of PFC activity have demonstrated its involvement in the highest level of cognitive, or executive, processing (Miller and Cohen, 2001). This includes cognitive functions that are neither exclusively sensory nor motor, such as short-term “working” memory, inhibition of prepotent responses, and the learning and representation of rules. The PFC is comprised of a number of anatomically distinct areas that are directly interconnected with a wide variety of cortical and subcortical brain areas involved in sensory, motor, emotional and reward processing. The PFC is therefore perfectly situated to monitor the activity across a wide array of sensory and motor processing systems, and exert a supervisory, or executive, influence over our behavior. Based on its pattern of connections with a wide range of sensory and motor brain areas, it is not surprising that PFC neurons are activated by diverse stimuli from virtually all sensory modalities (especially for stimuli that are relevant for performing the task at hand), prior to and during the execution of motor responses, during memory for previously encountered stimuli, and in anticipation of expected events. In addition, PFC neurons can convey information about internal factors such as motivation and attention (for a review, see Miller and Cohen, 2001). Thus, the PFC’s involvement in such a diverse set of sensory, motor, and executive functions suggests that it is also likely to play a role processing learning and encoding the behavioral relevance, or category, of stimuli.

3.2. Visual shape categorization and the prefrontal cortex

To test the hypothesis that the PFC plays a role in encoding the category membership of visual stimuli, we trained two rhesus monkeys to perform a visual shape categorization task and then recorded PFC neuronal activity during task performance (Freedman et al., 2001, 2002). Over the course of several months of training, monkeys were trained to group computer-generated “morphed” stimuli into two arbitrary categories, “cats” and “dogs” that were divided by a category boundary (Fig. 1a). We used a novel 3D morphing system developed in Tomaso Poggio’s laboratory to generate a large set of parametric blends of six prototype images (three species of cats and three breeds of dogs) (Beymer and Poggio, 1996; Shelton, 2000) by varying the relative proportions of the six cat and dog prototypes. This allowed us to smoothly control the visual similarity between stimuli and precisely define the category boundary (at the midpoint along cat–dog morph lines). The category boundary divided the set of cat/dog stimuli into two equal groups that the monkeys were then trained to categorize. Over the course
of training, the monkeys learned that stimuli that were more than 50% cat were in the “cat” category, and remaining stimuli were “dogs”. As a result, stimuli from different categories could be visually very similar if they were close to but on opposite sides of the category boundary. Likewise, stimuli from the same category could be visually dissimilar (e.g. the “cheetah” and “housecat” prototypes). This allowed for a disassociation between the visual similarity and category membership of stimuli.

Monkeys were trained to perform a delayed-match-to-category task (DMC, Fig. 2a). During the DMC task, the monkeys were required to indicate whether two successively presented sample and test stimuli (separated by a one second delay) were in the same category. If the sample and test were in the same category, the monkeys had to release a lever (during the test-stimulus epoch) to receive a juice reward. If the sample and test were from different categories, the monkeys had to withhold a response during the test and wait until a second test stimulus appeared (after an additional short delay) that was always a match to the sample (and required a lever release). During training, stimuli were chosen from throughout the cat and dog morph space. After several months of training, the monkeys’ DMC task performance was excellent, even for stimuli close to the category boundary. For example, the monkeys correctly categorized dog-like cats (60% cat, 40% dog) about 90% of the time, and miscategorized them only 10% of the time (Fig. 2b).

After the monkeys had completed the training process, we recorded from 525 neurons in the lateral PFC, the PFC region that is directly interconnected with temporal lobe visual-shape processing areas (including the ITC), and
found that many PFC neurons showed activity that reflected stimulus-category: sharp differences in activity between the two categories, and little variance in activity within each category. An example of a category-selective PFC neuron is shown in Fig. 3a. This neuron’s activity sharply differentiated between dog-like (60%) cats and cat-like (60%) dogs, yet showed a relatively homogeneous level of response to stimuli within each of the categories. In other words, PFC activity mirrored the monkeys’ behavior: both showed sharp differences between categories and similar responses within each category.

Fig. 2. Delayed-match-to-category task. (a) A trial began with central fixation (500 ms) after which a sample stimulus appeared at the center of gaze for 600 ms. This was followed by a one second delay and then by a test stimulus (600 ms). If the category of the test matched that of the sample, monkeys had to release a lever to the test stimulus within 600 ms of its presentation to obtain a juice reward. If the test was a non-match, there was another delay interval (600 ms) followed by a presentation of a match, which required a lever release for a reward. There were an equal number of match and non-match trials and they were randomly interleaved. (b) Average performance of both monkeys during neurophysiological recordings for the two-category task. Dark gray bars indicate the percent of samples classified as cat and light gray bars the percent classified as dog.

Neuronal category selectivity was observed in a sizable fraction of PFC neurons. Across the population, PFC activity tended to reflect the category membership of stimuli, and was less sensitive to shape differences between individual stimuli that were in the same category. This effect was observed using a correlation analysis across the PFC population shown in Fig. 3b. This analysis was applied to the population of stimulus-selective neurons (defined as neurons that showed significantly different activity among all sample stimuli according to a one-way ANOVA) in each time epoch (sample, delay and test). For each neuron we calculated its average firing rate to each of the sample stimuli. Then, across the neuronal population, we computed the degree of correlation between neuronal firing rates to all possible pairs of sample stimuli. A category-selective neuron would show similar firing rates to pairs of stimuli that were in the same category (giving high correlation values for the activity elicited by pairs of stimuli in the same category), while the firing rates would differ greatly between stimuli that were in different categories (giving low or negative correlation values for
between-category stimulus-pairs). This pattern is exactly what we observed across the PFC population (Fig. 3b). The small patches (42 × 42 = 1764) show the correlation coefficient values between each pair of sample stimuli during the sample (left panel), delay (middle) and test (right). The four large 21 × 21 square patches of high and low correlation values (the light and dark gray regions, respectively) reflect the relative similarity in activity within categories, and the dissimilarity of activity between stimuli in different categories. While a tendency for category encoding was observed during all three time epochs, we observed especially strong category signals during the delay and test epochs, indicated by the more uniform regions of high correlation values (for pairs of stimuli within category) and low correlation values (between categories).

When the test stimulus appeared, the monkeys had to decide whether it was a category match to the previously presented sample stimulus (and whether it required a lever release). This required the monkey to determine the category membership of the currently visible test stimulus,
and to remember the category of the previously presented sample stimulus. To investigate the types of information encoded by PFC activity during the test-epoch, we computed a two-way ANOVA (factor 1: match/non-match status of test stimulus; factor 2: category of the test stimulus) on each neuron’s average activity during the test epoch. Nearly 30% of PFC neurons (N = 152) showed a main effect of, or interaction between, these factors. Of these, one third of neurons (N = 48) had test-epoch activity that reflected the match/non-match status of the test stimulus, and approximately 20% (N = 31) were selective for the category membership of the currently visible test stimulus. The remaining neurons showed significant interactions between the category of the test stimulus and whether that stimulus was a category match to the sample. These included neurons that showed match/non-match effects that were stronger for one category than the other, and also neurons that, during the test epoch, showed category selectivity for the previously presented sample stimulus (like the neuron in Fig. 3a, and across the population in Fig. 3b). In sum, neuronal activity in PFC during the test epoch of the task conveyed all the relevant information that, in principle, the monkeys needed to solve the DMC task.

Since our monkeys had no experience with cats or dogs prior to learning the DMC task, it seemed highly likely that these neuronal category effects resulted from training. Nevertheless, we verified that these effects were learning-dependent by retraining one of the monkeys to reclassify the same stimuli into three new categories that were defined by two new category boundaries that were orthogonal to the original cat/dog boundary (Fig. 1a). These three new categories each contained morphs that spanned the space between one cat prototype and one dog prototype (e.g., the cheetah and the “doberman”). After several months of training, the monkeys performed the DMC task at a high level of performance (> 85% correct), even for stimuli that were close to one of the two category boundaries. After retraining, we recorded 103 PFC neurons from the same sites as in the original two-category experiment, and found that they now were category selective for the newly learned three categories, but no longer encoded the old two categories (that were no longer relevant for the task) (Freedman et al., 2001, 2002). This demonstrated a dramatic plasticity of PFC shape-selectivity as a result of experience, and indicates that PFC category selectivity was indeed a result of training on the DMC task.

These results are compatible with those of several recent studies that have also found that PFC neurons can encode relatively abstract information about the behavioral relevance of stimuli during a variety of behavioral tasks. For example, studies by Andreas Nieder and colleagues (Nieder et al., 2002) suggest that the PFC plays a role in encoding category-like information about the numerical quantity of items visible on a computer screen. In this study, monkeys were trained to perform a delayed-match-to-number task that was similar to the delayed-match-to-category task (described above), except that the monkeys indicated whether two sequentially presented stimulus arrays (clusters of 1–5 visual items) contained the same number of stimuli. Following training, the monkeys could perform the task well for small numbers (e.g., 1–3 items), though their performance dropped sharply for larger numbers. Recordings from the lateral PFC (including recordings from the same PFC region as in the cat/dog categorization studies) found a population of PFC neurons that grouped stimuli according to the number of items that they contained (even though the arrays of items that contained a given number of items could vary widely in their visual appearance). This suggests that PFC neurons can show visual selectivity during a numerical matching task that was qualitatively similar to that seen during the cat/dog categorization task. Although, it remains to be seen whether these effects might be due, in part or in their entirety, to an innate numerical ability in monkeys and whether they share a common neuronal mechanism as the PFC shape-category effects.

In another related study, Wallis et al. (2001) taught monkeys two rules: “match” and “non-match”. During the task, the monkeys indicated (with a lever release) whether two sequentially viewed visual images were the same—if monkeys were cued to use the match rule on that trial—or different—if monkeys were cued to use the non-match rule. As compared with shape-categories, rules like “match” and “non-match” are more abstract—since they can be applied to any stimuli, even to novel images that the monkeys had never seen before. PFC recordings during the abstract rule task found a population of neurons that reflected the rule (match or non-match) that the monkey was cued to use on that trial. This points out a remarkable ability for PFC neurons to encode abstract rules (that are not explicitly and rigidly tied to particular stimuli or features) as a result of learning. Further, this raises the possibility that both visual categories (like the cats and dogs) and rules may share common neural mechanisms in the PFC.

Taken together, these studies suggest that the activity of individual PFC neurons has an impressive capacity to encode meaningful information about visual stimuli. PFC responses were similar for stimuli from the same category even if those stimuli differed greatly in their physical features. Likewise, PFC activity showed sharper discrimination between stimuli from different categories, even if those stimuli were visually similar to one-another. PFC category effects almost certainly developed as a result of learning. Retraining the monkeys to re-group stimuli into new categories caused a dramatic reorganization of PFC stimulus selectivity that resulted in neuronal encoding of the stimuli according to the newly learned categories.

A number of important questions remain about the neuronal processes underlying visual category recognition and learning. One of the primary goals of our research is to gain an understanding of the progression from feature-based encoding of stimuli in primary sensory brain areas to more malleable and abstract encoding like that observed in
PFC. What other areas might be involved in the categorization process, and how does the PFC fit into the brain-wide circuit underlying visual categorization? One possibility is that shape categories are first encoded in areas known to be involved in visual shape processing, such as the ITC. In that case, PFC category information might arise via category-selective inputs relayed via its interconnections with the ITC. Another possibility is that the PFC might play a more active role in the initial processing of stimulus-category, while the ITC would primarily represent high-level visual shape features, but not more abstract information about their category membership. The next section of this article will describe studies in which we tested these competing hypotheses by directly comparing PFC and ITC activity during the cat versus dog categorization task, and found that the two brain areas likely play different, though complimentary, roles in visual categorization and object recognition.

3.3. Inferior temporal cortex

Decades of neuropsychological and neurophysiological studies have firmly established that the ITC is an important component in the neural machinery underlying visual form processing and shape recognition. The ITC, located in the anterior ventral portion of the temporal lobe, receives substantial inputs from “ventral stream” visual form processing areas such as V4 and posterior IT cortex. The ITC is also interconnected with a number of areas, including medial temporal structures, the frontal lobe (including PFC) and the parietal cortex (Ungerleider and Mishkin, 1982; Ungerleider et al., 1989; Webster et al., 1994; Murray et al., 2000). The ITC’s role in visual shape processing was first suggested by the observation that damage to the ITC in monkeys results in pronounced behavioral deficits in visual discrimination and recognition (Kluver and Bucy, 1938, 1939; Blum et al., 1950; Mishkin, 1954, 1966; Mishkin and Pribram, 1954), and in humans it can cause category-specificagnosias (most notably for faces) (Damasio et al., 1982).

Neurophysiological recordings from ITC neurons have found further evidence supporting their involvement in visual shape processing. They often exhibit robust selectivity for complex visual stimuli such as faces, familiar objects, and geometric patterns (Gross, 1973; Bruce et al., 1981; Perrett et al., 1982; Desimone et al., 1984; Tanaka, 1996; Brincat and Connor, 2004; Hung et al., 2005). Furthermore, ITC shape selectivity can be highly specific for particular classes of stimuli, most notably for faces (Perrett et al., 1982; Desimone et al., 1984; Baylis et al., 1987; Tsao et al., 2006). ITC stimulus selectivity can be modified through visual experience, usually resulting in enhanced tuning for familiar or trained stimuli (Logothetis et al., 1995; Kobatake et al., 1998; Booth and Rolls, 1998; Sigala and Logothetis, 2002; Baker et al., 2002; Freedman et al., 2005). In addition, familiarization or training with a set of stimuli can result in clustering of neurons with similar stimulus preferences in anterior ventral ITC (perirhinal cortex) (Erickson et al., 2000). Thus, the plasticity of ITC shape selectivity as a result of experience suggests that it could play a key role in learning and encoding shape categories.

3.4. Visual shape categorization and the inferior temporal cortex

Because of its well-established role in high-level shape processing and learning, most prior neurophysiological investigations of visual categorization have focused on the temporal lobe. Despite this, it has remained uncertain whether ITC neurons show category encoding like that observed in the PFC. Recent studies have provided evidence that categories are reflected in the activity of neurons in the human MTL, which is directly interconnected with the ITC. In these studies, neurophysiologists teamed up with neurosurgeons to record from MTL neurons in human epileptic patients that had MTL recording electrodes implanted for precise anatomical localization of seizure foci (Kreiman et al., 2000; Quiroga et al., 2005). These studies found examples of MTL neurons that were remarkably selective for stimuli from a particular category (e.g., famous people, tools), but showed little difference to stimuli within-category.

Several recent studies have also investigated the responses of ITC neurons during shape categorization in monkeys. In one study, Vogels (1999) trained monkeys to categorize trees versus non-trees and fish versus non-fish and found a population of ITC neurons that responded well to many of the stimuli from the trained category, but responded weakly to distracter objects (e.g., randomly chosen objects or images that did not contain trees or fish). However, even neurons that showed the strongest category effects in this study failed to show the tight clustering of responses to stimuli within a category and sharp distinctions between categories observed in the PFC. This suggests that the category selectivity in this study might be due primarily to the visual similarity between stimuli in each of the trained categories (i.e. trees tend to be visually more similar to one another than randomly chosen objects). Another possibility is that signals related to feature and category processing might be intermixed in the ITC.

In a second recent study that examined ITC neurons during shape categorization, Sigala and Logothetis (2002) trained monkeys to group line drawings of either faces or fish into two categories. Neurophysiological recordings revealed that ITC neurons showed enhanced tuning for the stimulus features that the monkeys were trained to use to make their category judgments. However, this study did not report more abstract category effects like those seen in the PFC (e.g., binary-like responses that encoded the category membership of stimuli but did not differentiate between stimuli within each category). Instead, ITC responses seemed to become more sharply tuned for
specific stimulus features as a result of experience. However, some caution is warranted in comparing effects across these different experiments, since they differed in several important ways from the DMC task we had used in our PFC studies. For example, neither the Vogels nor Sigala tasks required the monkeys to remember the category of stimuli during a delay period, or to compare and match the category of two successively presented stimuli. Thus, it remained unclear whether the ITC might encode more explicit category information during the DMC task as we had observed in the PFC, or whether the ITC’s role in categorization is instead more limited to visual feature processing. The next section of this article will describe experiments aimed at understanding the relative roles of the PFC and ITC during visual shape categorization.

3.5. Comparison of prefrontal and inferior temporal cortices during visual shape categorization

To investigate the ITC’s role in visual shape categorization, we recorded the activity of 443 ITC neurons in area TE from two monkeys while they performed the DMC task (Freedman et al., 2003). In order to more directly compare PFC and ITC activity, we conducted simultaneous recordings from the PFC and ITC for a subset of the ITC recording sessions \(N = 130\) PFC and 117 ITC neurons. This allowed us to evaluate whether category signals, like those that we had observed in the PFC, were evident in the ITC, and whether it seemed likely that PFC category selectivity might arise via inputs from the ITC. As described below, the results of these PFC–ITC comparisons are compatible with previous ITC findings, and suggest that ITC neurons did not show strong category selectivity as we had observed in PFC. Instead, the pattern of ITC selectivity seemed more suited to a role in shape and/or feature processing and perceptual learning, but not more abstract and flexible category encoding.

The pattern of ITC activity differed from that in the PFC in several important ways. First, while there were several examples of ITC neurons that showed relatively strong category selectivity (though even those did not show effects as strong as in many PFC neurons), most ITC neurons showed activity that differed among the sample stimuli but that selectivity did not correspond in an obvious way to the two categories. Instead, most ITC neurons typically responded strongly to their preferred stimulus with gradually weaker responses to stimuli that were progressively more dissimilar to that preferred stimulus. It should be noted that we did find, on average, significantly sharper tuning for stimuli across the category boundary than within-category, though this effect was much less pronounced than in PFC. This trend for shape/feature selectivity was even evident among ITC neurons that exhibited the strongest category effects. For example, the ITC neuron shown in Fig. 4a (one of the ITC neurons that showed the strongest sample-epoch category selectivity) responded more strongly to stimuli in the “dog” category. However, a more detailed examination of the responses to each of the individual sample stimuli (shown in the grayscale plot to the right of the average histogram) showed a higher degree of variability among the stimuli within each category (as compared with the PFC neuron example in Fig. 3a) that likely indicates greater sensitivity to differences in visual similarity between stimuli within each category.

This trend for weaker category selectivity and sharper tuning for individual stimuli as compared with the PFC was also observed across the ITC population. We computed the same correlation analysis used for the PFC (shown in Fig. 3b) across the population of stimulus-selective ITC neurons during the sample, delay and test epochs. As shown in Fig. 4b, the ITC displayed a markedly different pattern of selectivity than in PFC. During the sample epoch (Fig. 4b, left panel), the ITC population did not show strong correlations between all stimuli within the same category as we had observed in the PFC (Fig. 3b). Instead, the ITC showed highly correlated activity between sample stimuli that were visually similar to one-another. This is indicated by the six 7 × 7 patches of higher correlation values along the diagonal in Fig. 4b (left panel) (corresponding to the seven stimuli closest to, and most visually similar to, each of the six prototype images). Thus, sample-period ITC activity reflected the visual similarity between stimuli, and not necessarily their category membership. In the subsequent memory delay epoch, there were comparatively fewer neurons \(N = 38/443\) that showed selectivity for the previously presented sample stimulus. Among that population of stimulus-selective neurons during the delay, ITC selectivity was clearly much weaker than in PFC, and showed only a hint of category selectivity (Fig. 4b, middle panel). Interestingly, significant category selectivity (for the previously presented sample stimulus) emerged in a relatively small population of stimulus-selective neurons \(N = 23\) during the test epoch (Fig. 4b, right panel). This raises the possibility that these ITC category signals late in the trial might arise due to feedback from the PFC, though this is merely a hypothesis that needs to be tested through further experiments.

An important difference between the pattern of results in PFC and ITC was apparent during the test epoch of the task, while the test stimulus was visible and the monkeys had to decide whether its category matched that of the previously presented sample stimulus (and required a lever-release). While test-period activity in PFC encoded all the information that was needed to solve the DMC task (e.g., sample category, test category and match/non-match status of the test stimulus), a two-way ANOVA (as above, with test-stimulus category and match/non-match status as factors) revealed few ITC neurons that showed match/ non-match effects (7%, or 10/151 neurons that showed any significant effects). Instead, the modal group of ITC neurons (59%, \(N = 89/151\)) showed an effect of test-stimulus category (most likely due to stimulus-selectivity...
among the test stimuli, and not necessarily more explicit category encoding). The remaining neurons had test epoch activity that showed an interaction between test-category and match/non-match factors. These consisted mainly of neurons that showed category selectivity for the previously presented sample stimulus during the test epoch (as indicated by the correlation analysis during the test epoch, above and Fig. 4b). Thus, test-epoch activity in the ITC seemed primarily involved in visual encoding of the currently visible test-stimulus, and seemed less involved in encoding factors related to the match/non-match or release/hold decision-related responses.

These results are compatible with previous studies of visual learning, recognition and categorization in the ITC, and suggest that the PFC and ITC play different roles in behaviors involving visual object recognition and
categorization: the ITC seems better suited to a role in visual feature and shape analysis, while the PFC may be more involved in explicit category encoding, memory signals, and a greater tendency to encode motor or decision-related factors related to the task-at-hand. While these results suggest that the ITC is an unlikely candidate for providing explicit category information (that is independent of visual similarity) to the PFC, it is possible, perhaps even likely, that other brain areas may play a more direct role in transforming visual feature-based encoding into more explicit category representations. Areas that are candidates for playing such a role include MTL areas such as the perirhinal cortex and the hippocampus, both of which receive substantial inputs from the ITC and are directly interconnected with the PFC. Thus, these areas deserve further investigation through future experiments.

Another candidate for involvement in the categorization process is the PPC, which is directly interconnected with dorsal stream visual areas such as area MT and MST (Lewis and Van Essen, 2000), and with a wide range of cortical and subcortical areas, including the PFC, ITC, basal ganglia, and areas involved in the control of eye movements (Felleman and Van Essen, 1991; Webster et al., 1994; Lewis and Van Essen, 2000). The PPC is traditionally thought to be centrally involved in visuo-spatial and attentional processing, such as directing spatial attention and planning visually guided action. However, several recent studies have raised the possibility that the PPC may also be more widely involved in a diverse set of non-spatial visual processing and executive functions, including visual shape processing, rule encoding, and even visual category representations. This will be the focus of the next section of this article.

3.6. Posterior parietal cortex

The PPC, particularly the lateral intraparietal (LIP) area, has been one of the most studied brain areas among primate neurophysiologists in recent years. Decades of neurophysiological studies in monkeys have firmly established that LIP neurons are activated by a wide range of tasks and behaviors, particularly those that involve spatial attention and visually guided actions (Colby and Goldberg, 1999; Andersen and Buneo, 2002; Assad, 2003).

Although the PPC is typically studied in the context of visuo-spatial processing and spatial attention, recent studies suggest that LIP neurons may also be involved in visual and/or more abstract cognitive processing of non-spatial stimuli. For example, several studies by Anne Sereno and John Maunsell have found that a substantial fraction of LIP neurons are strongly and selectively activated by complex visual shapes during both passive viewing and shape-matching tasks (Sereno and Maunsell, 1998; Sereno and Amador, 2006), perhaps due to LIP’s direct interconnections with the ITC. In another study, Nieder and Miller (2004) taught monkeys to recognize, report and match the number of visual items during a number-matching task (as in their studies of PFC, see above) and found many PPC neurons that selectively encoded the number of visual items in much the same way as in their PFC studies.

Further evidence that the PPC may be involved in more abstract and flexible encoding of non-spatial cognitive factors comes from several recent studies that investigated the responses of PPC neurons while monkeys applied different task—rules to a set of visual stimuli. For example, Toth and Assad (2002) trained monkeys to make a saccade in one of two directions according to either the location or color of a cue. At the start of each trial, monkeys were given a cue instructing them to attend to either the color or location of a stimulus during that trial. Recordings from LIP revealed color selectivity that varied dynamically according to whether or not the monkey had been cued to attend to color on that trial. In other words, LIP neurons were selective for stimulus-color when color was relevant, but not when it was irrelevant. In another study, Stoet and Snyder (2004) trained monkeys to discriminate the orientation or color of stimuli. At the beginning of each trial, the monkeys were instructed by a cue to attend to either the color or orientation of a subsequent sample stimulus. Recordings from the PPC (including LIP and surrounding areas) found a population of neurons that differentiated between the two “rules” (attend to color or orientation). Together, these two studies indicate that PPC neurons are likely to play a role in cognitive functions beyond their traditional role in spatial attention and planning eye movements. These studies also demonstrate that PPC neurons can show marked and rapid plasticity in their encoding according to changing task demands.

3.7. Visual motion categorization and the posterior parietal cortex

The results of these prior studies raise the possibility that PPC neurons might also encode meaningful information about the behavioral relevance, or category, of visual stimuli as a result of experience. To determine whether PPC activity might show similar category effects to what we observed in PFC, we used a similar experimental design and behavioral paradigm (delayed-match-to-category) as in the PFC and ITC. Rather than using complex shapes, we trained the monkeys to group visual-motion patterns into two categories based on their direction of motion. We chose motion rather than static shapes as stimuli for two reasons. First, it is known that many LIP neurons are activated by dynamic visual stimuli and are direction selective, even for stimuli that are “passively viewed” outside the context of an active behavioral task (Fanini and Assad, submitted for publication). It is likely that this is due to LIP’s direct interconnection with the MT and medial superior temporal (MST) areas (Lewis and Van Essen, 2000), which are known to be centrally involved in visual motion processing (Born and Bradley, 2005). Second, it can be argued that the neuronal processing...
underlying visual direction selectivity is better understood than that for complex shapes. Thus, it may be easier to identify how visual direction selectivity in areas such as MT and MST is transformed into experience-dependent and meaningful encoding of the category membership of visual-motion stimuli.

In this study, we trained two monkeys to group 12 directions of random-dot visual motion patterns into two categories that were defined by a learned “category boundary” (Fig. 5a). Monkeys performed a delayed-match-to-category (DMC) task (Fig. 5b) that was similar to that used in the PFC and ITC studies described earlier. In this task, the monkeys had to indicate (with a lever release) whether two successively presented (sample and test) stimuli were in the same category. After several weeks of training, the monkeys correctly categorized sample stimuli that were $75^\circ$ or $45^\circ$ from the category boundary with greater than 90% accuracy on average, and performed at better than 70% correct for stimuli closest to ($15^\circ$) the category boundary (Fig. 5c). As with the cat versus dog DMC task, this experimental design allowed us to evaluate whether neuronal activity encoded the visual features of

![Fig. 5. Visual motion stimuli and motion categorization task. (a) Monkeys grouped 12 motion directions into two categories (the light and dark gray arrows) separated by a ‘category boundary’ (black dotted line). The light gray dotted line is the boundary used for retraining with the new categories. (b) Delayed-match-to-category (DMC) task. A sample stimulus was followed by a delay and test. If the sample and test were in the same category, the monkeys were required to release a lever before the test disappeared. If the test was a non-match, there was a second brief delay that was always followed by a match (which required a lever release). (c) Monkeys’ average DMC task performance across all recording sessions was greater than chance (50%) for sample stimuli that were close to ($15^\circ$) and farther from ($45^\circ$ or $75^\circ$) the boundary.]
stimuli (e.g., direction of motion) and/or their category membership.

Once the monkeys were fully trained, we recorded from 156 LIP neurons during DMC-task performance. A striking number of these neurons were category selective: their activity differed sharply between the two categories and showed little variance in their responses to stimuli within each category (Freedman and Assad, 2006). The activity of two category-selective LIP neurons is shown in Fig. 6. The 12 traces indicate the 12 motion directions used as sample stimuli, and are colored red or blue according to their category membership. The pale red and blue traces indicate the four directions closest to (15° from) the category boundary. The neuron in Fig. 6a preferred category two during the sample, delay and test epochs, while the neuron in Fig. 6b showed a strong preference for category one during the sample, delay and test epochs.

To quantify the strength of category selectivity across the LIP population, we computed a category-tuning index from two parameters: a within-category-difference (WCD: the average difference in firing rates between pairs of directions within each category) and a between-category-difference (BCD: the average difference in firing rates between pairs of directions in different categories). From these values (WCD and BCD), we constructed a standard selectivity index that could vary from −1.0 to 1.0, where positive values indicate greater differences in firing rate between categories and negative values indicate more similar activity within each category. Across the LIP population (N = 122/156 neurons that were direction selective during the sample and/or delay), we found a positive shift of category-index values (indicating a tendency for neurons to group the stimuli according to their category membership) during both the sample and delay, with the strongest category selectivity apparent during the late-delay and early test epochs. Overall, the time-course of LIP category selectivity (Fig. 6c) showed a similar pattern to that in the PFC during the visual shape categorization task (Freedman et al., 2002)—both LIP and PFC showed category encoding during the sample epoch that persisted during the memory delay, and peaked in strength during the late-delay and early-test epochs.

To ensure that LIP category effects were a result of learning rather than an innate bias in LIP directional representations, we retrained both monkeys to re-group the same 12 motion-directions into two new categories that were separated by a new category boundary that was perpendicular to the original boundary. After several weeks of re-training the monkeys, we recorded an additional population of 64 LIP neurons while the monkeys performed the DMC task with the new category boundary. As a result of retraining, LIP population activity shifted dramatically and reflected the new (now relevant) category boundary and not the old (now irrelevant) categories. This effect was quantified for each neuron by determining which of the six possible category boundaries (that divided the 12 directions into two equal groups) gave the greatest difference in average activity among the six directions on either side of the boundary. Among neurons recorded with the original category boundary, the majority of neurons showed activity that was best classified by the actual category boundary that the monkeys were currently using and not the other five “irrelevant” boundaries. Following retraining, neuronal activity no longer reflected the old category boundary, but rather was best characterized by the new, now relevant, boundary (Freedman and Assad, 2006).

These studies of the parietal cortex show striking qualitative similarities with our results from the PFC during visual shape categorization. It was not previously known whether neuronal activity in brain areas typically considered to be more involved in sensory processing (as compared with PFC), such as LIP, could reflect more abstract and experience-dependent information about stimuli, or whether signals about the meaning of stimuli are exclusively encoded in more executive areas such as PFC. These results from parietal cortex also left open the possibility that motion-category signals might initially arise in motion processing areas, such as area MT, that are directly connected with LIP. On the other hand, area MT might be chiefly involved in low-level visual motion processing. In that case, more flexible and abstract information about the meaning of visual-motion stimuli would arise in downstream areas such as LIP. To test these two alternatives, we compared the respective roles of MT and LIP during the visual motion DMC task, as described in the next section of this article.

3.8. The middle temporal area

Since its initial characterization decades ago (Dubner and Zeki, 1971; Allman and Kaas, 1971), area MT has been among the most extensively studied brain areas apart from the primary visual cortex. It has been firmly established that area MT plays a key role in visual-motion processing. MT neurons typically show strong visual responses to moving spots, bars and drifting gratings, and its neurons are highly sensitive to the direction and speed of both simple and complex visual motion patterns. Area MT is directly interconnected with primary visual cortex and with areas V2, V3, the LGN and the pulvinar (Felleman and Van Essen, 1991). Outputs from MT include direct projections to the PPC, including area LIP (Lewis and Van Essen, 2000). For a recent review on MT, see Born and Bradley (2005).

3.9. Comparison of areas lip and MT during motion categorization

We recorded from 67 MT neurons during performance of the DMC task, from the same monkeys used during the LIP studies described above. As in LIP, most MT neurons were activated during DMC task. While the visual-motion stimulus was visible during the sample epoch, nearly all
Fig. 6. LIP single neuron and population activity during DMC task. (a, b) LIP single neuron examples. Average activity to the 12 sample directions for two LIP neurons is shown. The red and blue traces correspond to directions in the two categories (red, category 1; blue, category 2), and pale traces indicate the directions closest to (15°) the boundary. The three vertical dotted lines indicate (from left to right) the timing of sample onset, sample offset and test-stimulus onset. The neuron in (a) was recorded with the original category boundary. The neuron in (b) was recorded after the monkey had been retrained on the new categories. The plots at the right of each peri-stimulus time histogram (PSTH) show activity (means ± s.e.m.) for the 12 directions during the late delay and test (a), and delay (b). (c) Time-course of LIP category selectivity. A category index measured the strength of neuronal category selectivity. Positive index values indicate greater selectivity between categories and/or more similar activity within categories. The time-course of average category index values across 122 direction-selective LIP neurons (during sample and/or delay) is shown. The shaded area around the solid black line indicates the standard error of the mean.
MT neurons \((N = 66/67)\) responded selectively among the 12 directions of motion. However, the overall pattern of MT direction selectivity differed in several important ways from that in LIP. First, MT neurons did not encode the motion-directions according to their category membership. Instead, they showed sharper direction tuning than in LIP, and showed a more uniform distribution of preferred directions (rather than the highly biased distribution according to the two categories as seen in LIP). Secondly, MT neurons did not show elevated firing rates or direction selectivity during the memory delay epoch. These effects are seen in the two MT single neuron examples in Fig. 7. Both MT neurons showed classic direction tuning: strong responses to their preferred direction, and progressively weaker activity for directions that were progressively farther from the preferred direction.

As with the LIP data, we asked whether MT neurons showed sharper differences in activity across the category boundary and more similar activity within each category, we computed the same category-tuning index as used for

![Fig. 7](image-url)

Fig. 7. MT single neuron and population activity during DMC task. (a, b) Examples of two direction-selective MT neurons. Peri-stimulus time histograms (PSTH) in figures (a, b) show the average activity to the 12 motion directions for two single MT neurons. The red and blue colored lines correspond to directions in the two categories. The pale red and blue lines indicate those directions that were close to \(15^\circ\) the category boundary. The three vertical dotted lines indicate (from left to right) the timing of sample onset, sample offset and test-stimulus onset. The plots at the right of each PSTH show the average firing rate to the 12 directions during the sample epoch. Error bars indicate the standard error of the mean. (c) Time-course of MT category selectivity. A category index measured the strength of neuronal category selectivity. Positive index values indicate greater selectivity between categories and/or more similar activity within categories. The time-course of average category index values across the entire population of 67 MT neurons is shown. In contrast with LIP (Fig. 6c), category selectivity (i.e. category index values shifted, on average, towards positive values) was not observed in MT during the sample, delay or test epochs.
LIP. As suggested by the MT single neuron examples, MT category-tuning indices were not shifted significantly toward positive values (Fig. 7c). Instead, the distribution of MT category-index values was centered about zero, indicating that MT neurons did not, on average, show sharper distinctions between categories or sharper direction selectivity near the category boundary. This indicates that MT neurons did not explicitly reflect the category membership of stimuli, but instead showed a more faithful encoding of visual motion-direction similar to that observed in most previous MT studies in monkeys that had not been trained to categorize stimuli based on motion-direction.

Taken together, our results from areas LIP and MT suggest that learning to group visual stimuli into arbitrary categories based on their direction of motion causes neurons in LIP to strongly and robustly encode stimuli according to their category membership. LIP neurons responded similarly to motion directions of the same category even when those directions were visually dissimilar, and showed sharp distinctions between visually similar directions that belonged to different categories. By contrast, area MT activity was highly direction selective, but that selectivity did not show any obvious relationship to the category boundary or the categorization task. This suggests that areas LIP and MT likely play different roles in visual motion perception and in behaviors that depend on visual motion. While area LIP showed a great degree of flexibility in its directional representations as a result of experience, MT direction selectivity was comparatively rigid, and seemed better suited to a role in early-stage processing of visual-motion direction.

4. Discussion

The results of these studies indicate that learning to group visual stimuli into behaviorally relevant categories can cause a dramatic reorganization of neuronal selectivity properties, resulting in populations of neurons that show explicit encoding of the category membership of stimuli. We compared neuronal activity in both the “ventral” and “dorsal” visual streams, which are thought to be relatively specialized for shape and spatial/motion processing respectively, and found striking similarities in their patterns of neuronal activity as a result of visual categorization training. During the cat versus dog shape categorization task, PFC activity differed sharply between stimuli that were in different categories and was much less sensitive to differences in appearance between individual stimuli that were in the same category. In contrast, activity in the ITC (which provides input to the PFC) seemed to be more involved in visual analysis of shapes and/or features and did not show more generalized, or abstract, encoding of category membership. During the motion-direction categorization task, LIP neurons encoded motion-directions according to their category membership. In contrast, neurons in area MT showed very strong direction selectivity, but not more abstract category signals, consistent with a role in low-level motion processing that is less influenced by learning and experience. This suggests that, for both visual shape and motion processing systems, there may be a relatively distinct division between visual feature encoding and more abstract and learning-dependent encoding of the meaning of stimuli.

Important questions remain about the roles of the prefrontal, parietal and temporal lobe areas in visual recognition, categorization and learning. One question is whether PFC and LIP function as “general purpose” categorizers for many types of visual stimuli, or whether they are more specialized for processing the specific types of stimuli that we used in our studies. One possibility is that the PFC and LIP are each specialized for visual shape (PFC) and motion (LIP) processing, and that we would not observe category effects in these areas for other types of stimuli. Alternatively, either of these areas might play a more general role in encoding the category membership of other types of stimuli. This seems particularly likely in the PFC, since it is directly interconnected with both the dorsal and ventral visual processing streams. In addition, the PFC receives projections from virtually all sensory modalities, including both auditory and somatosensory processing areas (Pandya and Yeterian, 1998). Because of this, it is not surprising that many studies have shown that PFC neurons respond selectively to a wide range of visual, auditory and tactile stimuli, especially when those stimuli are relevant for performing the task-at-hand (Miller and Cohen, 2001). Thus, it seems highly probable that PFC neurons would encode the category of motion direction in a similar fashion as in LIP. However, it is more difficult to predict whether LIP might show encoding of visual shape categories like that observed in PFC. On one hand, anatomical and neurophysiological studies suggest that LIP is more directly linked with dorsal stream visual areas as well as oculomotor structures such as the frontostriatal eye fields and superior colliculus (Lewis and Van Essen, 2000). This suggests that LIP might be better suited to visual-spatial processing. On the other hand, LIP is also interconnected with the PFC and temporal lobe areas such as V4 and the ITC (Webster et al., 1994; Lewis and Van Essen, 2000) which are known to be involved in visual form processing. In addition, a small but growing number of studies have found that posterior parietal neurons (including LIP) can respond selectively to simple and complex shapes during both passive viewing and active tasks (Sereno and Maunsell, 1998; Stoe and Snyder, 2004; Nieder and Miller, 2004; Sereno and Amador, 2006). Clearly, further studies are needed to determine whether LIP might play a more general role in visual learning and categorization for other types of stimuli.

In some ways, it is surprising that the ITC did not seem to play a more central role in encoding visual shape categories. Prior to these studies, it had been widely assumed that the ITC was a likely—if not the most likely—candidate for the learning and storage of abstract...
information about the meaning of visual shapes. This idea had developed because it was discovered that temporal lobe damage in humans and monkeys (often including a number of brain areas including those examined in our studies) resulted in deficits in visual shape recognition and learning, and even category-specific recognition deficits (e.g. facial agnosia). Furthermore, neurophysiological recordings from ITC have consistently found exquisite selectivity for complex shapes that was sometimes extremely specific for stimuli of a specific category (especially faces). Along these lines, the PFC is not typically thought to play a central role in visual shape processing or perceptual categorization. For example, damage to the PFC does not generally result in visual-recognition or categorization deficits, but instead leads to deficits in more cognitive or executive functions such as short-term working memory, rule learning and suppressing inappropriate or impulsive behaviors. This raises the possibility that the PFC may not be the source of the category signals that we observed in the cat/dog shape categorization experiments. The PFC may instead receive highly processed category information via its inputs from other brain areas that might be more involved in the initial processing of shape categories. It is possible that abstract category information is, in fact, encoded elsewhere in the ITC, in areas that we did not study in our experiments. Alternatively, it could be that signals about stimulus-category are initially encoded by neurons in medial temporal areas such as perirhinal cortex. The perirhinal cortex receives direct projections from the ITC and has been shown to be involved in both perceptual- and memory-related functions (Murray et al., 2000). Further studies are needed to better understand the transformation of visual-shape encoding (like that in the ITC) into more abstract category representations.

Additional work is also needed to develop a better understanding of the process of learning new categories. In the categorization studies described above, neuronal activity was evaluated only after the monkeys had been fully trained and the learning process was complete. While both PFC and LIP activity reflected the category of familiar stimuli after substantial training, they may play very different roles during the learning process. For example, it has been proposed that novel information and skills are primarily processed by frontal lobe brain areas such as the PFC, and that that neuronal processing shifts to more posterior brain areas such as the PPC or subcortical structures for highly familiar information and behaviors (Miller and Cohen, 2001). This idea could underlie the common experience that it is difficult to “multitask” when learning a new skill; for example, carrying on a conversation while learning to drive a car. In contrast, carrying out multiple tasks simultaneously becomes much easier as those tasks become more familiar and well rehearsed. To better understand the roles of PFC and PPC during the learning process, future studies are needed that directly compare their patterns of neural activity during real-time learning of new visual information.

Categorization tasks have been quite useful and productive tools for comparing the respective roles of brain areas in visual learning and recognition. While there is a great deal of work that needs to be done in order to fully understand the brain-wide circuitry underlying this process, we are hopeful that research of this type will result in a better understanding about how the brain makes sense of our surroundings.

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