

**Figure 24-7** Perceptual constancy is reflected in the behavior of neurons in the inferior temporal cortex. The responses of many inferior temporal neurons are selective for stimuli with a particular frequency (number) of lobes but invariant to object size, position, and reflectance. (Reproduced, with permission, from Schwartz et al. 1983.)

**A. Size constancy.** An object is perceived to be the same even when the retinal image size decreases with the distance of the object in the visual field. The response of the vast majority of inferior temporal neurons to substantial changes in retinal image size is invariant, as illustrated here by the record of a single cell.

**B. Position constancy.** An object is perceived to be the same despite changes in position in the retinal image. Almost all inferior temporal neurons respond similarly to the same stimulus in different positions in the visual field, as illustrated here by the record of a single neuron.

**C. Form-cue invariance.** An object is perceived to be the same despite changes in reflectance. Most inferior temporal neurons respond similarly to the two images illustrated, as shown in the record of an individual neuron.

## Categorical Perception of Objects Simplifies Behavior

All forms of perceptual constancy are the product of the visual system's attempts to generalize across different retinal images generated by a single object. A still more general type of constancy is the perception of individual objects as belonging to the same semantic category. The apples in a basket or the many appearances of the letter *A* in different fonts, for example, are

physically distinct but are effortlessly perceived as *categorically identical*.

Categorical perception is classically defined as the ability to distinguish objects of different categories better than objects of the same category. For example, it is more difficult to discriminate between two red lights that differ in wavelength by 10 nm than to discriminate between red and orange lights with the same wavelength difference.

Categorical perception simplifies behavior. For example, it usually does not matter whether an apple

is completely spherical or slightly mottled on the left side or whether the seat we are offered is a Windsor or a Chippendale side chair. Similarly, reading ability requires that one be able to recognize the alphabet in a broad variety of type styles. Like the simpler forms of perceptual constancy, categorical perception relies on the brain's ability to extract invariant features of objects seen.

Is there a population of neurons that respond uniformly to objects within a category and differentially to objects of different categories? To test this, David Freedman and Earl Miller and colleagues created a set of images in which features of dogs and cats were merged; the proportions of dog and cat in the composite images varied continuously from one extreme to the other. Monkeys were trained to identify these stimuli reliably as either dog or cat. Miller and colleagues then recorded from visually responsive neurons in the dorsolateral prefrontal cortex, a region that receives direct input from the inferior temporal cortex. Not only did these neurons exhibit the predicted category-selective responses—responding well to cat but not dog, or vice versa—but the neuronal category boundary also corresponded to the behaviorally learned boundary (Figure 24–8). By contrast, neurons in inferior temporal cortex represented similarity of features, not categories.

The fact that category-specific agnosias sometimes follow damage to the temporal lobe suggests there are neurons in the inferior temporal cortex that are category-selective similar to those of neurons in the prefrontal cortex. Face-selective cells in the temporal cortex appear to meet this criterion, because their responses to a range of faces are often similar. Yet, these may constitute a special case, whereas for most stimulus conditions, category-selective responses may be characteristic of neurons in the prefrontal cortex, where visual responses are more commonly linked to the behavioral significance of the stimuli.

## Visual Memory Is a Component of High-Level Visual Processing

Visual experience can be stored as memory, and visual memory influences the processing of incoming visual information. Object recognition in particular relies on the observer's previous experiences with objects. Thus, the contributions of the inferior temporal cortex to object recognition must be modifiable by experience.

Studies of the role of experience in visual perception have focused on two distinct types of experience-dependent plasticity. One stems from repeated exposure or practice, which leads to improvements

in visual discrimination and object recognition ability. These experience-dependent changes constitute a form of implicit learning known as perceptual learning (Chapter 23). The other occurs in connection with the storage of explicit learning, the learning of facts or events that can be recalled consciously (Chapter 54).

## Implicit Visual Learning Leads to Changes in the Selectivity of Neuronal Responses

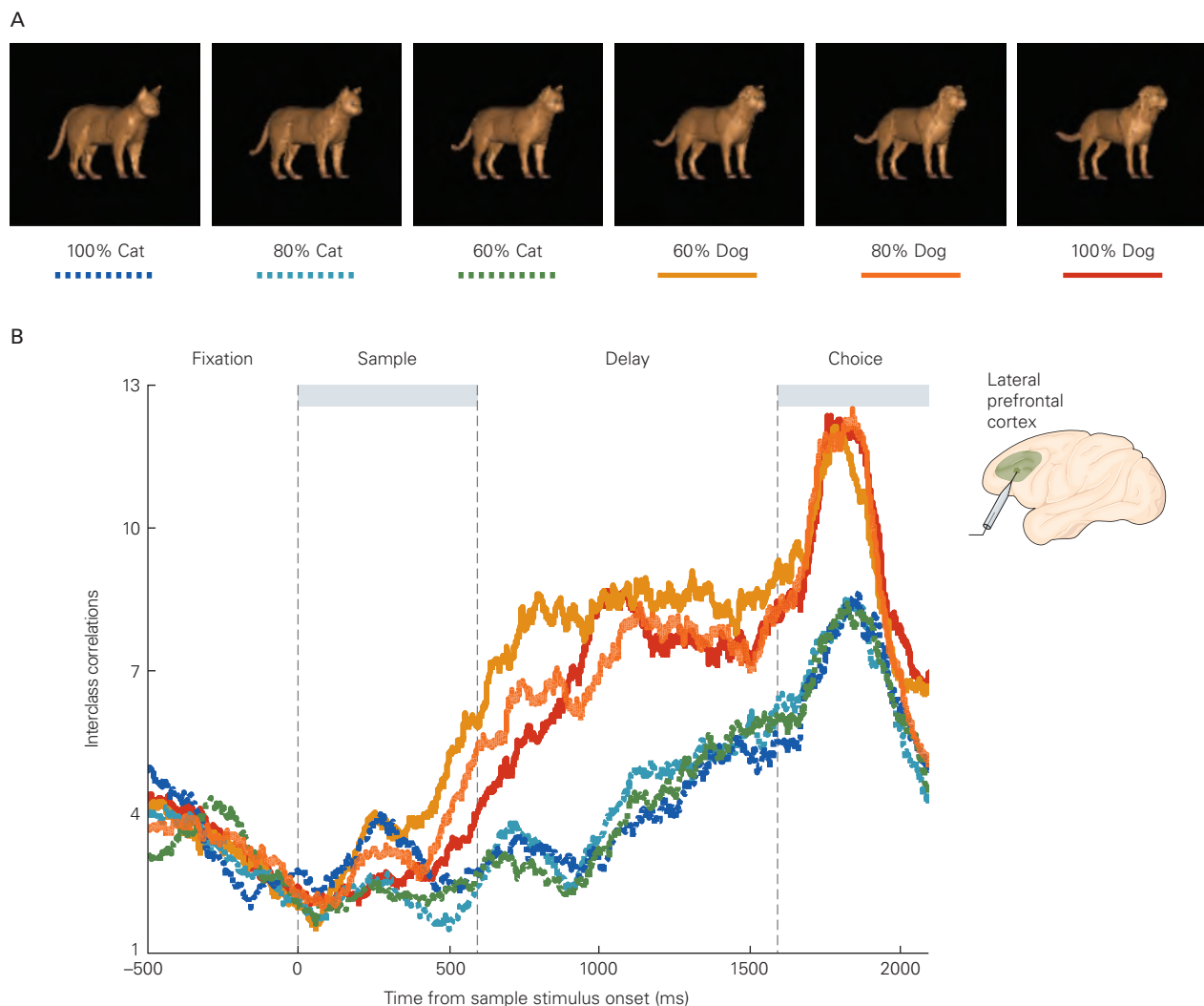
The ability to discriminate complex visual stimuli is highly modifiable by experience. For example, individuals who attend to fine differences between automobile models improve their ability to recognize such differences.

In the inferior temporal cortex, neuronal selectivity for complex objects can undergo change that parallels change in the ability to distinguish objects. For example, in a study by Logothetis and colleagues, monkeys were trained to identify novel three-dimensional objects, such as randomly bent wire forms, from two-dimensional views of the objects. Extensive training led to pronounced improvements in the ability to recognize the objects from two-dimensional views. After training, a population of neurons was found that exhibited marked selectivity for the views seen earlier but not for other two-dimensional views of the same objects (Figure 24–9).

Other studies with monkeys have shown that familiarization with novel faces alters the tuning of face-selective neurons in the inferior temporal cortex. Similarly, when an animal has experience with novel objects formed from simple features, inferior temporal neurons become selective for those objects. Such neuronal changes have been found as a consequence of the animal engaging in active discrimination or simply passive viewing of visual stimuli, and they are often manifested as a sharpening of neural selectivity rather than changes in absolute firing rate. Sharpening is precisely the sort of neuronal change that could underlie improvements in perceptual discrimination of visual stimuli.

## The Visual System Interacts With Working Memory and Long-Term Memory Systems

Object recognition and learning are intricately linked. In fact, learning can generate entire areas of functional specialization within inferior temporal cortex. For example, monkeys who learn at a young age to associate specific shapes (eg, a number symbol) with particular reward magnitudes develop specialized brain areas that process these specific shapes. These brain regions



**Figure 24–8** Neural coding for categorical perception.  
(Reproduced, with permission, from Freedman et al. 2002.)

**A.** The images combine cat and dog features in varying proportions. Monkeys were trained to categorize an image as cat or dog if it had 50% or more features of that animal.

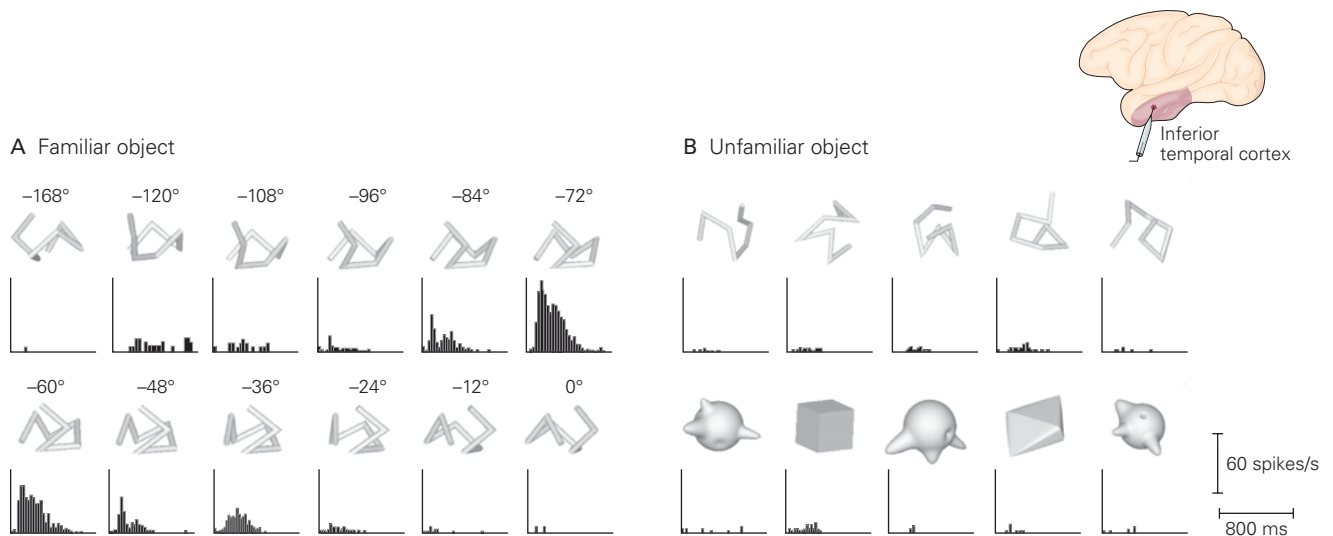
**B.** Peristimulus time histograms illustrate the responses of a prefrontal cortex neuron to the images shown in part A.

The neuron responded much more weakly to images of cats (100%, 80%, and 60%) than to images of dogs (60%, 80%, and 100%). Responses to images from the same category were very similar despite variations in retinal images that were as large as or even larger than the differences in retinal images between categories. Thus, the cell was category-specific. Such category-specific responses were common among visual neurons of the lateral prefrontal cortex.

develop close to the temporal lobe face patches discussed earlier.

Two issues concerning interaction between vision and memory have been investigated. First, how is visual information maintained in short-term working memory? Working memory has a limited capacity, acting like a buffer in a computer operating system, and consolidation into long-term memory is susceptible to interference (Chapter 54). Second, how are long-term visual memories and the associations between them stored and recalled?

In a visual delayed-response task requiring access to stimulus information beyond the duration of the stimulus (Box 24–1), many vision-related neurons in both the inferior temporal and prefrontal cortices continue firing during the delay. This delay-period activity is thought to maintain information in short-term working memory (Figure 24–11). Delay-period activity in the inferior temporal and prefrontal cortices differs in a number of ways. For one, activity in the inferior temporal cortex is associated with the short-term storage of visual patterns and color information, whereas



**Figure 24-9** Familiarity with particular complex objects leads inferior temporal neurons to respond selectively for those objects. (Reproduced, with permission, from Logothetis and Pauls 1995. Copyright © 1995 Oxford University Press.)

**A.** Monkeys were trained to recognize a randomly bent wire from a set of two-dimensional views of the wire. The wire form was rotated 12° in successive views. Once recognition performance was stable at a high level, recordings were made from

neurons in the inferior temporal cortex while each view was presented. Peristimulus time histograms show the responses of a typical neuron to each view. This neuron responded selectively to views that represented a small range of rotation of the object.

**B.** When the same neuron was tested with two sets of stimuli that were unfamiliar to the monkey, it failed to respond to any of these stimuli.

activity in the prefrontal cortex encodes visuospatial information as well as information received from other sensory modalities. Delay-period activity in the inferior temporal cortex also appears to be closely attuned to visual perception, for it encodes the sample image, but can be eliminated by the appearance of another image.

In the prefrontal cortex, by contrast, delay-period activity depends more on task requirements and is not terminated by intermittent sensory inputs, suggesting that it may play a role in the recall of long-term memories. Experiments by Earl Miller and colleagues support this view. In these experiments, monkeys were trained to associate multiple pairs of objects. They were then tested on whether they had learned these pairwise associations, using the following procedure. First, a single (sample) object was presented; then, after a brief delay, a second (test) object appeared. The monkey was instructed to indicate whether the test object was the object paired with the sample during previous training.

There are two possible ways to solve this task. During the delay, the animal could use a sensory code and keep a representation of the sample object online until the appearance of the test object, or it could remember the sample object's associate and keep information

about the associate object online in a “prospective code” of what might appear as the test object. Remarkably, neuronal activity appears to transition from one to the other during the delay. Neurons in the prefrontal cortex initially encode the sensory properties of the sample object—the one just seen—but later begin to encode the expected (associated) object. As we shall see, such prospective coding in the prefrontal cortex may be the source of top-down signals to the inferior temporal cortex, activating neurons that represent the expected object and thus giving rise to conscious recall of that object.

The relation between long-term declarative memory storage and visual processing has been explored extensively in the context of remembered associations between visual stimuli. Over a century ago, William James, a founder of the American school of experimental psychology, suggested that learning visual associations might be mediated by enhanced connectivity between the neurons encoding individual stimuli. To test this hypothesis, Thomas Albright and colleagues trained monkeys to associate pairs of objects that had no prior physical or semantic relatedness. The monkeys were later tested while extracellular recordings of neurons in the inferior temporal cortex were made. Objects that had been paired often elicited similar neuronal

### Box 24-1 Investigating Interactions Between Vision and Working Memory

The relationship between vision and memory can be studied by combining a neuropsychological approach with single-cell electrophysiological methods.

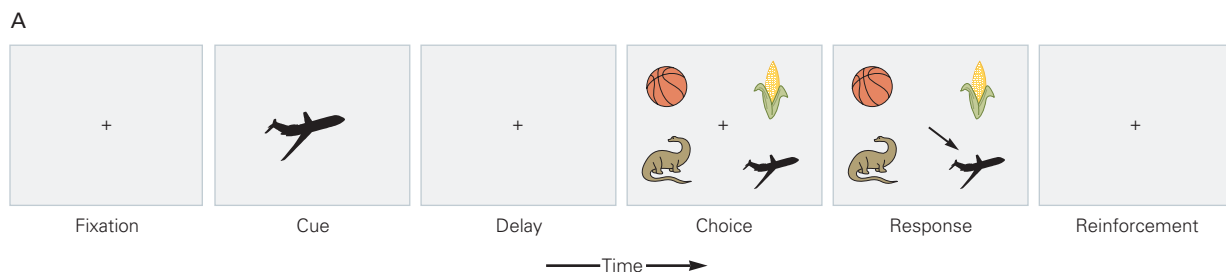
One behavioral paradigm used to study memory is the *delayed-response task*. A subject is required to make a specific response based on information remembered during a brief delay. In one form of this task, known as *delayed match-to-sample*, the subject must indicate whether a visual stimulus is the same or different from a previously viewed cue stimulus (sample) (Figure 24-10A).

When used in conjunction with single-cell recording, this task allows the experimenter to isolate three key components of a neuronal response: (1) the sensory component, the response elicited by the cue stimulus; (2) the short-term or working-memory component, the response that occurs during the delay between the cue

and the match; and (3) the recognition-memory or familiarity component, the difference between the response elicited by the match stimulus and the earlier response to the cue stimulus.

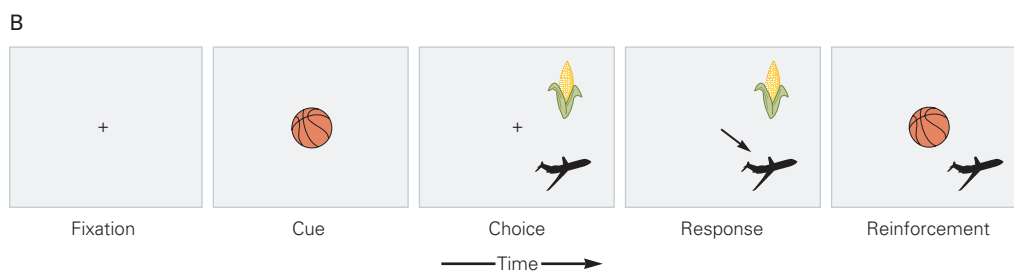
A second behavioral paradigm, the *visual paired-association task*, has been used in conjunction with electrophysiology to explore the cellular mechanisms underlying the long-term storage and recall of associations. This task differs from the delayed match-to-sample task in that the match and cue are two different stimuli (Figure 24-10B).

The sample stimulus might consist of the letter *A* and the match stimulus the letter *B*. Through repeated temporal pairing and conditional reinforcement, subjects learn that *A* and *B* are predictive of one another: They are associated.



**Figure 24-10A** Delayed match-to-sample task. In this paradigm, a trial begins with the appearance of a fixation spot that directs the subject's attention and gaze to the center of the computer screen. A cue stimulus (the "sample") then appears briefly, typically for 500 ms, followed by a delay in which the display is blank. The delay can be varied to fit the experimental goals. Following the delay, the choice display appears, which contains several images, one of which is the cue (the "match"). The subject must respond by choosing

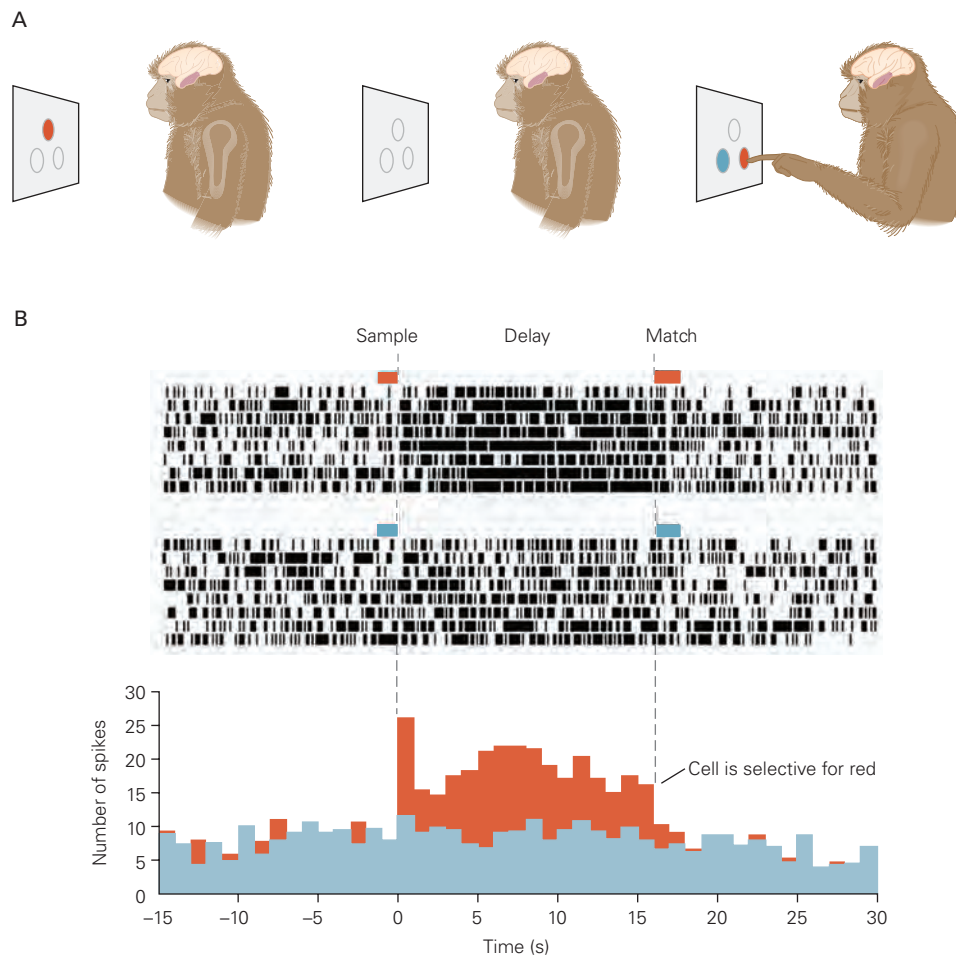
the cue stimulus, typically either by pressing a button or by a saccade to the stimulus. In the task illustrated here, all of the test images appear at once (a simultaneous match-to-sample task). They can also be presented sequentially (a sequential match-to-sample task). Although the trial's duration may be longer for the sequential task, this paradigm can be advantageous for electrophysiological studies by limiting the visual stimuli present at any time.



**Figure 24-10B** The paired-association task. This paradigm resembles the match-to-sample paradigm except that the cue and match are different stimuli. In the illustrated example, the basketball is the cue stimulus and the airplane is the experimenter-designated match stimulus. Because these stimuli have no inherent association, the

subject must discover the designated association through trial-and-error learning. The task is thus to establish an association between nonidentical stimuli. The paired-association task can also incorporate a delay between presentation of the sample and test stimuli, and it can be used in both simultaneous (shown) and sequential forms.





**Figure 24-11** Neural activity representing an object is sustained while the object is held in working memory. (Reproduced, with permission, from Fuster and Jervey 1982. Copyright © 1982 Society for Neuroscience.)

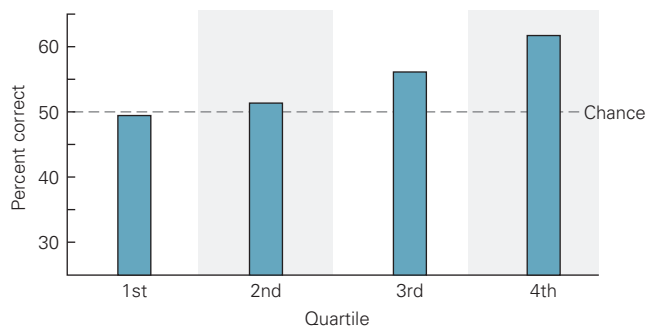
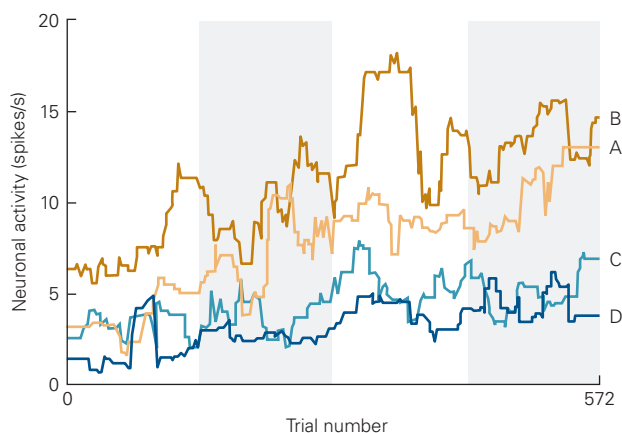
**A.** Monkeys were trained to perform a color match-to-sample task. For example, a red stimulus was first presented and the animal later had to choose a red stimulus from among many colored stimuli. The task incorporated a brief delay (1–2 seconds) between display of the sample and the match, during which information about the correct target color had to be maintained in working memory. The purple area in the monkey's brain indicates the inferior temporal cortex.

**B.** Peristimulus time histograms and raster plots of action potentials illustrate responses of a single neuron in the inferior temporal cortex during the delayed match-to-sample task. The upper record is from trials in which the sample was red, and the lower record is from trials in which it was green (shown here as blue). The recordings show that the cell responds preferentially to red stimuli. In trials with a green sample, the activity of the neuron does not change, whereas in trials with a red sample, the cell exhibited a brief burst of activity following presentation of the sample and continued firing throughout the delay. Many visual neurons in the inferior temporal and prefrontal cortices exhibit this kind of behavior.

responses, as one would expect if functional connections had been enhanced, whereas responses elicited by unpaired objects were unrelated. Recordings from individual inferior temporal neurons while monkeys were learning new visual associations showed that a cell's responses to paired objects became more similar over the course of training (Figure 24-12). Most importantly, the changes in neuronal activity occurred on the same timescale as the changes in behavior, and the changes in neural activity depended on successful learning.

These learning-dependent changes in the stimulus selectivity of inferior temporal cortex neurons are long-lasting, suggesting that this cortical region is part of the neural circuitry for associative visual memories. The experimental results also support the view that learned associations are implemented rapidly by changes in the strength of synaptic connections between neurons representing the associated stimuli.

We know that the hippocampus and neocortical areas of the medial temporal lobe—the perirhinal, entorhinal, and parahippocampal cortices—are

**A** Animals learn to associate pairs of stimuli**B** After training neurons respond similarly to paired stimuli

**Figure 24–12** Object recognition is linked to associative memory. Monkeys learned associations between pairs of visual stimuli while activity was recorded from a neuron in the inferior temporal cortex. (Reproduced, with permission, from Messinger et al. 2001. © 2001 National Academy of Sciences.)

**A.** Behavioral performance on a paired-association task is plotted for each quartile of a single training session (572 trials). The animal was presented with four novel stimuli (A, B, C, D) and was required to learn two paired associations (A–B, C–D). As expected, performance began at chance (50% correct) and gradually climbed as the animal learned the associations.

**B.** Mean firing rates of an inferior temporal neuron recorded during the behavioral task described in part A. Each trace represents the firing rate during presentation of one of the four stimuli (A, B, C, or D). The responses to all stimuli were of similar magnitude at the outset. As the paired associations were learned, the neuronal responses to the paired stimuli A and B began to cluster at a different level from responses to the paired stimuli C and D. The neuron's activity thus corresponded to the learned associations between the two pairs.

essential both for the acquisition of associative visual memories and for the functional plasticity of the inferior temporal cortex. In fact, work by Yasushi Miyashita and colleagues showed that the aforementioned pair-association neurons are much more prevalent in perirhinal cortex than in anterior inferior temporal cortex.

Thus, although learning changes the stimulus selectivity of neurons in both areas, the association between visually associated pairs grows stronger from inferior temporal to perirhinal cortex (Figure 24–2C). The hippocampus and medial temporal lobe may facilitate the reorganization of local neuronal circuitry in the inferior temporal cortex necessary to store associative visual memories. The reorganization itself may be a form of Hebbian plasticity (Chapter 49) initiated by the temporal coincidence of the associated visual stimuli.

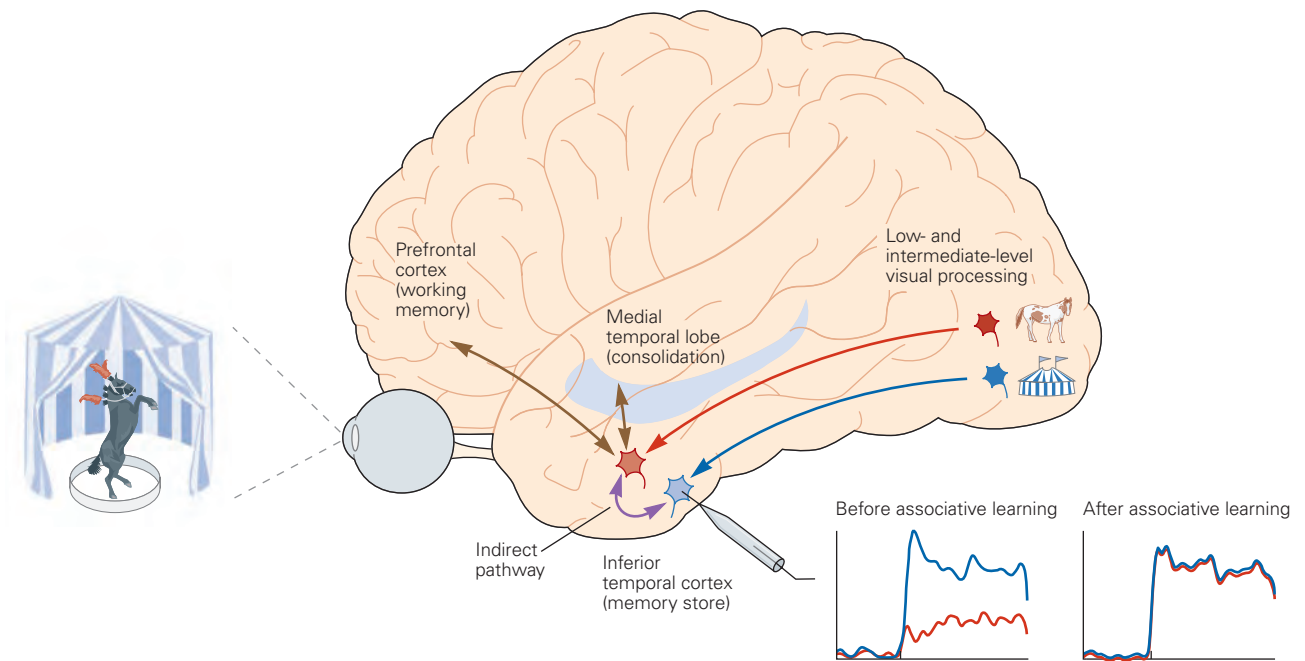
### Associative Recall of Visual Memories Depends on Top-Down Activation of the Cortical Neurons That Process Visual Stimuli

One of the most intriguing features of high-level visual processing is the fact that the detection of an image in one's visual field and the recall of the same image are subjectively similar. The former depends on the bottom-up flow of visual information and is what we traditionally regard as vision. The latter, by contrast, is a product of top-down information flow. This distinction is anatomically accurate but obscures the fact that under normal conditions afferent and descending signals collaborate to yield visual experience.

The study of associative visual memory has provided valuable insights into the cellular mechanisms underlying visual recall. As we have seen, visual associative memories are stored in the visual cortex through changes in the functional connectivity between neurons that independently represent the associated stimuli. The practical consequence of this change is that a neuron that responded only to stimulus A prior to learning will respond to both A and B after these stimuli have been associated (Figure 24–13). Activation of an A-responsive neuron by stimulus B can be viewed as the neuronal correlate of top-down recall of stimulus A.

Neurons in the inferior temporal cortex exhibit precisely this behavior. The activity correlated with cued recall is nearly identical to the bottom-up activation by the stimulus. These neurophysiological findings are supported by a number of brain imaging studies that have identified selective activity in the visual cortex during cued and spontaneous recall of objects.

Although learned associations between images are likely to be stored through circuit changes in the inferior temporal cortex, activation of these circuits for conscious recall depends on input from the prefrontal cortex. The afferent signal for one of a pair of images might be received by the inferior temporal cortex and relayed to prefrontal cortex, where the information



**Figure 24–13** Circuits for visual association and recall. Bottom-up signals—afferent signals conveying information about objects in the observer’s visual field—are combined into object representations in the inferior temporal cortex. Before associative learning, a neuron (blue) responds well to the circus tent but not to the horse. Learned associations between objects are mediated in the inferior temporal cortex by strengthening connections between neurons representing

each of the paired objects (the indirect pathway in the figure). Thus, recall of the circus tent following presentation of the horse is achieved by activating the indirect pathway. Indirect activation can also be triggered by the contents of working memory (feedback from the prefrontal cortex). Under normal conditions, visual perception is the product of a combination of direct and indirect inputs to inferior temporal neurons.

would be maintained in working memory. As we have seen, the continued firing of many prefrontal neurons during the delay period of a delayed match-to-sample task initially represents information about the sample image but changes to the associated image that is expected to follow. Signals from prefrontal cortex to the inferior temporal cortex would selectively activate neurons representing the associated image, and that activation would constitute the neural correlate of visual recall.

## Highlights

1. A key function of high-level vision is object recognition. Object recognition imbues visual perception with meaning. As the eminent neuropsychologist Hans-Lukas Teuber once wrote, failure of object recognition “would appear in its purest form as a normal percept that has somehow been stripped of its meaning.”
2. Object recognition is difficult, primarily because of changes in appearance with changes in

position, distance, orientation, or lighting conditions, possibly rendering different objects similar in appearance. Building computer models mimicking primate object recognition capabilities is a major challenge for current and future research.

3. Object recognition relies on a region of the temporal lobe called inferior temporal cortex. Visual information reaching inferior temporal cortex has already been processed through mechanisms of low- and mid-level vision.
4. Lesions to inferior temporal cortex cause visual agnosia, a loss in the ability to recognize objects. Apperceptive agnosia, the inability to match or copy complex objects, is distinguished from associative agnosia, the impairment of the ability to recognize an object’s meaning or function. Predicting the exact nature of an agnosia from the pattern of lesioned or inactivated areas, and thus to go from understanding the *correlates* to the *causes* of neural object representations, is a major goal for the field of object recognition and neurology.



5. Individual cells in inferior temporal cortex can be highly shape-selective and respond selectively, eg, to a hand or a face. They can maintain selectivity across position, size, and even rotation—properties that might explain perceptual constancy.
6. Inferotemporal cortex comprises a yet-unknown number of areas with very different functional specializations. While the functional logic of the overall organization remains unknown, we do know that cells with similar selectivity group into cortical columns and that face cells are organized into larger units called face areas.
7. Face recognition is supported by multiple face areas, each with a unique functional specialization. Face areas are selectively coupled to form a face-processing network, which has emerged as a model system for high-level vision.
8. Inferotemporal cortex is interconnected with perirhinal and parahippocampal cortices for memory formation, with the amygdala for the assignment of emotional valence to objects, and with prefrontal cortex for object categorization and visual working memory. If associative memories are stored as patterns of connections between neurons, what then are the specific contributions of hippocampus and neocortical structures of the medial temporal lobe, and by what cellular mechanisms do they exert their influences? The confluence of molecular-genetic, cellular, neurophysiological, and behavioral approaches promises to solve these and other problems.
9. Objects are perceived as members of a category. This simplifies the selection of appropriate behaviors, which often do not depend on stimulus details. Neurons with categorical selectivity are found in dorsolateral prefrontal cortex, a main projection site of inferior temporal cortex.
10. Object recognition relies on past experience. Perceptual learning can improve the ability to discriminate between complex objects and refine neural selectivity in inferior temporal cortex.
11. Visual information can be held in short-term working memory to be available beyond the duration of a sensory stimulus. Neurons in temporal and prefrontal cortex can exhibit delay-period activity after the disappearance of a stimulus. How these networks establish the ability to keep information online is an open question.
12. High-level visual information processing changes with top-down modulation. The sensory experience of an image in view and the recall of the same stimulus from memory are subjectively

similar. Neurons in inferior temporal cortex exhibit similar activity during bottom-up activation and cued recall.

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### Selected Reading

- Freedman DJ, Miller EK. 2008. Neural mechanisms of visual categorization: insights from neurophysiology. *Neurosci Biobehav Rev* 32:311–329.
- Gross CG. 1999. *Brain, Vision, Memory: Tales in the History of Neuroscience*. Cambridge, MA: MIT Press.
- Kanwisher N, McDermott J, Chun MM. 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J Neurosci* 17:4302–4311.
- Logothetis NK, Sheinberg DL. 1996. Visual object recognition. *Annu Rev Neurosci* 19:577–621.
- McCarthy G, Puce A, Gore J, Allison T. 1997. Face-specific processing in the human fusiform gyrus. *J Cog Neurosci* 9:605–610.
- Messinger A, Squire LR, Zola SM, Albright TD. 2005. Neural correlates of knowledge: stable representation of stimulus associations across variations in behavioral performance. *Neuron* 48:359–371.
- Miller EK, Li L, Desimone R. 1991. A neural mechanism for working and recognition memory in inferior temporal cortex. *Science* 254:1377–1379.
- Miyashita Y. 1993. Inferior temporal cortex: where visual perception meets memory. *Annu Rev Neurosci* 16:245–263.
- Schlack A, Albright TD. 2007. Remembering visual motion: neural correlates of associative plasticity and motion recall in cortical area MT. *Neuron* 53:881–890.
- Squire LR, Zola-Morgan S. 1991. The medial temporal lobe memory system. *Science* 253:1380–1386.
- Ungerleider LG, Courtney SM, Haxby JV. 1998. A neural system for human visual working memory. *Proc Natl Acad Sci U S A* 95:883–890.

### References

- Baker CI, Behrmann M, Olson CR. 2002. Impact of learning on representation of parts and wholes in monkey inferotemporal cortex. *Nat Neurosci* 5:1210–1216.
- Brown S, Schafer ES. 1888. An investigation into the functions of the occipital and temporal lobes of the monkey's brain. *Philos Trans R Soc Lond B Biol Sci* 179:303–327.
- Damasio AR, Damasio H, Van Hoesen GW. 1982. Prosopagnosia: anatomic basis and behavioral mechanisms. *Neurology* 32:331–341.