

Object-based vision and attention in primates

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In forming a representation of a visible object, the brain must analyze the visual scene pre-attentively, select an object through active attention, and form representations of the multiple attributes of the selected object. During the past two years, progress has been made in understanding the neural underpinnings of these processes by means of single-neuron recording in monkeys.

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Abbreviation

MT middle temporal

Introduction

Object-based representations in the cerebral cortex are far removed from the earliest representations of visual information at the level of the retina. Rather than encoding the welter of details spread through the visual scene, neurons in higher-order cortical areas encode the attributes of a selected object. Their activity is the culmination of processes that include structuring the details of the visual scene into objects, selecting one object for attention, and computing the attributes of that object. These processes are intertwined and distributed. They certainly depend on inferotemporal cortex, which plays a pre-eminent role in the recognition of objects, but they also depend on several occipital, parietal and frontal areas (Figure 1). Here, I review advances during the past two years in our understanding of the cortical mechanisms that underlie object-based vision in the monkey.

Perceptual organization

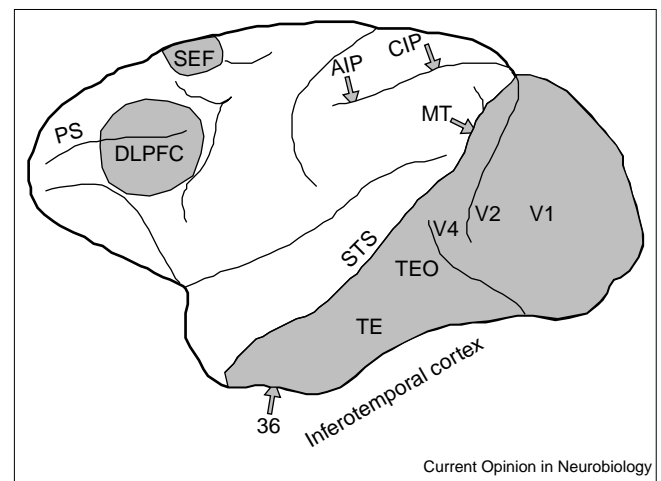
To pass from representing the visual scene as a welter of local details to representing it as a collection of objects, the visual system must put together information distributed throughout the scene. Which local features belong to one object and which to another cannot be resolved without considering all of the features together. Nevertheless, and surprisingly, even neurons with small receptive fields in early cortical visual areas participate in these processes.

The involvement of area V1, primary visual cortex, in the representation of whole objects has become particularly clear from recent experiments involving modal and amodal completion. ‘Completion’ refers to cases in which an object is perceived as complete even when it is only partially visible. Modal completion underlies certain visual illusions in which viewing fragments of an object induces a vivid perception of

the object as a whole including contours not actually shown in the display. Neurons in area V1 fire when such modally completed contours are present in their receptive fields [1•]. Amodal completion arises in cases where one object is partially occluded by another. Viewers amodally complete a square, seeing it as a thing with four corners, even when one corner is covered by another object. Neurons in area V1 fire in response to the presence in their receptive fields of amodally completed contours such as the occluded corner [2]. In areas beyond V1, recent studies have afforded evidence for involvement in another aspect of whole-object perception: border ownership. A vertical contour may be the left edge of an object to its right or the right edge of an object to its left. It is owned as a border by whichever adjacent surface is in the foreground, and thus possesses occlusion precedence. When occlusion precedence is signaled by textural [3] or stereoscopic [4] cues in the receptive field, neurons in area V2 fire at different levels according to which object owns the border. Even when precedence is signaled by cues outside the receptive field, many neurons in areas V2 and V4 signal border-ownership [5••]. Figure 2 shows data from a neuron signaling border-ownership under these conditions.

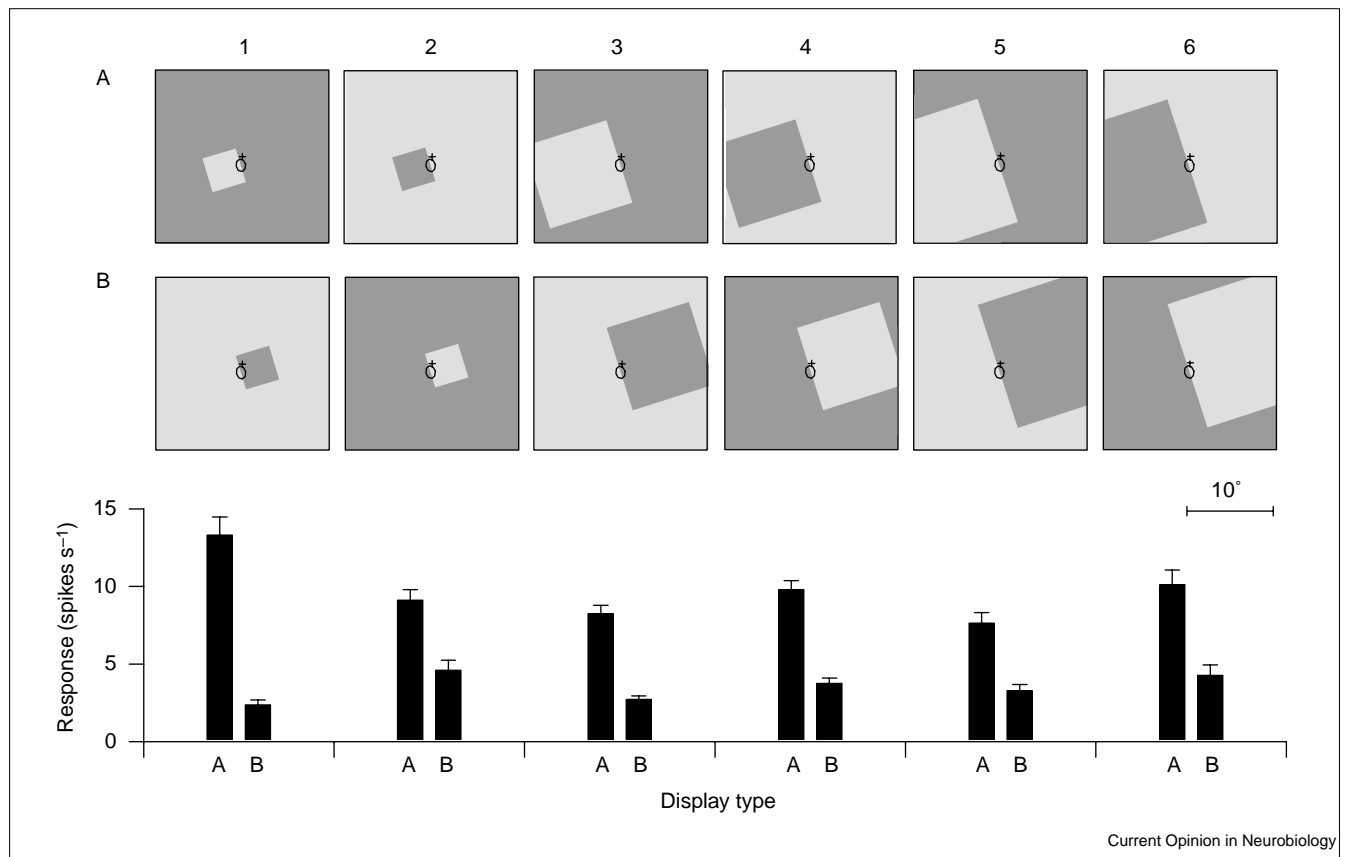
A related effect occurs in the middle temporal (MT) area. In the so-called ‘barber-diamond’ display, the direction in which a section of grating is perceived as moving is strongly

Figure 1



Cortical areas involved in object representation include ones indicated by highlighting in this lateral view of a macaque monkey's left cerebral hemisphere. Arrows indicate areas hidden from view. 36, area 36 of perirhinal cortex; AIP, anterior intraparietal area; CIP, central intraparietal area; DLPFC, the region of dorsolateral prefrontal cortex containing object-selective neurons; PS, principal sulcus; SEF, supplementary eye field; STS, superior temporal sulcus; TE and TEO, cytoarchitecturally distinct subdivisions of temporal lobe cortex. The term ‘inferotemporal cortex’, where used without qualification in the text, refers to the zone encompassing areas TE and 36.

Figure 2



Data from a neuron in area V2 that is sensitive to border ownership (adapted with permission from [5•]). In the top two rows, the dark gray and light gray areas represent the visual stimulus and the small circle indicates the location of the neuron's receptive field. In the displays of row A (versus B), the contour in the receptive field constitutes the right (versus left) edge of an object. In the histogram

on the bottom row, the height of each bar represents the strength of the neuron's response to A or B in the display above. Note that the neuron responds more strongly to displays of type A, in which the contour in the receptive field forms the right edge of an object. This was found to be true across a succession of scales (1 and 2 versus 3 and 4 versus 5 and 6).

influenced by the depth ordering of adjacent sectors of the display. Some neurons in area MT signal the perceived motion of the grating even when the inducing sectors lie outside their receptive fields [6•]. In showing that neurons with small receptive fields are influenced not just by the detail in their receptive fields but by the perceptual organization placed on the scene as a whole, these findings provide support for the long-standing idea that there is interactive activation between areas where neurons represent small parts of the visual scene and areas where neurons represent larger regions [7].

Voluntary attention

Activity in cortical visual areas reflects not only pre-attentive organizational processes, but also the active selection of one object by attention. There is growing agreement that the neuronal mechanisms of voluntary visual attention conform to certain basic principles: namely, that objects compete to control the activity of neurons; that they succeed in proportion to their salience; and, that attention acts by enhancing

the salience of the selected object. These principles are incorporated in the biased competition model [8], for which several recent findings have provided support.

The principle that objects compete for neuronal representation has been verified in areas V2 and V4 [9•] and in inferotemporal cortex [10]. Reynolds *et al.* [11•] tested and confirmed the principle that attention enhances the salience of selected objects in a study showing that the impact of attention on neuronal activity in area V4 is indistinguishable from the impact of an increase in luminance contrast. The functional significance of the latter effect has been clarified in a study by McAdams and Maunsell [12•] showing that neurons in area V4 discriminate orientation more effectively when salience is enhanced by attention. The multifaceted nature of factors controlling the neural effects of attention has been emphasized in another study by the same authors [13] showing that response strength in area V4 is affected additively by the location and the feature dimension to which attention is allocated.

There has been considerable debate over the past decade concerning whether attention is space-based, spreading uniformly through a selected region of the visual field, or object-based, spreading within the irregular confines of a selected object [14]. It now seems clear that under some circumstances the relationship between attention and object representations is intimate and reciprocal in the sense that the effects of attention are confined within the limits of the selected object to the exclusion of overlapping and interdigitated objects. A recent electrophysiological study has now shown for the first time object-based attentional effects at the level of single neurons in area V1 of the monkey [15]. Roelfsema *et al.* [15] recorded from neurons in area V1 while monkeys performed a task requiring them to attend to one irregular curve and to ignore another overlapping curve. They found that neurons with receptive fields containing segments of the selected curve exhibited enhanced visual responsiveness, whereas neurons with receptive fields containing segments of the distractor curve did not.

Attention can be directed not only to specific objects but to selected locations within those objects. Command signals that may underlie this process have now been detected by single-neuron recording in the supplementary eye field, an area located medially on the dorsal surface of the frontal lobe. In monkeys trained to select as the target for an eye movement either one or the other end of a horizontal bar, some neurons in this area fire differentially as a function of the end of the bar that has been selected, regardless of the bar's absolute location, thus encoding the object-centered location to which the monkey is attending [16]. The signals carried by these neurons do not depend on the specific visual properties of the instructional cue [17] or the reference object [18•]. Rather, they constitute a pure spatial signal reflecting the locus of attention relative to an object-centered frame.

Covert search

Visual search comes into play when we know the properties of a sought object (round and white in the event of a hunt for mushrooms) without knowing its location. Human studies of 'covert visual search' (search unaided by eye movements) have indicated that it occurs quickly if the target is distinguished from surrounding distractors by low-level features such as color (e.g. red circle among green circles) but slowly if the target is distinguished only by a conjunction of low-level features, none of which alone is diagnostic (e.g. red circle among red squares and green circles).

Why conjunction search is slow is an issue of perennial debate. One possibility is that attention must be focused on one object after another in serial order until the target is found. Another possibility, recently defended by Chelazzi [19•], is that parallel search simply requires more time when the target is defined by a conjunction of features. It may be possible to resolve this issue by single-neuron recording in the monkey. Monkeys can be trained to engage in both feature and conjunction search and, like humans, are slower

when searching for a conjunction [20,21]. Furthermore, a monkey's attentional state can be monitored moment by moment by recording in inferotemporal cortex, where neurons signal the identity of the selected object, or in frontal cortex, where neurons signal its location.

In a search task involving one target and one distractor, inferotemporal neurons were found to signal the identity of the target, indicating that it had captured attention, about 200 ms after the appearance of the search pair [22]. This time was relatively invariant from trial to trial — not bimodally distributed as would be expected if the monkey were scanning serially, selecting the distractor first on some trials and the target first on others [19•]. Even during strict conjunction search, the timing of neuronal activity in the frontal eye field appears to be consistent from trial to trial and not multimodal [23••]. Thus, the bulk of evidence from recent primate studies seems to favor a parallel model of conjunction search.

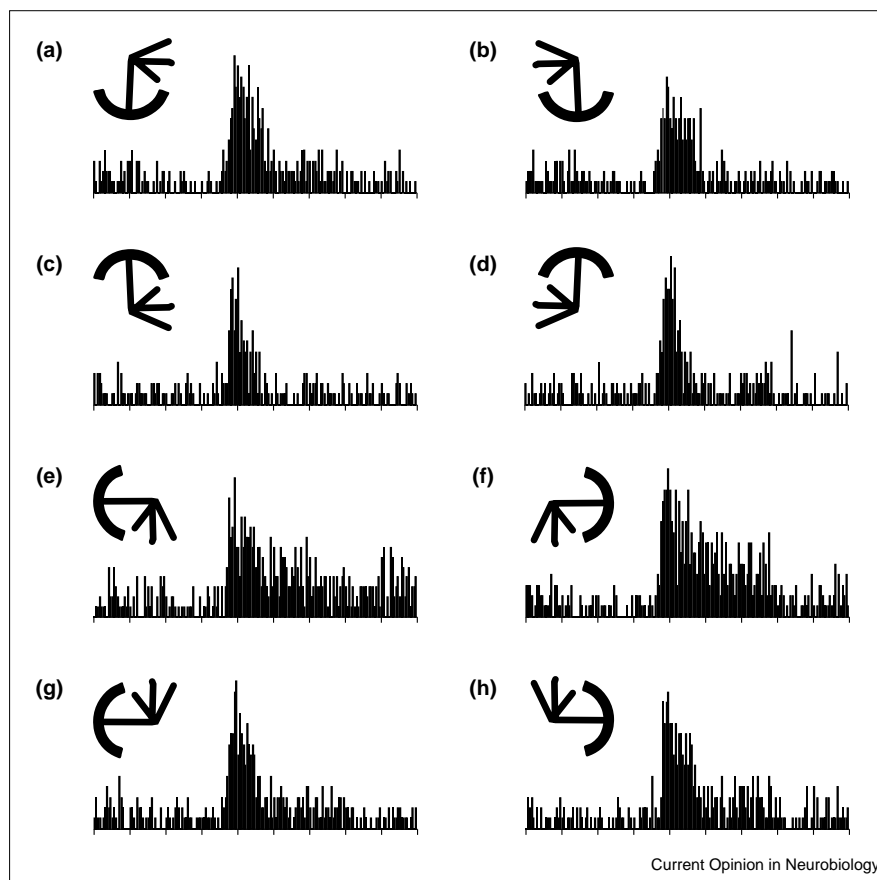
Free viewing

Several recent studies have addressed whether inferotemporal neurons represent objects in a fundamentally different way under natural conditions (oculomotor scanning of a cluttered scene) than under the reduced conditions commonly used in recording experiments (exposure to a single flashed image during steady fixation). Eye movements exert a strong influence on neuronal activity in areas V1, V2 and V4 [24,25]; however, at the level of inferotemporal cortex, their influence is minor. Microsaccades occurring during fixation have little impact on neuronal activity even when they jitter a preferred image in the neuron's receptive field [24]. Furthermore, neuronal visual responses elicited when a large saccade brings an object onto the fovea are virtually identical to responses elicited by turning the foveal stimulus on during steady fixation [26••].

Clutter does exert an effect on inferotemporal visual responses — even responses to an object selected by attention; however, this effect is not so great as to substantially alter the population activity signaling the object's identity. The response to a foveal target is nearly unaffected by a row of low-contrast flanking distractors [26••]. Even when monkeys scan a richly detailed scene in search of a tiny embedded object, neuronal activity begins to encode the identity of the object at the moment when the monkey notices it and begins to direct the next eye movement to it [27••]. Because noticing the target relies on visual search [28], this effect appears to be much the same as that observed during covert search with gaze fixed. Whether the impact of clutter is reduced in inferotemporal cortex as compared with areas of lower order [29] is not known.

In conclusion, the incidental details that distinguish complex natural conditions from the reduced circumstances of most visual neurophysiological experiments seem to exert little influence on neuronal activity in inferotemporal cortex.

Figure 3



Data from a neuron in inferotemporal cortex (TE) that responds more similarly to lateral than to vertical mirror images (adapted with permission from [35••]). Each histogram represents the mean firing rate as a function of time during the trial for 16 trials in which the juxtaposed stimulus was presented. Tick marks on the x-axis are 200 ms apart. The stimulus was turned on at 600 ms and off at 1200 ms. Note the similarity in the response profile for stimuli that were lateral mirror images of each other ([A and B], [C and D], [E and F] and [G and H]). Note the dissimilarity for stimuli that were vertical mirror images ([A and C], [B and D], [E and G] and [F and H]).

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Perceived similarity

How is it that some pairs of objects are perceived as being similar to each other while other pairs are not? At least in part, the neural underpinnings of perceived similarity reside in inferotemporal cortex. Each inferotemporal neuron fires at different rates in response to different images, so that its firing rate carries a formally definable amount of information about the identity of the image currently being viewed [30–32]. It is possible that images resemble each other perceptually to the degree that they elicit activity in overlapping populations of inferotemporal neurons. This possibility can be assessed in monkeys because they, like humans, tend to confuse some pairs of images more than others [33].

The notion that confusable or similar images excite overlapping populations of inferotemporal neurons was put to the test by Miyashita *et al.* [34], who assessed neuronal responses to fractal images rated for similarity by human observers. They discovered a moderate tendency for images rated as highly similar by humans to excite overlapping populations of inferotemporal neurons in monkeys. One might argue that the activity of neurons in this experiment was related to the physical similarity of the images rather than to their perceptual similarity; however, these factors have been dissociated in a recent experiment

taking advantage of the phenomenon of mirror-image confusion [35••].

Many species, including humans and monkeys, confuse lateral mirror images (e.g. p and q) more often than vertical mirror images (e.g. p and b) although, by any isotropic measure of physical attributes, lateral and vertical mirror images are equally similar. On recording in inferotemporal cortex during presentation of mirror-image stimuli, Rollenhagen and Olson [35••] found that the neurons respond more similarly to the members of lateral than vertical mirror-image pairs. Figure 3 shows data from a neuron conforming to this pattern. It thus appears that perceptual similarity and overlapping representation in inferotemporal cortex go hand in hand.

Learning

The well established observation that presenting an image repeatedly leads to a reduction in the strength with which inferotemporal neurons respond to that image [36] cannot in itself account for the ability to recognize and discriminate among familiar images. These skills are widely thought to depend on the development in inferotemporal cortex of neurons selective for images viewed repeatedly. Reports, including recent ones [37,38], describe neurons that are selective for trained objects or categories; however, without

systematically comparing responses elicited by images in the training set with responses elicited in the same neurons by control images equated for geometric properties, the results are difficult to interpret.

Kobatake *et al.* [39], on comparing neuronal responses to a standard set of objects in untrained monkeys and monkeys trained for a period of months, did find a subtle trend toward greater object selectivity in trained monkeys. In contrast, Erickson *et al.* [40**] compared responses of the same neurons to familiar and unfamiliar objects, after days of exposure, and found absolutely no enhancement of selectivity for trained objects. Rather, they observed a tendency for neurons recorded from the same electrode to prefer the same familiar images, as if experience had induced a rewiring of intracolumnar connections. Erickson *et al.*'s finding adds strength to other recent evidence emphasizing the importance of local connections [41] and columnar organization [42] for image processing in inferotemporal cortex. Perhaps changes of the sort observed by Erickson *et al.* [40**] occur rapidly whereas changes of the sort observed by Kobatake *et al.* [39] develop over a longer period of exposure.

Over the past decade, Miyashita and colleagues have used the visual paired associate task as a probe for examining the plasticity of object representations in inferotemporal cortex. Their central finding is that inferotemporal neurons responsive to one member of an associated pair tend also to respond to the other member [43].

A major thrust of recent research has been to examine the role in pair coding of the perirhinal division of inferotemporal cortex (area 36). Recent studies have yielded three main findings: first, lesions that extend through area 36 block the expression of pair coding in area TE (another subdivision of inferotemporal cortex) [44]; second, brain-derived neurotrophic factor is upregulated specifically in perirhinal cortex during paired associate learning [45*]; and third, neuronal indices of pair coding are higher in perirhinal cortex than in area TE (Naya Y, Yoshida M, Ihara T, Nagao S, Miyashita Y, *Soc Neurosci Abstr* 2000, 26:286). Erickson and Desimone [46], using a novel task variant that allowed new pairs of images to be introduced each day, found signs of pair coding in area 36 as early as one day after exposure to a new pair of images. The conclusion from this work is that pair coding is expressed strongly in, and probably depends critically on, perirhinal cortex.

Parietal cortex

Parietal contributions to object vision are closely related to the role of parietal cortex in representing three-dimensional space and mediating visuomotor integration. Visually responsive neurons in the caudal intraparietal area (CIP) are sensitive to the tilt of an object's plane or axis, including tilt in depth [47], while some neurons in the anterior parietal area (AIP) are selective for the three-dimensional shape, orientation and size of graspable objects, such as

rings, plates and cylinders [48*], even when the monkey is viewing them without being permitted to grasp.

Neuronal activity in these areas, while of use in motor guidance, may also provide the foundation for a form of awareness of object structure based on the movements required for manipulating the object. Pathways linking parietal cortex to the temporal lobe are focused on dorsal areas in and around the superior temporal sulcus. This finding fits with the observation that inferotemporal neurons selective for shape in depth [49*] tend to be located dorsally [50]. Perhaps these neurons mediate depth-cue-based recognition as distinct from structural awareness and motor guidance.

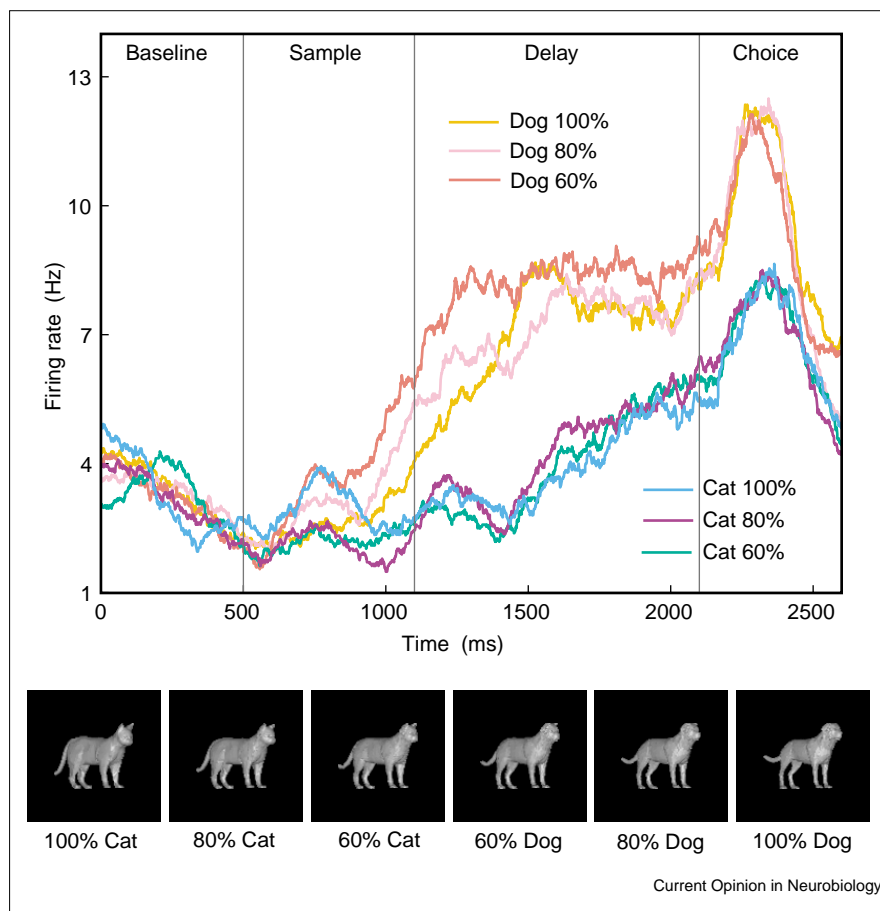
Prefrontal cortex

The dorsolateral prefrontal cortex of the monkey contains neurons that respond selectively to objects presented visually. These neurons are distributed broadly across a region surrounding and including the principal sulcus [51,52], but appear to be most densely aggregated in more ventral areas, where connections to and from inferotemporal cortex are strongest [53]. That prefrontal neurons represent objects with a high degree of fidelity — indeed, with a degree of fidelity approaching that of inferotemporal neurons — has been demonstrated indirectly by Tomita *et al.* [54**] in a recent elegant and technically demanding experiment. These authors found that inferotemporal neurons respond to objects with an almost normal level of selectivity, even when their input is relayed through prefrontal cortex. A further experiment by the same group showed that the trans-prefrontal pathway can support normal levels of behavioral pattern discrimination [55].

Prefrontal object-selective neurons are distinguished from their inferotemporal counterparts by at least two functional traits. In a delayed-match-to-sample task with serial presentation of probes, non-matching probes abolish the object-selective activity of inferotemporal but not of prefrontal neurons [56]. Furthermore, the baseline activity, response strength and selectivity of some object-selective neurons in prefrontal cortex are affected by the task context in which the images are presented [57,58]. Other recent studies of prefrontal cortex have revealed functional traits that seem to be shared with inferotemporal cortex.

Like inferotemporal neurons, prefrontal neurons encode the identity of a stimulus to which the monkey expects to respond at the end of a trial [47] and of a stimulus selected from among distractors during visual search [59,60]. Changes in visual responsiveness observed in prefrontal cortex as a result of experience and learning include a reduction in response strength [61], an enhanced imperviousness to noise [52], and a respect for category boundaries placed at an arbitrary point along a stimulus continuum during training [62**]. Figure 4 shows data from a neuron selectively active on trials in which the sample was on the dog side of an arbitrary line placed along a morphing continuum extending from a cat image to a dog

Figure 4



Data from a neuron in prefrontal cortex (DLPFC) carrying categorical information during the delay period of a categorical delayed-match-to-sample task (adapted with permission from [62]). The six curves represent mean firing rate as a function of time during trials in which the stimulus was an image of 100%, 80% or 60% cat, or 100%, 80% or 60% dog, like the examples at the bottom of the figure. Note the disjunction between high firing rates under any condition in which the sample was a dog and low firing rates under any condition in which the sample was a cat.

image. To what degree these traits are shared with inferotemporal neurons is an area for future study. In general, these observations are compatible with the view that prefrontal and inferotemporal cortex interact closely in representing objects, but that inferotemporal cortex plays a predominant role in recognition while prefrontal cortex contributes specifically to working memory and executive control.

Conclusions

There have been significant advances over the past two years in our understanding of how the brain represents objects. Some of these advances concern processes by which the brain selects the object to be represented. Principles that have emerged include the involvement even of early visual areas in perceptual organization, the usefulness of the biased competition model as a means of explaining how attention affects neuronal visual responses, the parallel nature of conjunction search, and the purity of the object representation at the level of inferotemporal cortex as achieved by eliminating the influence of eye movements and clutter.

Other advances concern the nature of the object representation itself. Noteworthy findings include: the relation between perceptual similarity and representational overlap

in inferotemporal cortex, the specific involvement of perirhinal cortex in visual paired associate learning, the contributions of parietal and dorsal inferotemporal cortex to structural awareness of objects, and the robustness of object representations in prefrontal cortex.

There are two areas in which substantial progress is needed and seems likely to occur over the next few years. First, the neural underpinnings of visual expertise, as studied up to this point primarily in humans [63], must be characterized in monkeys. Second, the distinctive functions of inferotemporal, prefrontal and parietal cortex must be clarified through a comparative approach involving the application of identical methods to multiple areas.

Update

Two papers that have appeared since this manuscript was submitted merit mention because of their direct relevance to the themes of attention and learning discussed above. Fries *et al.* [64] have added a new dimension to the discussion of neural mechanisms underlying voluntary visual attention by demonstrating that attention enhances not only the magnitude of visual responses in area V4 but also the degree of oscillatory synchronization in the gamma band (35–90 Hz) between neurons representing the

attended stimulus. Naya *et al.* [65] have shown that neurons in area 36 signal the identity of the associate of a given stimulus well before neurons in area TE, thus providing additional support of the view that area 36 plays a singularly prominent role in the representation of learned associations between visual stimuli.

Acknowledgements

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References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- of special interest
- of outstanding interest

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Using a novel form of the Kanizsa display – sudden onset of an illusory object against a stable background – the authors demonstrate that, contrary to previous reports, 14% of neurons in area V1 do respond to contours formed by modal completion in displays where the inducing detail is entirely outside the receptive field. The timing of the responses (later in area V1 than V2) suggests that they are mediated by feedback from visual areas hierarchically superior to V1.
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The authors record neuronal responses in areas V1, V2 and V4 while presenting displays in which the contour in the receptive field is held constant but its global properties (surroundedness and convexity) are manipulated, thus determining whether that contour belongs to the right or left edge of an object. Although the inducing cues are outside the receptive field, around 50% of neurons in areas V2 and V4 fire differentially as a function of boundary ownership. Because many other cues (depth and motion among them) can affect boundary ownership, a subject for future work will be the degree to which boundary-ownership signals are invariant across cue-type.
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Recording from neurons in area MT, the authors first characterize each neuron's preferred direction of motion using standard displays. They then record neuronal activity while presenting a compelling illusion in which the perceived direction of motion of a grating is affected by its depth relative to bounding regions of the display (see <http://www.cnl.salk.edu/~gene/>). They discover a highly significant tendency for the direction signaled by the neuronal population to match the perceived direction.
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Previous studies by this group, in which they presented one maximally effective and one ineffective stimulus inside the neuron's receptive field, led to two conclusions: first, that the response to the stimulus pair was intermediate in strength between responses to the individual stimuli; and second, that attention to either stimulus within the pair could shift the response toward the level elicited by that stimulus when presented alone. In this paper, they show that the same principles apply for stimuli with intermediate levels

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This study assesses how attention affects the neuronal contrast-sensitivity function, a typically sigmoidal function relating response strength to stimulus contrast. The essential finding is that attention shifts the contrast-sensitivity function to the left. As a consequence, the effects of attention are maximal for stimuli around contrast threshold.
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The authors record from single neurons in the supplementary eye field of monkeys trained to make eye movements to the right or left end of a reference object. The object may be either a horizontal bar or a pair of dots in a horizontal array. Neurons fire differentially as a function of the object-centered location of the cued point (right end or left end) regardless of the absolute location of the object on the screen and, consequently, regardless of the physical direction of the impending eye movement.
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This study is notable for using a neurophysiological approach to characterize processes underlying conjunction search. Monkeys are presented on each trial with an array of four stimuli (red cross, red circle, green cross and green circle), one of which has to be selected as the target for an eye movement. The target is constant throughout a session. Recording from the frontal eye field, the authors obtain results that are generally consistent with a parallel search model: once a neuron begins to discriminate which stimulus is in its receptive field, it fires more or less according to the degree to which the stimulus resembles the target.
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The authors ask whether the neuronal visual response to a foveal target varies as a function of behavioral context (steady fixation versus saccadic acquisition) or visual context (isolated versus embedded in a row of distractors). The experiment is noteworthy for the extreme care in design, epitomized by adjusting the location of the target during each saccade so as to ensure accurate foveation when the eye comes to rest. The general conclusion is summarized in the paper's title.
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The authors record from inferotemporal neurons while monkeys scan digitized images of natural scenes in search of target objects embedded at locations randomized from trial to trial. Bursts of activity detectable by Poisson spike-train analysis are consistently correlated with the monkey noticing any target to which the neuron is responsive. The background scene does exert some influence on neuronal activity in a substantial minority of neurons, reducing the strength or altering the selectivity of the response to a foveal target.
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