Object vision and visual awareness
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Conscious experience involves perceiving, attending, remembering, and recognizing. Recent neuroscientific research has made significant contributions to our understanding of the mechanisms that mediate such capacities. Physiological and neuropsychological investigations have provided increasingly detailed descriptions of the location and functional properties of the brain structures involved in conscious perception, in attentive behavior and working memory, and in the recognition of objects. Such studies suggest that awareness of a visual stimulus probably reflects the interconnectivity and the type of cells involved in the representation of this stimulus, rather than the activity of specific circumscribed visual areas or processing streams.

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Abbreviations
IP intraparietal
IT inferior temporal cortex
MT middle temporal area
STS superior temporal sulcus
TE anterior IT
TEO posterior IT
TPO superior temporal polysensory area

Introduction
The primate visual system is conceptualized as a hierarchical series of processing stages, each consisting of different highly interconnected areas or modules that work—to some extent—parallel to each other in analyzing different visual attributes [1]. These areas are organized in two anatomically distinct and functionally specialized cortical streams of visual processing emanating from the primary visual cortex, or V1, in the occipital lobe: a dorsal, occipito-parietal stream stretching through the visual association areas of the parietal lobe, and a ventral, occipito-temporal one through the visual areas of the temporal lobe [2,3]. Both streams maintain reciprocal connectivity with a number of limbic structures and the prefrontal cortex [4], where information from different modalities is integrated.

Behavioral studies investigating the correlation between visual discrimination ability in monkeys and lesions in areas of the temporal or parietal lobe suggested that the dorsal stream deals with the processing of spatial information, whereas the ventral stream is involved in the representation of visual objects [2]. Later brain imaging studies confirmed the existence of such a functional dissociation in the human visual system [5], but a different explanation of this dissociation was also proposed on the basis of neuropsychological investigations in human patients [6]. According to this hypothesis, the dorsal pathway serves to control visually guided action and may often process information of which we are unaware, while the ventral pathway mediates conscious visual perception, including that experienced during action.

Here, I review recent research examining correlations between different types of conscious, cognitive actions of monkeys and the activity of single neurons in the ventral pathway, including the associated areas in the superior temporal polysensory and the prefrontal cortices. Emphasis is placed on the activity of those cells that encode complex configurations and may therefore be constituents of explicit object representations. I will review evidence showing that such complex stimulus selectivity is not limited to animate objects, but may instead reflect the extensive requirements of recognition tasks at the subordinate level. The responses of these configuration-selective neurons are most closely correlated with a monkey’s conscious perception, its short-term memory, its recognition of objects, and its ability to represent associations between various pairs of visual stimuli. The functional properties of such cells most probably reflect not only local processing in each cortical area, but also each area’s diverse and complex reciprocal connectivity with a number of other brain structures involved in sensory processing, decision-making, and memory. I will, therefore, first briefly review the anatomical organization of the occipito-temporal pathway, and then go on to describe the cellular response types encountered therein and their possible role in conscious behavior.

The anatomy of the object pathway
Object-related information is transmitted from the primary visual cortex through multiple pre-striate areas to the inferior temporal (IT) cortex of the temporal lobe [7]. Hierarchically, the IT cortex is the highest exclusively visual area. It is roughly co-extensive with Brodmann areas 20 and 21, extending from just anterior to the inferior occipital sulcus (IOS) to a couple of millimeters posterior to the temporal pole, and from the fundus of the superior temporal sulcus (STS) to the lateral wall of the occipito-temporal sulcus (Figure 1a–d). On the basis of cytoarchitectonic criteria [8] and later also on the deficits that follow focal lesions [9], the IT cortex was initially subdivided into a posterior (TEO) and an anterior (TE) part. Later, area TE was further subdivided into five more or less parallel, rostrocaudally oriented cortical
Visual areas of monkey cortex. (a) Lateral, (c) medial, and (d) ventral view of the Macaca mulatta brain. Superimposed on these outlines are various shadings depicting the major visual areas described by Felleman and van Essen [1]. The acronyms for the von Bonin and Bailey [8] subdivisions are depicted on the brain, and the labels used by other investigators appear next to the relevant area. The bold labels starting with a ‘W’ depict the prefrontal cortical areas described by Walker [68]. (b) The parcellation of the ventro-lateral temporal cortex, as suggested by Seltzer and Pandya [67]. The STS (gray area in the inset showing the lateral view of the macaque brain) has been opened to reveal the location of the sensory areas within it. AIT, anterior IT; CIT, central IT; DP, dorsal prelunate; FST, floor of superior temporal; IO, inferior occipital; La, lateral; Lu, lunate; PIT, posterior IT; Pro, temporopolar proriscortex; TE1, TE2, TE3 and TEO, architectonic subdivisions of the inferotemporal region [10]; TPO1–TPO4, architectonic subdivisions of the upper bank of STS [67]; V1–V4, visual areas 1 through 4; VP, ventral posterior. Adapted from von Bonin and Bailey [8].

sectors termed areas TE1, TE2, TE3, TEM, and TEm (Figure 1b) on the basis of cyto- and myelo-architectonic criteria and of afferent cortical connections [10]: the first three areas lie on the inferior temporal gyrus; area TEm lies entirely within the lower bank of the sulus; and TEm straddles the lower lip of the STS. The fundus and the upper bank of STS are subdivided into a number of other areas, such as intraparietal IPA and TPO (superior temporal polysensory area), which receive visual, auditory, and somatosensory inputs.

Microelectrode recordings have shown that the different subdivisions of IT have neurons with different physiological properties [11]. While visual responses in TPO and IPA may also be elicited by moving stimuli, the dominant stimuli of areas TE1–TE3, TEM and TEm are complex stationary visual patterns, including faces and hands of humans and monkeys. The diversity of response properties in this area reflects the extensive reciprocal connectivity of areas TEO and TE with a number of cortical and subcortical structures of diverse functionality.

Input to area TEO comes primarily from area V4 (although direct inputs from V2 and V3 also exist) [3,12–15] and is topographically organized [12]. In addition, sparser inputs to TEO come from areas V3A, V4t, and MT (middle temporal) [12]. Feedback projections to TEO arise from area TE [15], from the parahippocampal area TH, area TG, and the perirhinal cortex (areas 35 and 36) [16]. Fibers from TEO, on the other hand, project back to areas
V2, V3, V3A, V4, and V4t [12,17,18]. Moreover, TEO is interconnected with a number of areas of the dorsal stream, such as areas MT, FST, IPa, PP, and LIP.

Input to area TE comes primarily from area TEO [12,13,16,19], but also directly from V4 [13]. More specifically, fibers from TEO project to areas TEm and TEa [10,12]. The latter areas relay visual information to the rostral IT, the parahippocampal gyrus, and through area IPa to TPO [20].

Both TEO and TE send fibers to area 12 on the inferior convexity of the prefrontal cortex and area 45 on the anterior bank of the inferior limb of the arcuate sulcus [21], as well as to various structures of the limbic system, such as the perirhinal cortex (areas 35 and 36), the entorhinal cortex [18], parts of the striatum, and the amygdala [22]. Most of these connections are reciprocal.

Finally, both TEO and TE are also connected to a large number of subcortical structures and receive nonreciprocal inputs from several nuclei of the thalamus, from the hypothalamus, locus coeruleus, reticular formation, basal nucleus of Meynert, and the dorsolateral and median raphe nuclei. Both are also reciprocally connected with the pulvinar and the ventral portion of the claustrum [23]. The main nonreciprocal output of both areas is a projection to the striatum, whereas TEO alone projects to the superior colliculus, and TE to the medial dorsal magnocellular nucleus of the thalamus [23].

In short, area IT is interconnected, on the one hand, with the peristriate cortex, and on the other, with the polysensory areas of the STS such as TPO and IPa, with the temporopolar proisocortex, the prefrontal cortex, and with the limbic system. It is thus in a position to integrate multiple aspects of vision, to relay visual information to multisensory convergence zones, and to interact with structures that play a critical role in decision-making, in short- and long-term memory, and in feelings and emotional reactions.

This critical role of IT in visual object recognition has been convincingly demonstrated in a large number of behavioral and physiological investigations in monkeys, as well as in numerous clinical and brain imaging studies in humans. Damage to this area causes profound pattern or object agnosias in both humans [24] and monkeys [2]. Recent human brain imaging studies have shown that some areas in this pathway exhibit significant object-specific activation (see [25,26]). Similarly, single-unit recordings have shown that neurons in this area exhibit a striking pattern selectivity (for a review, see [7,27]). The representational capacity of these neurons depends on their connectivity with other areas. For instance, the ability of IT neurons to encode an association between picture pairs depends on feedback signals from the limbic cortex. Disruption of the inputs from the entorhinal and perirhinal cortices abolishes the neurons’ responses to a paired associate, but leaves intact the responses to either stimulus [28]. Neurons in IT are thus capable of representing the complex patterns and abstract forms of a stimulus. Are their responses, however, contingent upon the monkeys’ awareness of a visual stimulus? Before considering evidence directly bearing on this question, it is worth reviewing the response types of the IT neurons that have been implicated in the representation of objects.

Responses of neurons to views of animate objects

The responses of IT neurons to animate objects, such as human and monkey faces, hands or other body parts, are striking (for a historical review, see [29]). Cells responding to faces are found predominantly in IT areas TEm and TEM, with fewer selective neurons in areas TE1–TE3 [11]. However, cells responding to different aspects of faces are also found in various areas that are interconnected with IT, including the polysensory areas of STS (e.g. area TPO), the amygdala [30], the ventral striatum (which receives a projection from the amygdala [31]), and the inferior convexity of the prefrontal cortex [32,33]. Selectivity has been reported for face identity, facial expression, gaze direction, and, recently, for body form and motion [34]. Thus, an extensive network for processing facial information exists in the ventral pathway and its associated brain structures.

Without a doubt, faces are critically important for primates, whose ability to recognize faces appears to begin very early in life [35,36]. Face-specific processing, which has also recently been identified in humans [37–39], may be of great evolutionary advantage. However, these results also raise questions. Does face recognition rely on functionally and anatomically distinct neural mechanisms, or is complex configurational selectivity used for representing any arbitrary visual object?

Responses of neurons to object features

Careful experiments by Tanaka and colleagues (see [27,40–41]) have demonstrated that almost all responses that may be initially characterized as selective for various three-dimensional objects can also be elicited by a greatly simplified version of these objects, often just a combination of one or two simple visual features (see [27,40–41]). Selectivity to moderately complex features is evident as early as in area V4 [41], although the frequency of neurons that are selective to such features is found to be increasingly higher in the posterior and anterior IT.

Experiments in which penetrations were made parallel or perpendicular to the cortical surface have shown that neurons responding to similar features are clustered in modules spanning the entire thickness of the cortex [42]. The regional clustering of neurons with similar feature selectivity has also been confirmed in optical imaging of
intrinsic signals, which demonstrates that cortical columns activated by different but related features tend to overlap spatially [43].

The picture that emerged from all these studies is that the neural representation of nonface objects is accomplished by the co-activation of many neurons in IT, none of which is specific enough to itself to represent views of natural objects [40**]. Yet, these studies never used stimuli that were of particular importance to the animal, nor were the monkeys ever involved in recognizing exemplars of any of the stimulus classes used, as they typically do with the class of faces.

**Is complex configurational selectivity specific to animate objects?**

To determine whether complex configurational selectivity is specific to animate objects, we [44] trained monkeys to recognize individual exemplars from a novel class of computer-generated objects. The objects were spheroids or wire-like structures composed of seven segments of the same length, thickness, and color [45], and they were presented from different vantage points on a screen in front of the animal. After several months of training, the monkeys became experts at recognizing individual exemplars of this class despite a great similarity between targets and distractors—a task not unlike the recognition of individual faces. Much as in face recognition [46], wire-recognitio performance was found to be view-dependent, with object constancy accomplished only after exposure to different views of the objects [44]. Recording from the anterior IT (mostly in the upper bank of the anterior medial temporal sulcus) during this recognition task actually revealed a number of cells that were highly selective to familiar views of these recently learned objects [47,48]. The neurons responded best to one object view and showed the characteristic view-tuning that was previously described for face cells (Figure 2).

To find out the minimum stimulus configuration that would still elicit significant responses from the neurons, Pauls [49] developed a method of eliminating, scrambling, or occluding the displayed wire segments. By systematically reducing the complexity of the stimulus with this technique, he found that some cells were actually selective to a simple feature, such as an angle (Figure 3a), rather than to the entire wire configuration. In sharp contrast to such cells, however, other wire-selective neurons exhibited extreme sensitivity to alterations in the stimulus configuration (Figure 3b,c). In other words, reduction of the stimulus was impossible without significantly reducing the cell's response. Moreover, some neurons exhibited distinctly different responses to targets and distractors, despite the great degree of similarity (up to five sequential
Figure 3

The effects of object reduction on the responses of single inferotemporal neurons. (a) Recording from a cell responding to a simple feature, here an 'angle' element. (b) Recording from a cell responding to a moderately complex feature. (c) This cell discharges maximally when the view is complete (left panel). Removing even a single segment, such as the top segment (depicted here with dotted lines) — although it can be any of the seven segments — greatly reduces the neuron’s response (right top panel). Presenting any of the segments alone elicits a minimal response (right bottom panel). (d) Recording from a neuron that responds strongly to a view of the target but that does not discharge a single spike for a distractor view that shares a five-segment part with the target.

segments with very similar orientation in space) between them (Figure 3d).

The properties of such neurons closely resemble those of face-selective cells, a finding suggesting that the encoding of visual objects by the brain may be determined not only by the biological significance of an object class, but also by the nature of the recognition task. The latter hypothesis is supported by recent observations that areas closely corresponding to those previously implicated in the processing of faces are sensitive to manipulations of nonface objects at the categorization level [50], and that areas in the medial temporal lobe of humans react selectively to complex configurations, such as a spatial layout of local space similar to that of face areas [51*].

The firing of an ensemble of face-selective neurons has often been thought to provide the representation of a face [52]. Similarly, the firing of neurons that respond to complex nonface patterns or views may be thought of as providing the representation of any given object. This type of encoding may be specific to faces or simply to those object classes whose structurally similar members must be systematically identified by the animal. But is the response of such object-specific neurons contingent upon the monkeys’ awareness of a visual stimulus?

Inferotemporal neurons and visual perception
To determine the role played by IT neurons in visual perception, we [53**] trained monkeys to report their percepts while viewing ambiguous stimuli. Ambiguity was
introduced by presenting a different image to each eye. Rarely, if ever, are such nonmatching stimuli binocularly fused into a stable, coherent stimulus. Instead, each monocular pattern takes its turn at perceptual dominance, only to be overtaken by its competitor after a number of seconds (for a review, see [54**]).

Recordings in striate cortex using simple patterns such as sinusoidal gratings as the visual stimuli showed that only a small proportion of the neurons changed activity during the perceptual alternations [55]. In area V4, on the other hand, 38% of the recorded neurons modulated their activity with the monkey's report. Curiously, however, about one-third of the response-modulating cells fired more strongly when their nonpreferred stimulus was perceived; only two-thirds of the neurons were excited when their preferred stimulus was visible [55]. The neurons whose activity appears to be in anti-correlation with the animals' perception of the driving stimulus may be part of an inhibitory mechanism that is separate from, and to some extent independent of, the mechanisms of perception. Taken together, the physiological results of recording in early visual cortices suggest that the response of a large number of cells (about 80% in V1/V2, and 60% in V4/MT) in the visual cortex is independent of the perceptual dominance of the stimulus.

In sharp contrast with the neurons of the early extrastriate cortex, the vast majority of the inferotemporal or STS neurons (approximately 90% of the recorded cells) exhibited responses that were contingent upon the perceptual dominance of an effective visual stimulus [53**]. No cells in IT were found to be active exclusively during the phenomenal suppression of the stimulus, a finding also suggesting that the studied areas represent a stage of processing beyond the resolution of ambiguities, where neural activity may indeed be the physiological correlate of conscious perception.

Do neurons responding only when a stimulus is perceived actually mediate the conscious experience of this stimulus? The current data, although they favor such an interpretation, cannot prove it unequivocally. It is worth noting that even if such neurons prove to underlie directly the recognition of an object, their activity may still be insufficient to mediate the object's conscious experience, as recognition itself and the 'awareness of recognition' may involve different neural mechanisms. For instance, investigations of visual recognition impairments attributable to brain injury suggest that patients with preserved covert recognition may suffer a selective loss of awareness of recognition [56]. Such patients exhibit electrophysiological responses (e.g. galvanic skin responses) when exposed to familiar objects, and their recognition performance is facilitated by associative priming [57], just as in normal subjects, yet they are not aware of any familiarity with the objects. An interesting dissociation between single-unit activity and explicit recognition has also been reported recently in an electrophysiological study in the medial temporal lobe of human epilepsy patients [58**]. In this study, about one-fifth of the sampled neurons differentiated between novel and familiar stimuli. However, the activity of most cells was related to past exposure to the stimulus rather than to the subject's conscious recollection. In other words, the cells 'remembered' a previously seen stimulus and fired selectively when it was presented again, even when familiarity with this stimulus was denied by the subject.

Organisms never stop sensing their environment, matching its contents against memory, and constructing appropriate responses, often with no concomitant awareness of the events affecting the senses or the actions employed in the response. The brain must process information efficiently without relying on conscious experiences. It is thus hardly surprising that a great deal of subcortical and cortical activity accurately represents the organism's environment, even if many of the representations are kept outside of awareness. The question of interest is how this is done, and where the difference in neural activity between the conscious and unconscious states lies.

**Prefrontal cortex: knowing what is where**

Cell activity that is directly correlated with conscious behaviors has been demonstrated in various types of experiments. Here, I briefly review some results from recordings in the prefrontal cortex that have provided us with new insights into the mechanisms of working memory and the type of transient storage that is used when performing cognitive behavioral tasks, such as problem solving, calculating, or responding in delayed response or delayed matching to sample tasks.

In the macaque, the prefrontal cortex is subdivided into the cytoarchitectonic areas 8–13, 45 and 46 [58**]. The dorsolateral areas 9 and 46 receive information from the posterior parietal lobe of the dorsal stream [59], whereas the ventrolateral areas 12 and 45 receive their inputs from the temporal areas TEO and TE [21]. In other words, ventral areas 12 and 45 belong to the 'high-level' targets of the object pathway and may thus have neurons with properties similar to those observed in IT or the upper bank of the STS; physiological studies have demonstrated this to be the case.

Prefrontal areas selectively process information related to the identity of faces [33**]. Interestingly, it was found that some of these neurons show a tendency to continue firing after the cessation of stimulation, whereas others do not even begin firing until after stimulation has ended. Tcacer injections at the termination of the recording showed that the prefrontal region, including the face-selective neurons, receives its inputs from the ventral bank of STS (areas TEm and TEn). In sharp contrast to areas 12 and 45, area 46 is involved in stimulus location [60,61**]. It thus appears that, to some extent, 'what' and 'where' information remains segregated in the prefrontal cortex.
Moreover, this is the case for both monkeys [32] and humans [62**,63]. But how is information regarding the identity and the spatial location of a stimulus integrated to guide behavior?

A recent clever experiment by Miller and colleagues [61**] shows that integration may actually occur within the prefrontal cortex. Recording from monkeys performing a task requiring both object and spatial working memory revealed that neurons in this area show both spatial and object tuning in the delay period of the task. Such cells may indeed underlie the unified representation of 'objects in their places' required to guide appropriate action.

Conclusions

Cortical areas at the highest level of the occipito-temporal processing stream contain neurons that may be increasingly more involved in the explicit representation of visual objects. Such neurons appear to encode holistic information about object views in such a manner that reducing the configurational complexity of the stimulus strongly reduces the cell responses. The existence of such cells does not imply that exemplars of all object classes are necessarily represented by the firing of highly specialized units in IT (or elsewhere). A plethora of objects that need only to be categorically described in the monkey's visual system may be neurally represented by encoding moderately complicated conjunctions of simple features, as Tanaka and his colleagues (see [40**]) have suggested. In fact, encoding simple features and their spatial relationships is probably all that is required to represent most of the objects that the animal encounters in its entire life. Faces cannot be represented in this manner, as they all share the same basic features in the same spatial arrangement. As both face identity and the interpretation of facial expression are of paramount importance for a monkey's survival, a 'special' neural machinery may be used to recognize faces. Yet, the same mechanism may, in principle, be used to represent individuals of any homogeneous object class when subordinate recognition is required.

Interestingly, the response of the highly specialized IT cells best correlates with the perception of ambiguous stimuli. Whereas only a limited number of neurons in the early visual areas show patterns of alternating excitation and inhibition in synchrony with the perceptual dominance and disappearance of the cell's preferred visual pattern, almost all neurons selective to faces or other complex stimuli in IT fire exclusively when these stimuli are consciously perceived. The areas containing such neurons are interconnected with both the limbic system and areas of the prefrontal cortex, and thus integrate sensory information with object-related information. Prefrontal neurons, which also show complex configurational selectivity, most probably serve working memory, the type of memory that is crucial for cognitive tasks and the planning of actions. It will be interesting to investigate how cells in prefrontal or parahippocampal cortices behave when the perception of a stimulus is ambiguous. Does cell activity in these areas show the same strong correlation with the perception of the animal? Or is the activation of the cells continuous as long as the monkey can remember which stimulus is suppressed? When do prefrontal and temporal neurons that are selective for the same pattern disagree with each other? Given the increasing interest of the neuroscience community in the neural mechanisms underlying various conscious cognitive processes [65**], future studies are likely to shed light on many of these questions.

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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

15. Nakamura H,Gattass R, Desimone R, Ungerleider LG: The modular organization of projections from areas V1 and V2 to


The authors review evidence showing the importance of the temporal and occipitotemporal cortex in object recognition.


A review of functional magnetic resonance imaging (fMRI) studies on the anatomy and function of the visual system. The authors summarize evidence of hierarchical processing among visual cortical areas and describe relevant fMRI studies on higher cognitive processes, such as attention and memory.


33. O'Scaladhe SP, Wilson FAW, Goldman-Rakic PS; Areal segregation of face-processing neurons in prefrontal cortex. Science 1997, 278:1135-1138.

Monkeys were trained to maintain fixation while visual stimuli were presented on a display. Microelectrode recording during this task showed that many neurons respond to pictures of faces significantly more than to pictures of non-face objects. The cells were selective to entire configurations of the face. Scrambling the face greatly diminished the response of the units. Some cells continued to fire after the stimulus was discontinued, while others did not start firing until after the cessation of stimulation. This type of persistence was previously reported only in the context of a delayed matching to sample task. It appears, however, to reflect an intrinsic property of these prefrontal neurons, because the monkeys were not engaged in a memory task and one animal was not trained at all.


A review of recent neurophysiology, anatomy, and imaging studies in object recognition.


Functional magnetic resonance imaging study in humans. Subjects viewed intact and scrambled versions of black and white photographs of faces, houses, common objects, and scenes presented in separate epochs. Viewing was either passive or required pressing a button every time an image was seen two times in a row. In all subjects, significant bilateral activation was found during the presentation of intact but not of scrambled scenes in a region of parahippocampal cortex around the collateral sulcus. The same area was activated upon presentation of spatial layouts containing no discrete objects.


The activity of single neurons was recorded in monkeys trained to report their perceptions when viewing ambiguous stimuli. Visual ambiguity was induced by presenting incongruent images to the two eyes, a stimulation condition known to instigate binocular rivalry, during which one image is seen at a given time while the other is perceptually suppressed. Previous recordings in areas V1, V2, V4 and MT of monkeys experiencing binocular rivalry showed that only a small proportion of striate and early extrastriate neurons discharge exclusively when the driving stimulus is seen. In contrast, the activity of almost all neurons in the inferior temporal cortex and the visual areas of the cortex...
of superior temporal sulcus was found to be contingent upon the perceptual dominance of an effective visual stimulus.


The activity of neurons in the human medial temporal lobe was recorded during a recognition memory task. Recordings were carried out in patients with intractable epilepsy who underwent implantation of intracranial electrodes in order to identify the seizure focus for potential surgical resection. The cells discriminated faces from nonface objects, and often responded selectively to specific emotional expressions. Activity was dependent on novelty or familiarity. During the recognition task, the firing of some cells was more reliable than the person's conscious recollection.


Single-neuron activity was recorded while monkeys performed a delayed sequential reaching task, in which they needed to remember two cue positions out of three and their temporal order of presentation. Responses were found to be position-dependent. Interestingly, some cells exhibited delay-period activity only when the visual cues were presented at two positions out of three. The study shows the high spatial selectivity of this prefrontal area.


By using functional magnetic resonance imaging in humans, an area in the superior frontal sulcus was identified that is specialized for spatial working memory. This area is located more superiorly and posteriorly in the human brain than in the monkey brain.


Monkeys were trained to fixate while a sample object was briefly presented at the center of the screen. After a delay, two test objects were briefly presented at two of four possible extraregional locations. One object matched the sample, the other did not. After another delay, the monkey had to make a saccade to the remembered location of the match. The task required the animal to remember the object's identity over the first delay (object-delay), use that information to find the match, and subsequently remember its location over the second delay (position-delay) in order to perform the correct saccadic eye movement. Neurons were found that fired selectively during the object- or position-delay. About half of the population, however, appeared to contribute to both object and spatial working memory. Thus, the neurons of this area may contribute directly to the linking of the object and spatial information needed to guide the animal's behavior.


A review of a scientific approach to the problem of consciousness. The authors discuss visual awareness as a basic form of consciousness. They offer interesting neuroscientific explanations of awareness and discuss how function of neurons in the brain may be able to explain subjective experience.
