PART IV

Visual Attention

18

Primate Visual Attention

How Studies of Monkeys Have Shaped Theories of Selective Visual Processing

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Despite having highly developed visual abilities, even the visual systems of primates exhibit a limited capacity to process all of the information available in our cluttered visual environments. To overcome this limitation, primates have evolved sophisticated mechanisms of selection that allow limited-capacity resources to be focused on the most relevant objects, surfaces, and other organisms that surround us. A majority of the studies of nonhuman primate attention have focused on how it is that their visual systems select certain inputs for preferential perceptual processing while filtering other distracting inputs that are not relevant for the task being performed. For example, while foraging for fruit in trees, it is particularly important for diurnal primates to take advantage of their color vision to localize the ripe fruits that typically differ in color from the background canopy of leaves. In the laboratory, this ability to select information based on the visual features of task-relevant objects has been studied using visual attention tasks such as spatial cuing and visual search paradigms. Not surprisingly, data from behavioral and neurophysiological studies of such tasks by primates have played a primary role in shaping theories of attention. These theories are not only used to explain the behavior and neural activity recorded from the brains of monkeys but also dominate theories of attentional selection by humans.

Since the purely introspective definition of the concept of attention by William James (1890), numerous experimental paradigms have been developed to study the ability of humans and nonhuman primates to process a particular element in their visual field. These paradigms include spatial cuing tasks (e.g., Posner & Cohen, 1984), visual search (Wolfe, 1998), and studies of flanker interference (Eriksen, 1995). Although each of these paradigms has revealed important insights into how mechanisms of visual attention selectively process perceptual inputs, theories differ in how they explain capacity limits of processing in humans and nonhuman primates. In this chapter, we will focus our discussion primarily on four theories of attention and how studies of visual processing and attentional selection in primates have largely shaped these theories. The first theory that we will discuss is the feature-integration theory of Treisman and colleagues. We will then describe its offspring (the guided-search model and the ambiguity-resolution theory). Finally, we will discuss the biased-competition account of selection and the premotor theory of attention. This sequence roughly follows the chronological order in which they were introduced into the literature.

Hubel and Wiesel received a Nobel Prize for their work showing that occipital cortex of cats and nonhuman primates not only has a topographic representation of the visual field, but that, within this organization, the neurons selectively respond when a certain object feature is in the cell's receptive field (RF; Hubel & Wiesel, 1968). A neuron's RF is simply the area of space to which a neuron will respond to an effective stimulus. For example, when a horizontal line, like the edge of an object, passes through the RF of a certain V1 cell, it will respond vigorously. However, when the stimulus in the RF is a vertical line, this cell gives little or no response when such a feature appears. The neurons that code for different orientations in V1 also appear to have an orderly columnar structure, with cells coding for one orientation localized next to a column of neurons coding for a similar orientation. These neurophysiological findings, together with additional work examining the processing of visual information other than line orientation, were taken as evidence that the brain possesses modules for processing different visual features (Zeki, 1978). The map of color, in an area like V4 in the macaque, signals that a specific color is at a specific location in the visual field (De Valois & De Valois, 1975). A different topographic map in visual cortex links a specific line orientation to a location in the visual field. Similar properties have also been described for perceived motion, spatial frequency, and more (see Chapters 5 and 14 for overviews of monkey visual system). Samir Zeki's paper (1978) reviewed the empirical work that contributed to this emerging view of the role of different areas of visual cortex. He foreshadowed that one of the big questions for researchers in the future would be how information from these separate feature maps is combined to form the unitary percepts that primates experience.

FEATURE-INTEGRATION THEORY

It is telling that the first paper cited in the seminal work of Treisman and Gelade (1980) is Samir Zeki's summary of some of the neurophysiological evidence for the independent processing of visual features in the cortex of monkeys. As Treisman and Gelade note, this recent evidence supports a constructionist view in the longstanding debate over the nature of visual perception. Gestalt psychologists had long argued that we first visually process whole objects before the component parts (Wertheimer, 1924/1950). Intuitively, this view had the advantage of being consistent with our own experience of our visual environment, in which we are aware of integrated objects and not unbound features that are unassociated with a spatial location. Contrary to this view, the evidence emerging from the neurophysiological studies of visual cortex in monkeys supported the view that the visual system first analyzes the component visual features of objects. Only later do we form object representations of the type that we introspectively experience. What Treisman and her colleagues (Treisman & Gelade, 1980; Treisman, Sykes, & Gelade, 1977) proposed was that our perception of visual information was a result of bottom-up processing of simple features (color, line orientations, etc.) and top-down attentional deployment to a specific location in space. This seemingly simple idea still plays a large role in shaping the debates in the literature over the role that attention plays in the visual systems of primates (e.g., Treisman, 2006).

The notion that it is the output of attention mechanisms that dictates the nature of the information we perceive in our visual field may seem banal at this point. However, it is easy to underemphasize the degree to which the feature-integration theory of attention incorporated findings from other fields of study, built on previous work, and shaped the topics of study after it. With notable exceptions (e.g., Neisser, 1967), theories of attention had largely revolved around findings from studies of human attention using auditory stimulus presentation prior to the late 1970s and early 1980s (Deutsch & Deutsch, 1963; Treisman, 1969). The primary issue was whether attention selected information before or after stimuli had been recognized. This debate over early versus late selection had shaped how people viewed the role of attention. That is, did attention filter or attenuate task-irrelevant information from awareness before it had been processed to the point of extracting its meaning and categorizing it, or after this level of processing had been performed on all of the available stimuli (Broadbent, 1957; Kahneman, 1973; Treisman, 1969)? This debate had been largely driven by dichotic listening paradigms in which human subjects were to monitor stimuli presented to one ear and ignore stimuli that were presented to the unattended ear (e.g., Moray, 1959).

The linchpin of the feature-integration theory was the "master map" of locations. It is a spatial representation of the visual field in which attention was deployed to a given spot on the map. Once attention was deployed to a location in the master map, all of the features at the same location were bound together to form a representation of the multifeature object (see Figure 18.1; Treisman, 1988). Without deploying attention to a location in the master map, the visual system could detect the presence of a feature (e.g., the color red) in the visual field but did not have access to the other object features that were present at the same location as the task-relevant feature. It was this distinction that was used to explain the qualitatively different patterns of behavioral performance in visual search tasks (see Chapter 3 for an overview of visual search task performance in pigeons). When subjects have to detect the presence

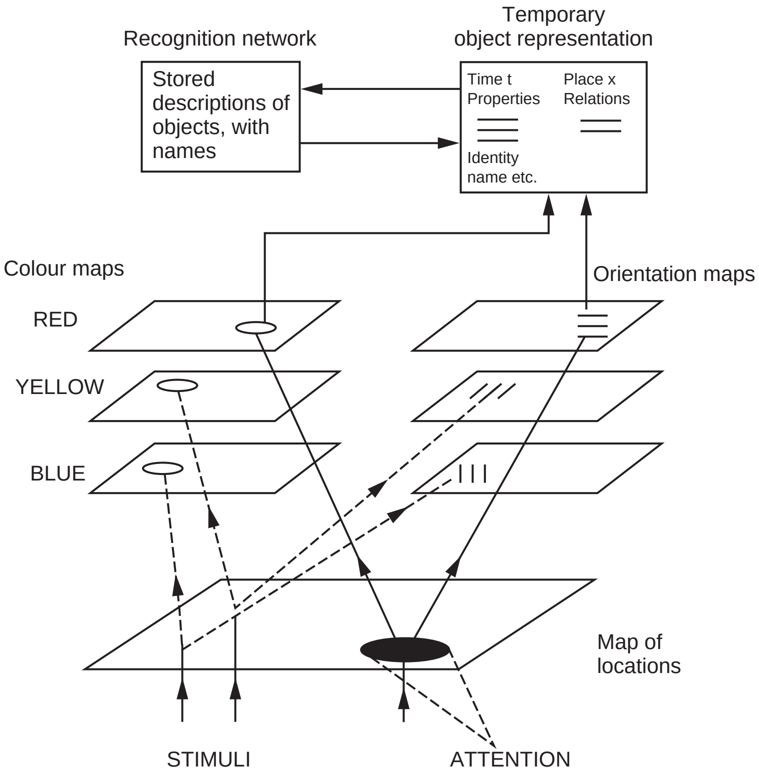

FIGURE 18.1 Diagram of the feature maps and master location map in feature-integration theory. From Treisman, A. (1988). Features and objects: The Fourteenth Bartlett Memorial Lecture. *Quarterly Journal of Experimental Psychology*, *40*, 201–237. Reprinted with permission.

of a simple feature (e.g., the color red among green) in the visual field, they respond much more quickly than when searching for objects that are a combination of features. When observers search for objects defined by a conjunction of features (e.g., a red square among red circles and green squares), performance becomes slower as more items are added to the visual field. Feature-integration theory proposes that is because attention needs to be deployed to each of the object locations in the master map in a serial manner, to bind together the features and recognize each object. This model also proposed that, to localize any visual information, even a simple feature like a spot of red, attention needed to be deployed to a point on the master map of locations. Thus, attention must also be summoned to select a specific location in the map to localize the object or bind its features.

GUIDED-SEARCH MODEL

The significance of feature-integration theory may be best demonstrated by the theories that it has inspired. The guided-search model of Wolfe and colleagues (Wolfe & Cave, 1989; Wolfe, Cave, & Franzel, 1989; Wolfe & Gancarz, 1996) shares many ~~features~~ with feature-integration theory. It differs in that the locations of feature information are tied to a map of locations that represents the likelihood that a given location contains the task-relevant target. For example, if the target is a red, large square, then the feature maps with connections to the master map of locations can feed their inputs forward to indicate that the relevant features are at a certain location in the visual field. This elaboration of Treisman's model allows the guided-search model to account for data that feature-integration theory cannot, such as the efficiency with which an observer can locate a target defined by a conjunction of three features versus two (Wolfe et al., 1989).

Instead of describing the map of locations in which attention is deployed as a master map of visual space, the guided-search model uses the term *saliency map,* coined by Koch and Ullman (1985). The idea is that a representation of visual space exists in the brain for the purpose of identifying the task relevance of visual features, but not the actual features themselves. Such an area would have cells that respond to a specific region of the visual field if a task-relevant feature was presented in the cell's RF, but respond much less when a task-irrelevant feature was presented. As evidence that theories of attention and empirical work with primates have fed off of one another, the activity of neurons in the lateral intraparietal area (LIP) and the frontal eye field (FEF) has been interpreted in this way (see Figure 18.2 for a schematic diagram of visual areas in the macaque brain). For example, neurons in the FEF will respond more vigorously to a red item when the target is red and the visual search distractors are green, and more vigorously to a green object when the target is green and the distractors are red (Schall & Hanes, 1993). This task-based but not feature-based selectivity also appears to be the case for LIP (Gottlieb, Kusunoki, & Goldberg, 1998) and the superior colliculus (SC; McPeek & Keller, 2002). However, it should be noted that most of these results are from experiments that required an eye movement response to the task-relevant item, and these areas also show activity that appears to be related to controlling eye movements. Nevertheless, the evidence does support the notion that the FEF cells are selective for task-relevant items even when the task-relevant item requires a manual response or a response needed to be withheld (Thompson, Bichot, & Schall, 1997; Thompson, Biscoe, & Sato, 2005).

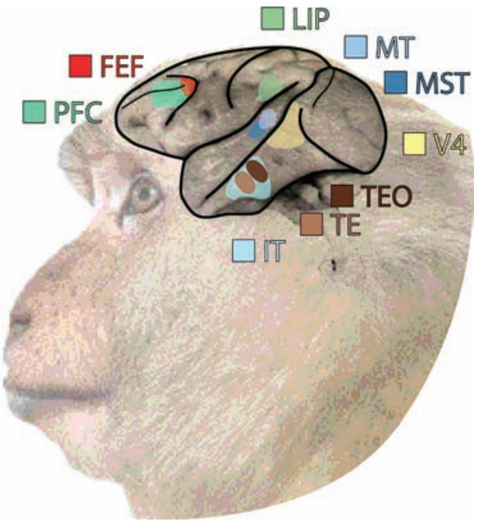

FIGURE 18.2 Schematic diagram of the location of visual areas in the neocortex of the macaque brain discussed in this chapter. Note that the specific locations, nomenclature, and spatial extent of these areas are still active topics of research.

AMBIGUITY-RESOLUTION THEORY

Feature-integration theory was a source of inspiration for another theory of attention that was also stimulated by studies of attention in macaque monkeys. The ambiguity-resolution theory (Luck, Girelli, McDermott, & Ford, 1997) was proposed with the goal of integrating monkey and human electrophysiology. Specifically, Chelazzi, Miller, Duncan, and Desimone (1993) recorded from the extrastriate area known as inferotemporal cortex (IT) in macaque monkeys. This area is in the ventral visual pathway, which appears to be specialized for processing objects, whereas the dorsal visual stream appears to be specialized for processing spatial information (Ungerleider & Mishkin, 1982). The ventral stream of visual information processing can be thought of as a hierarchy of visual areas that are selective for increasingly complex stimuli (Barlow, 1972; Felleman & Van Essen, 1991). That is, neurons in area V1 have small RFs and respond to basic features like line orientations. Cells in a downstream area like IT have large RFs, and its neurons are selective for more complex stimuli, such as objects composed of combinations of color and shape.

Chelazzi and colleagues (1993) trained macaque monkeys to perform a cued visual search task. As shown in Figure 18.3, each trial began with the monkey fixating a central point. Then, an object was presented at fixation, indicating what type of object the monkey was supposed to detect on that trial. After a blank cue-to-target interval, the array of items was presented. The matching item (target) could be presented within the RF of the IT cell or at a nearby location. In addition, the selectivity of each cell was determined a priori, so that the cued target either effectively drove the cell when presented in the RF (i.e., a good cue) or elicited a smaller response (i.e., a poor cue). The bottom panel of Figure 18.3 shows the firing rate of an example cell. The first striking effect occurred between the presentation of the cue and the visual search array. When the cued target was the preferred stimulus for the recorded cell, the cell responded more vigorously during the cue-to-target interval than it did when the non-preferred stimulus was cued on that trial. The theoretical

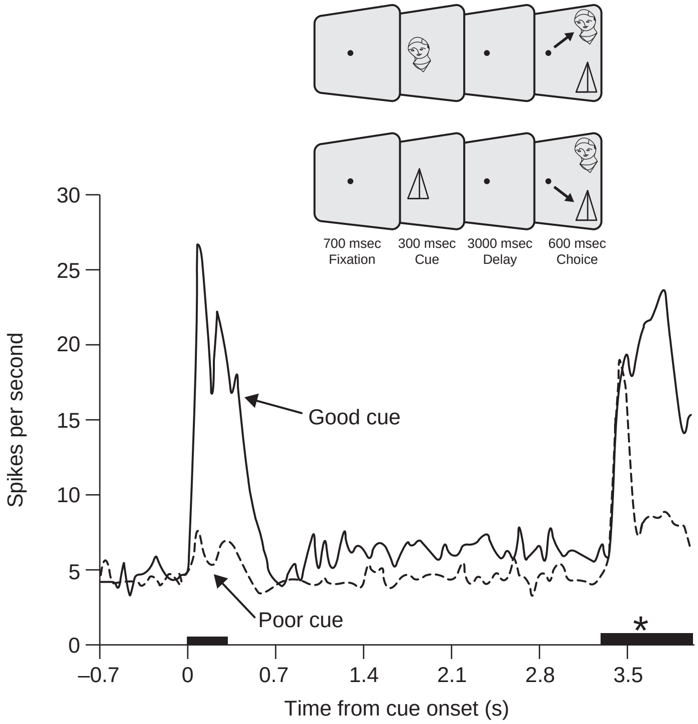

FIGURE 18.3 Example of the stimuli and results from Chelazzi et al. (1993). Top panel shows an example trial of stimuli in which the cue indicates the to-be-searched-for target followed after a retention interval by the two-item search array. Bottom panel shows the spike density function of an example cell recorded during this delayed-matched-to-sample search task. From Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience, 18*, 193–222. Reprinted with permission.

implications of this observation will be discussed further below. The primary finding of the study was that, when the search array was presented, the IT cells initially displayed a response that did not discriminate between whether the object presented in the RF was preferred or non-preferred stimulus. However, approximately 175 ms after the search array presentation, the neurons responded more vigorously when it was the preferred stimulus presented in the visual field. The amplitude of this target discrimination activity following the search array was increased by a number of factors. It was larger when the target was composed of one versus multiple features, when the target had to be localized with saccade to its location, and if distractors were presented nearer the target. These findings suggest that, after a period in which all items activate the ventral visual system similarly, there is a point at which cells come to signal the task relevance of the object in their visual field.

Luck worked with Chelazzi in Desimone's lab, so he was well aware of these findings from the visual search experiments recording from IT neurons. Prior to working with Desimone, Luck had worked with Steven Hillyard and discovered an event-related potential (ERP) component with a scalp distribution consistent with a source in the human homologue of macaque V4 or IT. This component of the visual ERP waveform is known as the N2pc, or N2-posterior contralateral. This component is a negative-going wave generally found in the second negative peak of the ERPs elicited by a visual stimulus (thus, in the N2 family of ERP components), with a posterior and contralateral distribution relative to where attention is deployed in the visual field (see Figure 18.4). To take a specific example, if a target item (a red square) is presented in the left visual field while distractors (green, blue, yellow, purple, and black squares) are presented in the rest of the visual field, then the right hemisphere will become more negative than the left hemisphere at approximately 175–200 ms after the search array is presented. If the target is presented right of fixation, then it is the left hemisphere that exhibits

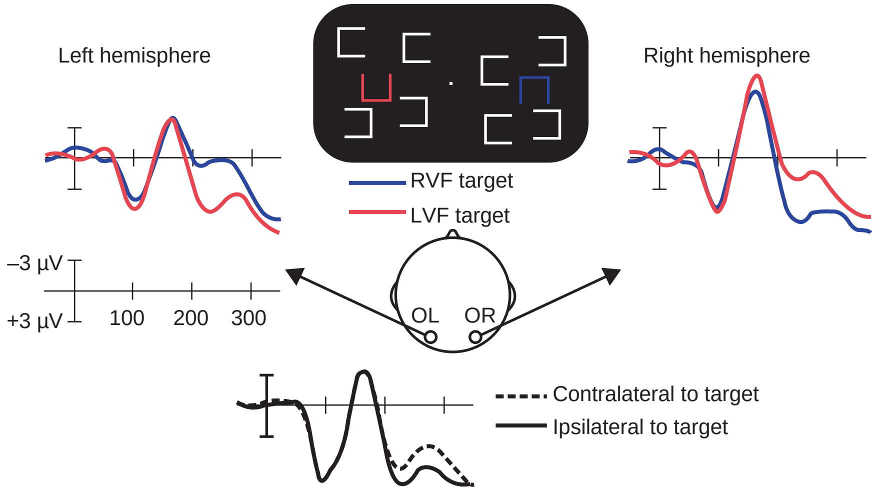

FIGURE 18.4 Example of a visual search array and pattern of N2pc activity recorded from humans, with the different colored targets being task-relevant in different blocks of trials. Contralateral and ipsilateral waveforms are averaged across electrodes relative to the target. From Woodman, G. F., & Luck, S. J. (1999). Electrophysiological measurement of rapid shifts of attention during visual search. *Nature*, *400*, 867–869. Reprinted with permission.

this relative negativity. If the target object is not presented in the array on a trial, then neither hemisphere becomes more negative following the search array presentation. That is, the posterior waveforms from both left and right hemispheres overlap. Upon setting up his own lab, Luck began testing the hypothesis that this N2pc component would behave similarly to the single-unit effects observed by Chelazzi et al. (1993).

To test the hypothesis that the N2pc component indexes the same mechanisms of selection studied during visual search studies of monkey IT cortex, Luck and colleagues had humans perform search tasks while manipulating the same stimulus and task variables that Chelazzi and colleagues had.

In one experiment, the search task was to discriminate the identity of a target defined by a conjunction of form and color while the target was presented with either distant or nearby distractors. This was contrasted with an experiment in which the task was to detect the presence of a target color that could have either distant or nearby distractors. Mirroring the results of Chelazzi et al. (1993), Luck et al. (1997b) found that the amplitude of the N2pc was increased when people searched for conjunction-defined targets compared to search-for-feature targets (see Figure 18.5). In addition, the amplitude of the N2pc was larger when subjects had to ultimately localize the target with a saccade than when a manual discrimination response was required. These findings are consistent with the original feature-integration theory, which was based on the distinction between feature and conjunction search and the unique processing requirements of target localization (Treisman & Gelade, 1980). However, the finding that nearby distractors further increased the amplitude of the N2pc component for both feature and conjunction search was difficult to reconcile with a model in which the role of visual attention in the primate brain was to bind together the features of objects. Instead, Luck and colleagues (1997) proposed that this was due to the N2pc being generated in a visual area with large RFs, such as IT.

When a target is presented without nearby distractors, the filtering of irrelevant information is relatively easy. However, when distractors are presented near task-relevant target stimuli, then the activity of cells coding for features of the nearby distractors needs to be suppressed. This filtering allows higher-level neurons of the visual system to accurately read out the information about the attended item to determine if it was in fact the target. Similar to the previous models of attention discussed, Luck and colleagues assumed that attention was deployed based on the presence of a target feature at a location. Luck et al. (1997b) proposed that the role of visual attention was to disambiguate the responses of neurons in the visual system that had large enough RFs to include both the target and distractor objects and complex enough response properties to code ~~to~~

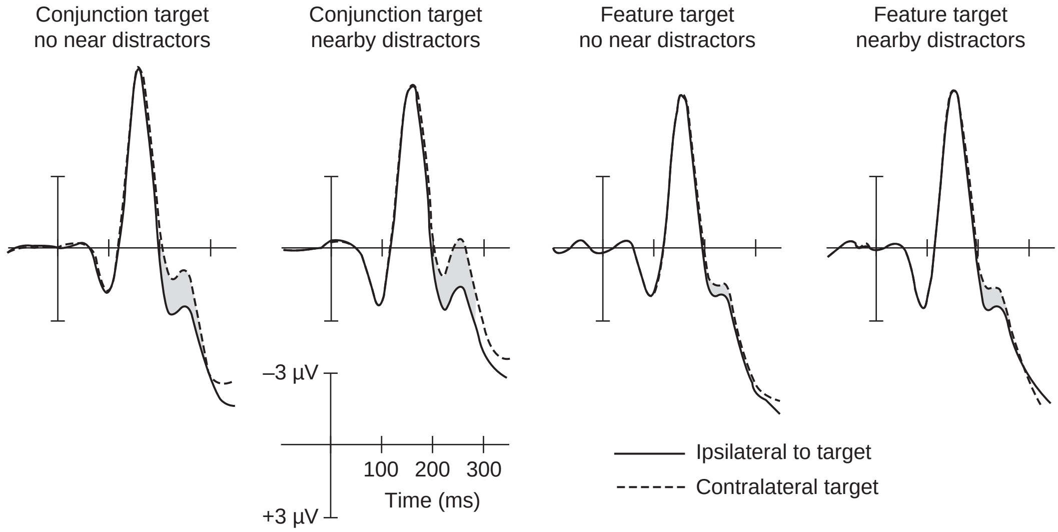

FIGURE 18.5 The results from Luck, et al. (1997b) recorded from human subjects during visual search tasks. Waveforms were recorded from lateral occipital electrode sites and elicited by targets that appeared in the lower visual field. Dashed lines indicate the waveforms recorded from electrodes contralateral to the target, and solid lines show the waveforms recorded ipsilateral to the target hemifield. From Luck, S. J., Girelli, M., McDermott, M., & Ford, M. A. (1997b). Bridging the gap between monkey neurophysiology and human perception: An ambiguity resolution theory of visual selective attention. *Cognitive Psychology*, *33*, 64–87. Reprinted with permission.

complex target objects. This forms the basis of the ambiguity-resolution theory (Luck et al., 1997b).

Areas like V4 and IT have relatively large RFs that are partially overlapping. This coarse coding of location makes it possible to suppress activity from the upstream neurons that include just the distractors surrounding the target. By coarse coding, we refer to the idea that the neurons in the ventral stream do have some degree of spatial resolution, but this is limited, particularly in cluttered visual scenes. This suppression of distractor activity, in turn, makes the responses of neurons that include multiple stimuli less ambiguous as to what visual features the possible target item possesses. Let us consider an example. A human or nonhuman primate is searching for a red letter T. If a specific IT neuron contains both a red T and a green L, then the output of this cell alone is ambiguous. There could be either a green T and red L, or it could in fact be the target object. To disambiguate the response of this cell, visual attention could suppress the activity of V4 neurons with RFs that overlap with the cell under consideration and contain only one of the two objects. If the cells that contain only the green L are suppressed, and these V4 cells feed information forward to the target IT neuron, then the IT cell will signal that the features of red and T are colocalized, thus signaling that the target is present.

Recent work has shown that macaque monkeys exhibit an apparent homologue of the human N2pc component. Woodman, Kang, Rossi, and Schall (2007) implanted surface electrodes into the most superficial layers of the skulls of monkeys trained to perform a demanding visual search task. They found that the posterior lateralized electrodes recorded a positive waveform contralateral to the target. Similar to the human N2pc, this component had a posterior distribution, and its onset became more variable as the search task was made more difficult by increasing the set size of the array. In addition, on trials in which no target was present (i.e., catch trials) this component disappeared, as in human studies of the N2pc (Luck & Hillyard, 1994). These findings suggest that the monkey visual system is a good model for that of the human, particularly given the centrality of this ERP component in accounts like the ambiguity-resolution theory.

The ambiguity-resolution theory is consistent with a large body of evidence. However, its role is as a framework for thinking about how findings from visual attention experiments could be interpreted based on the nature of neurons in the primate visual system. It is still unclear how attention mechanisms can select the relevant neurons to suppress from the mosaic of neurons that exist in high-level ventral stream areas like V4 and IT. Moreover, these neurons performing such selection would need a high degree of spatial resolution and would need to be driven by information regarding the target visual features. The idea that ventral stream areas could be driven by spatially specific, target-selecting areas is plausible based on studies showing that certain areas, such as the FEF, exhibit the connectivity and timing sufficient to implement this filtering (Schall, Morel, King, & Bullier, 1995; Schmolesky et al., 1998). Finally, it should be noted that this idea of using overlapping RF properties of higher-level ventral stream areas draws upon data recorded from macaque visual cortex across a number of studies. These studies suggest that when attention is deployed to one of two objects in a cell's RF, the cell responds as if the attended item is the only object present in the RF (Luck et al., 1997a; Moran & Desimone, 1985). This idea forms the backbone of one of the most influential theories of attention during the last several decades.

BIASED-COMPETITION THEORY

Probably no theory of visual attention was developed based on the experimental findings of nonhuman primates more than was the biased-competition theory of attention proposed by Desimone and Duncan. The biased-competition account is based on the idea that representations compete for access to the limited-capacity mechanisms of the brain. Examples of scarce resources for which representations might compete are the RFs of cells, representational space in working or long-term memory, and access to response execution mechanisms. Some stimuli win the competition to be attended or stored in working memory by virtue of their bottom-up salience. For example, when an object suddenly appears, it is processed with priority over the existing objects in the visual environment of a primate (Jonides & Yantis, 1988; Schmidt, Vogel, Woodman, & Luck, 2002). However, it is not always, or even frequently, the case that the most salient stimulus is the one that we primates are trying to process to complete the task at hand. Desimone and Duncan (1995) propose that the role of attention is to bias these competitions among various stimuli, such that behaviorally relevant representations obtain preferential access to the limited-capacity mechanisms of the brain. This overarching principle of competition between representations can be useful in tying together findings from cognitive psychology, neuropsychology, and neurophysiology (e.g., Bisiach & Vallar, 1988; Chelazzi et al., 1993; Duncan & Humphreys, 1989; Jonides & Yantis, 1988).

The biased-competition theory has gained a prominent place in the minds of visual attention researchers because it continues to provide convincing accounts of findings from single-unit recording studies of primate visual cortex. A study of Reynolds, Chelazzi, and Desimone (1999) provides an excellent example. Reynolds and colleagues recorded from neurons in V2 and V4 of macaques performing a target-detection task in which they were cued to monitor a specific spatial location for the presence of a target shape. The monkeys were either cued to attend away from or toward the RF of the neuron being recorded. To determine the selectivity of the cell being recorded from, the response of the neuron to objects presented individually in the neuron's parafoveal RF was assessed while the monkey fixated a central stimulus in the baseline condition. Some objects elicited more vigorous volleys of action potentials than others due to an individual cell's selectivity for certain stimulus attributes. Other stimuli elicited less vigorous volleys of action potentials. When both stimuli were presented in the RF of a neuron while attention was directed elsewhere, the response of the cell approximated the average of the cell's response to the two objects when presented individually in the RFs. However, when attention was directed to one of the two stimuli in the RF, the response of the cell came to resemble its response when only the attended object was present. This finding provides a near perfect fit with the predictions of the biased-competition account. That is, attention being directed to the location of one stimulus in the limited-capacity RF causes that stimulus to win the competition for representation by the cell. Note that the ambiguity-resolution theory also predicts such a finding, which probably is not surprising, given that these two models of attention are theoretically related.

The biased-competition account has been applied to visual search tasks in considerable detail. This theory proposes that the visual system becomes biased to process target-like objects by maintaining a representation of the expected target in visual working memory. This will tend to strengthen matching representations, allowing them to compete more effectively for limited resources. The strongest evidence for the maintenance of target templates during search comes from single-unit recording studies. Recall that Chelazzi et al. (1993) recorded from neurons in the temporal lobe of macaque monkeys while they performed a delayed match-to-sample visual search task. They found that the neurons coding the target maintained an elevated firing rate during the cue-to-target delay intervals. This elevated firing rate was interpreted as evidence that a memory representation was being maintained during the retention interval. In addition, it was hypothesized that this memory representation provides a biasing signal to those neurons that perform perceptual analysis. This biasing signal increases the baseline firing rate and therefore induces a competitive advantage for neurons that selectively respond to the searched-for target.

In the biased-competition theory, visual working memory essentially plays the role of the top-down biasing signal. By holding a representation of the target in visual working memory, the rest of the perceptual machinery of the visual cortex is biased to dedicate its limited capacity to similar inputs. Although the findings of the single-unit studies provide valuable insight regarding how visual search tasks are performed when the target is cued shortly before the presentation of the visual array, it is quite possible that visual search is performed differently when the task does not explicitly require visual working memory storage of the target. In addition, humans may have the ability to use intervening strategies that nonhuman primates either do not have available or do not avail themselves (see Woodman & Luck, 2007). It is also critical to note that typical visual search paradigms with human subjects use methods in which the target remains constant throughout the entire experiment. Thus, there is a potential problem in drawing conclusions about human visual search data based on electrophysiological data recorded from monkeys performing search tasks in which the target changed every trial or every several trials.

A recent study of humans performing a visual working memory task and visual search task concurrently emphasizes the limitations of cross-species generalizations when the tasks are qualitatively different. Woodman, Luck, and Schall (2007) had observers begin by maintaining four objects in working memory, thus filling working memory to capacity (i.e., the maximum number of representations that can be held in working memory, see Vogel, Woodman, & Luck, 2001); then, during the ensuing memory retention interval, they performed a visual search task. Following the search task, subjects had their memories tested for the four objects that were shown five seconds before. The crucial manipulation was that, in one condition, the identity of the target changed on every trial, similar to the paradigm used with monkeys (Chelazzi et al., 1993). To do this, each trial began with a cue indicating the shape of the target that subjects were to search on that trial. The other condition was identical, except that, for each observer, the cue was randomly chosen and did not change. That is, the cue was the same on every trial, as is typically done in visual search experiments with humans, in which the subjects usually search for the same object or pair of objects for the entire experiment (Wolfe, 1998).

Woodman et al. (2007) found that when the search target was the same across trials, there was almost no interference between the concurrent visual search and visual working memory task; that is, the efficiency of visual search was the same across conditions, and the size of the search array did not systematically change performance in the working memory task. This result replicates a previous report (Woodman, Vogel, & Luck, 2001). However, when the identity of the cued target changed from trial to trial, as in experiments with monkeys, the efficiency of visual search was significantly impaired. The concurrent memory task showed that the more demanding the search task, the worse performance got for remembering the existing visual working memory load. These findings suggest that when the visual system is set to search for the same object for trial after trial, very little demand is placed upon visual working memory with long-term memory representations apparently biasing attention mechanisms to the targets. These long-term memory representations are likely playing the role of preparing the visual system to select the task-relevant item (Logan, 1978).

The findings of Woodman et al. (2007) using behavioral measures of processing in humans fit nicely with a recent lesion study of macaque monkeys. These studies converge in showing that attentional selection by cells in ventral stream areas like V4 need only draw upon working memory mechanisms during frequent target-identity changes in a visual search task. Rossi, Harris, Bichot, Desimone, and Ungerleider (2001) trained monkeys to perform a visual search task in which the color of the fixation point indicated the identity of the target in the search array. The monkeys made a manual response to indicate the orientation of the target-colored item. The brains of these monkeys were then split along the corpus callosum, and the entire prefrontal cortex of one hemisphere was removed. By making a split-brain preparation, the intact hemisphere served as a within-animal control for the lesioned hemisphere. By all accounts, the prefrontal cortex is the part of the brain in which working memory functions originate (Goldman-Rakic, 1996; Miller & Cohen, 2001; Miller, Erickson, & Desimone, 1996). Thus, if visual working memory is essential for monkeys to perform visual search, then search in the lesioned hemifield should be impossible. However, Rossi and colleagues found that when the cued target-defining color rarely changed (e.g., every 100 trials), performance in the lesioned hemifield was essentially as good as when the search items were presented to the good hemifield. However, when the search target changed frequently (such as every trial), performance was severely impaired in the lesioned hemifield compared to the good field. This finding is consistent with the findings from the dual-task experiments with humans described above.

Rossi and colleagues (2001) report an additional finding that is truly groundbreaking. When recording from V4 cells in the hemisphere without prefrontal cortex, the cells responded more vigorously when the target is in their RF than when a distractor is present, provided the target changes rarely. In addition, the timing of this firing rate effect is essentially the same as that observed in the good hemifield and in previous reports (De Weerd, Peralta, Desimone, & Ungerleider, 1999). This evidence for intact target discrimination when prefrontal cortex is absent also supports the view that working memory resources are not necessary for visual attention to select the relevant target when target identity is stable. This provides another example of how findings from monkeys and humans converge on an answer to how the visual system can deploy attention in the absence of a visual working memory template of the searched-for item. Theories of automaticity propose that, with repeated task performance, the task can be performed via long-term memory retrieval (Logan, 1978, 1988).

At this point, the theories of attention and empirical studies of primates that we have focused on have sought to explain how the visual systems of animals find and localize task-relevant target objects. However, another theory of attention has avoided this question of selecting relevant features of objects, but instead has focused on how attention might select relevant locations.

PREMOTOR THEORY OF ATTENTION

The theory of biased competition and the previously discussed theories have been primarily concentrated on the mechanisms responsible for selection of the task-relevant features (i.e., the color red) in visual cortex via attention mechanisms. The premotor theory of attention differs in that it is primarily concerned with how certain locations are selected by covert attention. This will remind readers of feature-integration theory, in which location plays a special role in the selection of stimuli. The premotor theory of attention has its roots in studies of humans performing attentional cuing tasks, but has gained traction through neurophysiological studies in non-human primates.

The premotor theory of attention was first elaborated by Giacomo Rizzolatti and his colleagues (Rizzolatti, Gentilucci and Matelli, 1981; Rizzolatti, 1983). The basic assertion of this theory is that selecting a stimulus covertly (without moving the eyes) is performed by the same network of neurons in the brain that control overt selection (moving the eyes to something). In this way, it has the advantage of proposing a unitary superordinate system for selective attention. Rizzolatti and his colleagues (e.g., Rizzolatti et al., 1981) proposed that the premotor theory of attention can be viewed as a naïve explanation for behavioral effects of attention. This is supported by the lengths many attention researchers go to in order to rule out the explanation that supposed attention effects are not simply due to eye movements (Duncan, 1984), particularly in studies of monkey neurophysiology (Thompson et al., 1997).

The premotor theory of attention has been supported using observations made during both anatomical and physiological studies. One of the central thrusts of the premotor theory of attention is the observation that, during neurophysiological recordings, areas controlling gaze also contain cells that participate in the deployment of covert visual attention. As discussed previously, neurons in the FEF have been proposed to be a good candidate for the top-down attention effects observed in posterior visual cortex. The FEF is known to exert an important role in saccade generation (for a review, see Schall & Thompson, 1999), and the FEF has direct anatomical projections to visual areas that are modulated by spatial attention, including are-as V2, V3, V4, medial temporal area (MT), medial superior temporal area (MST), and areas in the temporal lobe (e.g., TE and TEO). The FEF also has connections to other potential sources of top-down attentional control, such as area LIP and the superior colliculus (Stanton et al., 1995).

In an important study that was interpreted using the premotor theory framework, Moore and Fallah (2001) measured changes in contrast sensitivity immediately following electrical stimulation of a region of the FEF. Electrical stimulation of the FEF causes the eye to move from the fixation point to a particular location. The specificity of the evoked movement observed when stimulating the FEF is sometimes referred to as the *movement field* of the stimulated neurons. In their study, Moore and Fallah determined the movement field of each stimulated region of the FEF. The monkey had been trained to detect a brief change in the luminance of a target stimulus to earn a juice reward. The visual target was presented such that it either fell inside or outside the movement field of the stimulated site in the FEF. The distractors were presented randomly at locations throughout the entire visual field, in order to increase the difficulty of the task. On a randomly selected subset of trials, some current was induced and then calibrated to be just too weak to evoke an eye movement. Then, a staircase procedure was used to determine the minimum luminance change required for the monkey to achieve a threshold level of performance on trials with and without stimulation. Moore and Fallah found that the stimulation of most of the FEF sites reduced the level of luminance contrast required to reliably detect the change. This finding is illustrated in an example session in Figure 18.6, which shows the contrast generated by the staircase procedure used to determine perceptual threshold. The effect of stimulation was to make the animal more sensitive to smaller changes in the contrast of the visual stimuli. In other words, they found that stimulating this oculomotor area also affected visual processing, thus supporting the theory that the same neuronal networks that control motor movement of the eyes also control attentional selection.

In a subsequent study, Moore and Armstrong (2003) recorded from neurons in V4 while performing stimulation in a region of the FEF. The authors first had to identify the specific site in the FEF whose movement field overlapped with the RF of a set of neurons in area V4. Then they measured the effect of the FEF microstimulation on neuronal responses in V4 neurons. Moore and Armstrong report that the FEF stimulation caused the neuronal response to increase in area V4. For most sites, the average response on microstimulation trials appeared clearly elevated following electrical stimulation relative to nonstimuluation trials. This increase in response did not simply reflect a tonic, antidromic activation from the FEF as there was no increase in baseline activity when the FEF stimulation occurred in the absence of a visual stimulus in the RF. Instead, these findings show that stimulation in the FEF changes the sensitivity of V4 neurons to processing perceptual inputs.

In a final set of conditions, Moore and Armstrong (2003) found that the FEF microstimulation appeared to filter out the influence of distractors. In this set of experiments, they tested the suppressive influence of distractor stimuli appearing outside the RF by placing a second stimulus outside the RF of the recorded neuron. The addition of a distractor outside the classical RF can lead to a reduction of the response elicited by the stimulus in the center. In particular, when the center stimulus was the preferred stimulus for the cell, the distractor outside the RF elicited surround inhibition. Moore and Armstrong found that when they stimulated the FEF, the neuronal response increased. This increase was more than twice the increase observed in the absence of an extra-RF stimulus, consistent with the proposal that stimulation modulated center-surround interactions in V4 neurons when microstimulation was delivered in the FEF.

Different psychophysical findings have also been proposed to support the premotor theory of attention. However, the most commonly cited evidence is the multiple behavioral experiments with human subjects that have shown that the sensitivity to a stimulus increases at the location targeted by an impending saccade (Chelazzi et al., 1993; Hoffman & Subramaniam, 1995).

Testing the premotor theory requires specifying the anatomical level at which the coupling mechanism between eye movement and attention maps onto the brain. If the premotor theory of attention

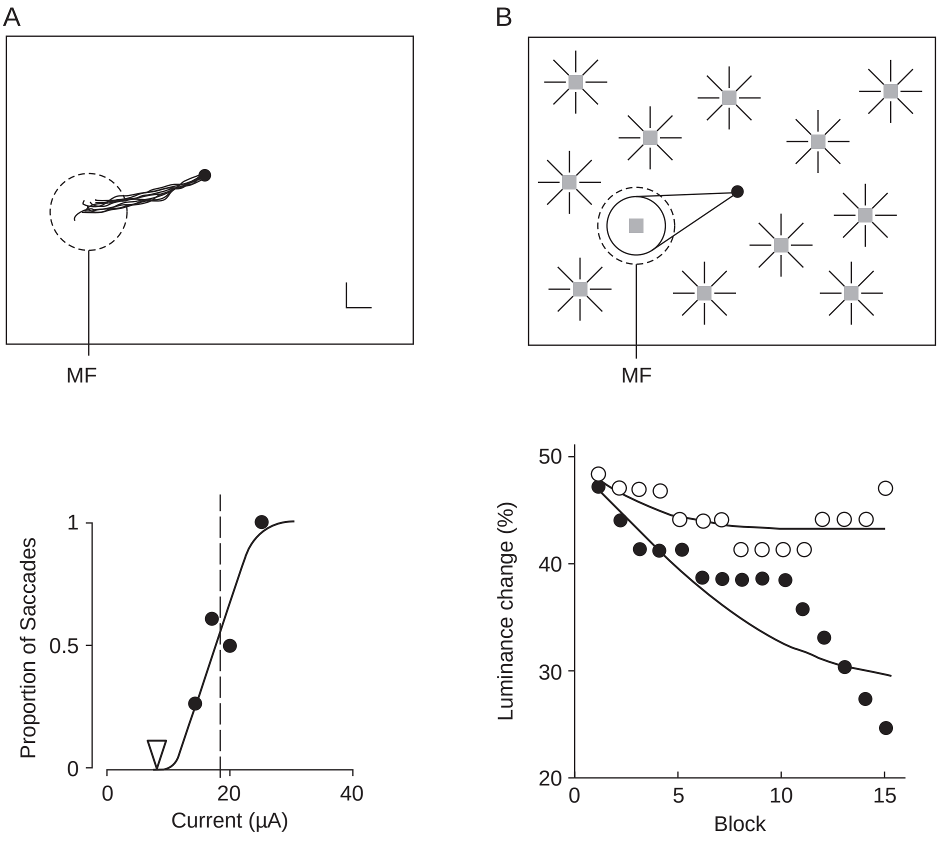

FIGURE 18.6 Representation of the different steps during the experiment session and the effect of stimulation on monkeys performance. **A**: *Top*: First, individual saccade vectors were found using suprathreshold stimulation in the frontal eye field (FEF). *MF* represents the movement field associated with the effect of microstimulation at that particular site in the FEF. The eye movement traces show saccades evoked on trials in which a suprathreshold current of 25 μA was used. Scale bar represents 2 degrees, visual angle vertical and horizontal. *Bottom*: The proportion of evoked saccades measured at different current levels. Open arrowhead indicates the subthreshold current (9 μA) used during the spatial attention task. **B**: *Top*: Depiction of the attention task performed with the target positioned in the MF. *Bottom*: Staircase functions used to obtain target change thresholds (% Michaelson contrast from background) with (*filled symbols*) and without microstimulation (*open symbols*). Each set of points is fitted with an asymptotic function to estimate threshold. From Moore, T., & Fallah, M. (2001). Control of eye movements and spatial attention. *Proceedings of the National Academy of Sciences of USA, 98,* 1273–1276. Reprinted with permission.

refers to a particular mechanism for which the populations of neurons instantiating saccade preparation are the same neurons that modulate the activity of extrastriate visual cortex, then some recent anatomical results challenge this claim (Pouget, Emeric, Leslie, & Schall, 2007). In their experiments, Pouget and colleagues examined the distribution of neurons in the FEF of macaque monkeys, labeled by simultaneous injections of different retrograde tracers in the superior colliculus (SC)—a subcortical structure that is known to receive motor signal from the FEF—and in extrastriate visual areas V4 and TEO—cortical structures that are known to be modulated by attention. As expected, the injection into the SC labeled numerous neurons in deep layers of the FEF, known to contain cells that contribute to eye movement control. In fact, all the neurons projecting from the FEF to the SC were found in layer 5 of the FEF.

The results were significantly different for the projection from the FEF to V4/TEO. In contrast to the neurons projecting to the SC, the labeled cells in the FEF that project to extrastriate visual cortex were mainly localized in the more superficial supragranular

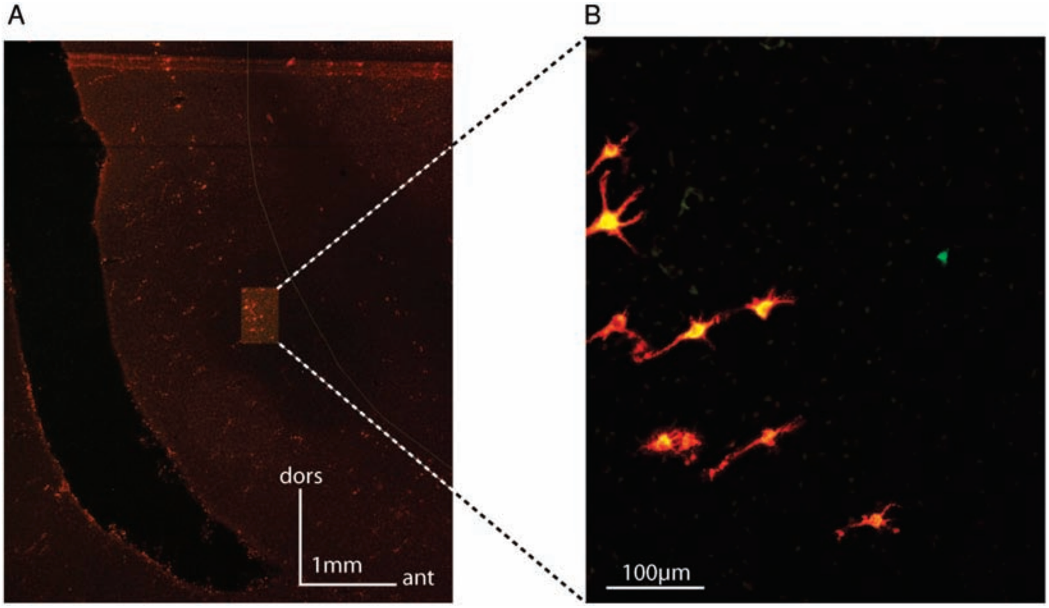

FIGURE 18.7 Low-magnification photomicrograph of the arcuate sulcus. Infragranular region of the frontal eye field (FEF), where neurons labeled with Diamidino yellow injected into V4 and Fluororuby injected into superior colliculus (SC), is highlighted. Limit occurs between cortex and white matter (*thin yellow line*). Scale bar representing 1 mm and orientation of the section are shown ant. (anterior), dor. (dorsal). *Left*: Superimposed photomicrographs of the FEF neurons labeled with Diamidino yellow and Fluororuby injected respectively into V4 and SC regions. The neurons labeled by injection of Fluororuby into SC (*red cells*) and Diamidino yellow into area V4 (*green nucleus*) are represented by a composite image of the same section photographed twice using different filters. Note the absence of double-labeled neurons and the depth of the neurons projecting to V4. Adapted with permission from Pouget et al. (2007).

layers. Furthermore, for the few neurons in the FEF that were found in deep layers and that do project to V4/TEO, none of them also projects to the SC. No double-labeled cells projecting to V4/TEO and the SC were found in the FEF (see Figure 18.7).

On one hand, the connectivity of the brain appears to challenge the premise that shifting attention is accomplished by the population of neurons that prepare saccades. On the other hand, if the mechanism proposed by the premotor theory of attention refers to entire brain structures or circuits comprised of heterogeneous populations of neurons performing different functions (e.g., some neurons shifting attention by selecting stimuli and others preparing saccades), then the premotor theory of attention can still be considered valid. However, by proposing such general mechanisms, the premotor theory of attention would lose the parsimony that is its hallmark. In addition, this would essentially make the premotor theory of attention mimic more traditional stage-like models of information processing (Sternberg, 2001).

Taken together, this recent neuroanatomical work suggests that it is not the same cells that control gaze and are connected with visual cortical areas like V4, contrary to the strong version of premotor theory. Supporting these conclusions, anatomical reconstruction of recording sites shows that neurons located in the supragranular layers of the FEF are active during the process of target selection and attentional allocation (Thompson, Hanes, Bichot, & Schall, 1996). These neurons select salient targets even if no saccade is produced (Thompson et al., 1997, 2005). Therefore, it is very likely that the signal extrastriate cortex receives from the FEF relates to target selection and not to saccade planning.

CONCLUSION

The notion of attention was proposed more than a century ago. However, in recent decades, a number of models of attention have been developed based on neurophysiological and anatomical data from monkeys. Monkeys serve as excellent models for the visual systems of all primates, including humans.

So far, comparative electrophysiological studies support this claim (Luck et al., 1997b; Woodman et al., 2007). Many of these models of attention attempt to explain how attentional deployment through space is directed to task-relevant objects. This is based on the logical assumption that what primates interact with in their environments are objects, and not points in space devoid of reward value.

Although studies of the monkey visual system and models of visual attention have begun to address many important issues about how we process the most pertinent information and deprioritize the rest, much is still unknown. For example, many models of the visual system assume a strictly feedforward architecture (e.g. Felleman & Van Essen, 1991), but this need not to be the case. Studies of timing and connectivity support the idea that information may be processed in a reiterative manner (e.g., Lamme, 1995; Schall et al., 1995). Indeed, a number of models have emerged that explicitly propose that a variety of cognitive operations are best accounted for by models with roles for both feedforward and feedback in the visual system (Di Lollo, Enns, & Rensink, 2000; Lamme & Roelfsema, 2000). Although neuroanatomy supporting the existence of feedback connections in the visual system is uncontroversial, much work still remains to determine exactly what mechanisms of selection are handled via feedforward and feedback of visual information.

Another lingering issue is how attentional selection is implemented at a mechanistic level. Specifically, the synaptic mechanisms that control dynamic attentional selection are unknown. However, it has been established from anatomical studies that the circuitry in primary visual cortex with direct excitatory inputs and indirect inputs from inhibitory interneurons might be sufficient to generate this type of control over the discharge of neuronal activity (Anderson & Van Essen, 1987; Crick & Koch, 1990; Desimone, 1987).

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