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GLOSSARY

attentional blink Following the identification of a target in a rapid sequential stream of stimuli, there is temporary impairment in identifying a second target stimulus that occurs shortly after the first. It is as if attention has “blinking” after identifying the first target, preventing subsequent target detection.

binding problem The problem of determining which elementary visual features, such as color, shape, or size, belong to the same stimulus. Spatial attention allows elementary features to be bound or grouped together.

grouped-array representation A spatial representation that contains perceptual grouping information. Image features (e.g., line segments) are grouped to form larger structures, such as surfaces or regions.

neglect (also extinction) A neuropsychological disorder of visual attention that follows damage to the posterior parietal region. Patients with neglect fail to attend to events on the side of space opposite the lesioned hemisphere. As patients recover from neglect, they demonstrate extinction, a form of transient neglect that occurs when events occur on both sides of space simultaneously.

object-centered representation A representation of an object that encodes the properties of the object, such as parts, relative to a reference point on the object itself, such as a principle axis.

visual search The process used to find a visual target (i.e., how you find what you are looking for). Both elementary visual features, such as color, shape, or size, and focal visual attention combine to guide the search for a target.

At any given moment, the sensory systems in your brain are receiving thousands of simultaneous environmental inputs. Some of these inputs are relevant to your current behavior and others are irrelevant. The visual words printed on a page are relevant to reading, but the visual impression of the desk on which the pages lie is irrelevant to reading. Furthermore, some of the inputs in one modality have correspondences with inputs in another modality, as in the link between a person’s visual appearance and the speech uttered by that individual. Because we cannot process all inputs simultaneously, there must exist processes that select some inputs and filter out others. These processes collectively are referred to as “attention.”

The study of attention has a long history in both the cognitive and brain sciences. Although early research implicitly assumed that attention is a single, monolithic process, an emerging view that we endorse is that there are multiple forms of attentional selection. Attention can select stimuli at specific locations in vision, audition, or touch; attention also can select entire objects, not just locations. Furthermore, attention selects not only stimulus inputs but also mental functions such as behavioral goals or tasks: You can attend to the task of reading instead of the task of identifying a font type. To understand attention requires studying these multiple forms of selection, their similarities and dissimilarities, and their neural foundations.
I. CONTROL OF VISUAL SPATIAL ATTENTION

A. Multiple Constraints on Selection: A Framework

Perhaps the most complete understanding of attentional selection is in the visuospatial domain, in which stimuli at specific locations are selected for processing. What are the critical parameters that determine those inputs that receive attention and those that do not? This is the question of attentional control.

There are different parameters or processes that can influence attentional control. Two general classes of control are top-down sources that arise from the current behavioral goals and bottom-up sources that arise from sensory stimuli present in a scene. These two sources can be illustrated by considering visual search, the act of looking for a visual target among distractors (e.g., finding a friend’s face in a crowd). In a typical visual search task, observers are instructed to search for a particular target, such as a black vertical line, that appears in a field of distractors (Fig. 1). The target description can be conceptualized as a “template” temporarily stored in memory that can influence visual search in a top-down manner; as an observer, you would actively attempt to look at black and vertical items. The scene presented in a visual search task provides the bottom-up information that is searched; this information indicates where objects are located and which features are present at each location. Effective visual search would require finding a balance between the top-down information and the bottom-up information. An example of an effective search is searching for a single feature, such as a black vertical line among white vertical lines (Fig. 1a). In this example of a feature search, color uniquely defines the target, and the bottom-up information is consistent with the top-down information in constraining where an observer should search. A less efficient search would involve searching for a conjunction of features, such as a black vertical line among black horizontal lines and white vertical lines (Fig. 1b). In this search, any single piece of bottom-up information is not unique to the target item, so the bottom-up constraints are weaker than in the feature search. Top-down constraints would be required to resolve the competition among the input items. In general, the control of spatial attention can be viewed as a “biased competition” model: Competition among bottom-up inputs is biased (i.e., some of the inputs are favored) by top-down inputs, such as a target template.

How is visual search controlled, particularly when search is inefficient and not determined by bottom-up information? Two possible control modes have been hypothesized for visual search. The serial search account proposes a sequential control of attention in which attention shifts from one item to the next until the target is found. The parallel search account proposes that attention is allocated to every item simultaneously, with less attention available for each item when a large number of items must be searched simultaneously. Much debate has surrounded the serial/parallel dichotomy, and current perspectives on the issue focus on the efficiency of search and not on an absolute dichotomy. Although there is evidence for a serial control process, this serial control process must be implemented in the brain’s parallel hardware. Furthermore, if multiple attention systems exist, then some forms of attentional control may be more serial and others may be more parallel.

The control of spatial attention has also been examined by directing attention to a location before a target event occurs. In these “spatial pre-cuing” tasks, observers are required to detect or identify a target item that appears at a peripheral location. Before the target appears, one location is precued by an arrow pointing to the location, a flash of light at the location, or some similar means. The subsequent target usually appears at the cued location (a “valid” trial), although it may occasionally appear at an uncued location (an “invalid” trial). Because the cue is usually valid, observers are motivated to attend to the cued location, and observers typically detect valid location targets more quickly and accurately than invalid location targets.

The type of precue used can bias attentional control to favor bottom-up factors or top-down factors. For example, if the precue is an abrupt luminance change (e.g., a flicker in the visual periphery), attention is automatically captured by the bottom-up input, irrespective of the observer’s intentions. Such “exogenous” cues are extremely difficult to ignore and they

Figure 1  Sample visual search task: search for a black vertical line. (a) Feature search in which the target pops out from a homogeneous background. (b) Conjunction search in which the target does not pop out because the distractors share both black and vertical features with the target.
are not interfered with by concurrent tasks such as a memory task. In contrast, if the precue is a symbol such as a centrally presented arrow that points to a location, attention will move to the cued location only if the observer wants to shift attention, and when attention does move it moves more slowly. These “endogenous” cues are not automatic: They can be ignored, and they are interfered with by concurrent tasks. Because endogenous cues are dependent on task-related goals and observers’ expectancies, they involve top-down control processes. In many spatial precuing tasks, the control of attention involves a balance between bottom-up and top-down factors. Although bottom-up onset cues capture attention, they may be influenced by top-down attentional control settings (e.g., expectations of where the target will appear).

B. Neuroanatomy of Control

1. Neuropsychology: Neglect and Extinction

There are undoubtedly several cortical and subcortical areas that participate in the control of spatial attention. The pulvinar nucleus of the thalamus, for example, is involved in filtering or suppressing irrelevant stimuli in a cluttered display. However, the cortical region that plays the most significant role in the control of spatial attention is the posterior parietal region. Damage to the parietal region (especially the right parietal region) in humans results in a profound attentional impairment referred to as neglect. Neuropsychological patients with neglect fail to pay attention to stimuli falling on the side of space opposite the lesion (the contralesional side). For example, a patient with damage to the right parietal lobe may fail to acknowledge a person sitting on the left, may fail to eat food on the left half of a plate, and may fail to read words on the left half of a page. Neglect occurs soon after damage to the parietal region. As a patient recovers and the neglect becomes less severe, patients can process a single stimulus presented in the contralesional visual field. These recovering patients show another disorder, however, referred to as extinction: When two stimuli are presented simultaneously in opposite visual fields, patients will extinguish, or fail to notice, the stimulus in the contralesional field. In other words, extinction patients exhibit neglect of contralesional stimuli only in the presence of ipsilateral stimuli. Both neglect and extinction appear to be disruptions of the ability to control spatial attention and deploy it to the contralesional field.

Neglect can be observed in spatial precuing tasks. In these tasks, extinction patients can detect and identify targets presented in the contralesional visual field; furthermore, these patients can use exogenous precues to allocate attention to the contralesional field prior to the appearance of the target. However, when a precue appears in the ipsilesional field and a target appears in the contralesional field, these patients are much slower to detect the target than when the contralesional field is cued and the target appears in the ipsilesional field. That is, they are impaired primarily when they are cued to the good field and then the target appears in the bad field. A straightforward interpretation of these results is that the contralesional and ipsilesional sides of space compete for attention. A bottom-up factor, such as a spatial precue, can bias the competition in favor of the cued field. The effect of parietal damage is to weaken the ability of the contralesional field to compete for attention. When both the cue and the target are in the same field, there is no competition and the target can be detected quickly. However, when the good field is cued and the target appears in the bad field, the good field wins the competition for attention even though the target is in the bad field, leading to abnormally slow responses.

What aspect of attentional control, bottom-up or top-down, is disrupted in these patients? Although parietal-damaged patients appear to have intact perceptual processing, the disorder of attention appears to involve bottom-up control parameters: Attention is not captured effectively by contralesional inputs. Furthermore, some forms of top-down attentional control appear to be intact in parietal-damaged patients. These patients can make use of top-down expectancies or task-relevant goals. For example, a contralesional stimulus may not be extinguished if the ipsilesional stimulus is irrelevant to a task and the patient is instructed to ignore this ipsilesional stimulus. Presumably, the top-down control of attention is intact in these patients and biases attention to select the relevant item in the bad field.

2. Neuroimaging Studies

Neuroimaging studies also indicate a central role for the posterior parietal lobe in spatial selection. Because the whole brain can be examined using some of these techniques, other brain regions that influence spatial attention can be observed. Observing multiple neural sites simultaneously may be useful for isolating the sources of bottom-up and top-down control.
Separate neuroanatomical sources for two forms of control is suggested by positron emission tomography (PET) studies of performance in the spatial precuing task. Observers were presented with sequences of visual targets that appeared in a predictable sequence that would engage endogenous attentional allocation. The predictable sequences were leftward or rightward appearances of the target; the target first appeared near fixation to the left or right and then continued to move in the same direction in a majority of the trials. For example, if the first target first appeared slightly to the right of fixation, the second target would likely occur to the right of the first target’s position; similarly, the third target would likely occur to the right of the second target, and so forth. A predictable sequence allows observers to anticipate the next target location and endogenously allocate attention to that expected location. Thus, the peripheral targets in this task involve both exogenous and endogenous components—the appearance of the target is an exogenous luminance change and the predictable sequence allows observers to anticipate the next target and allocate attention endogenously. Two neural regions of interest exhibited increased blood flow during this task: the superior parietal lobe near the postcentral sulcus (near Brodmann’s area 7) and the superior frontal cortex (near Brodmann’s area 6).

To distinguish the superior parietal and superior frontal areas by their sensitivity to the exogenous and endogenous components, observers performed a control task. This control task presented the same peripheral targets in a predictive sequence, but instead of detecting these peripheral targets observers detected targets presented at fixation. Exogenous orienting would occur to the peripheral targets, even though these targets were irrelevant to the observers’ task. However, endogenous attention would be directed to the central targets because these were the task-relevant stimuli. When endogenous shifts of attention were eliminated in this manner, the superior frontal areas were no longer active, but the superior parietal areas continued to be active. These results suggest that superior parietal regions are involved in the exogenous, bottom-up control of spatial attention and that superior frontal regions are involved in the endogenous, top-down control of spatial attention.

The bottom-up control of spatial attention coordinated by the superior parietal lobe appears to involve spatial selection only. If other visual attributes are selected, such as a color or a shape, the superior parietal lobe does not appear to show increased blood flow as measured by PET, although other extrastriate visual areas are activated in response to different visual attributes. For example, in searching for a target defined by color, blood flow increased in the left dorsolateral occipital lobe and in the left collateral sulcus. Searching for a target defined by movement or by shape resulted in increased blood flow in other extrastriate areas. Thus, there appears to be a large network of extrastriate visual areas that mediate bottom-up aspects of attention to different stimulus attributes. Furthermore, PET results suggest that each of these areas could receive feedback from frontal lobe areas—areas that may represent task-relevant goals useful for allowing one stimulus attribute (e.g., color) to be selected from an image containing many attributes (e.g., color, shape, and movement).

There may exist some extrastriate visual regions that participate in attentional control across different visual attributes. Recent functional magnetic resonance imaging (MRI) results have found activation in two parietal lobe areas across three very different attention tasks: (i) a spatial shifting task similar to that described previously, (ii) an object matching task in which observers reported whether two attended objects were the same or different, and (iii) a nonspatial conjunction task in which observers searched for a target letter in a sequential stream of colored letters. These two parietal subareas seem to be involved in a wide range of visual selection, contrary to the PET results discussed previously that demonstrated no parietal involvement in visual search for targets defined by color, shape, or motion.

However, there is a resolution to the apparent discrepancy between a general attentional involvement of parietal areas and a spatial-specific role for parietal areas: Parietal lobe attention areas may control the suppression of visual distractors. Functional MRI studies that exhibit parietal activation across attention tasks required irrelevant stimuli to be ignored; PET visual search studies that did not exhibit parietal activation across tasks involved displays containing only task-relevant stimuli. In the biased competition account, parietal lobe areas may receive feedback from frontal lobe areas that allow parietal regions to suppress distractors and act as a “gate” for other extrastriate visual areas.

C. Neurophysiology of Control

As with neuroanatomical studies of attentional control, there has been a substantial amount of research
on single-neuron recordings from a range of brain areas. Those regions relevant to the biased competition framework are regions in the parietal and frontal lobes; other important areas, such as the superior colliculus or pulvinar, will not be reviewed here.

Many neurophysiological studies investigate overt spatial attention, in which the eyes overtly move to an attended location, in contrast to covert spatial attention, in which the eyes do not move. One consequence of overt shifts of spatial attention is that stimuli in a visual scene occupy different retinal locations from one eye movement to the next. Covert spatial attention appears to shift before the overt eye movement, allowing the representation of a visual scene to be updated prior to the eye movement. Neurons in the parietal lobe appear to play a role in controlling the focus of spatial attention.

Evidence for parietal lobe involvement in covert shifts of spatial attention derives from single-unit recordings from the lateral intraparietal (LIP) area in monkeys. Neurons in LIP have topographically mapped receptive fields that respond to visual stimulation (Fig. 2a). When a monkey makes an eye movement to a new location, the receptive field of a LIP neuron will also fall in a new location (Fig. 2c). Prior to the eye movement, however, a LIP neuron will respond to visual stimuli at a location based on the planned eye movement that has not been executed (Fig. 2b). That is, the receptive fields of LIP neurons are remapped in anticipation of an eye movement. This shift of the LIP representation of space may provide the neural mechanism for covert shifts of attention that precede and anticipate overt shifts involving eye movements.

The ability of LIP neurons to update their representation of space implies that this area receives inputs regarding the intended eye movement. This input likely comes from the frontal eye fields (FEFs), suggesting that updating the spatial representation is based on endogenous, top-down factors. Neurons in LIP are also able to alter their firing based on exogenous, bottom-up factors, such as the abrupt appearance of a stimulus in a LIP neuron’s receptive field. The appearance of a new stimulus inside a LIP neuron’s receptive field results in a large increase in the neuron’s firing rate. However, if an eye movement brings a stationary stimulus into the neuron’s receptive field, only a weak neural response is produced. The abrupt appearance of a stimulus is the critical parameter for evoking a large neural response: If a stimulus appears shortly before an eye movement (approximately 400 ms), there is a large neural response when the eye movement brings the new stimulus into the LIP neuron’s receptive field. The “newness” or salience of the stimulus, indicated by the recency of its appearance, in part controls the response of LIP neurons and, presumably, covert spatial attention.

Finally, consistent with neuroimaging data, frontal lobe areas participate in the control of attention. In visual search, the FEF is involved in selecting the target to which an eye movement will be directed. Monkeys viewed displays that contained a target that differed from a field of distractors by one feature (Fig. 1a); they were trained to make an eye movement to this target. Prior to the saccade, FEF neurons discriminated target items from distractor items. If the target fell within a FEF neuron’s receptive field, the neuron

Figure 2 Remapping of receptive fields in area LIP in response to an intended eye movement. (a) The center tree is fixated, and the sun falls within an LIP receptive field. (b) An eye movement to the other tree is planned, and the LIP neuron’s receptive field is remapped in accordance with the intended movement. The cloud falls within the receptive field, even though the eyes remain fixated on the center tree. (c) The eye movement is performed, allowing the second tree to be fixated.
responded vigorously; if a distractor fell within the receptive field, the neuron responded weakly. Additional studies demonstrated that the enhanced firing of these FEF neurons was not in response to a bottom-up capture of attention by the odd item in the display. Other monkeys were trained to make eye movements to a target defined by color (e.g., make an eye movement to any white target). If a monkey trained to move to a white target viewed Fig. 1a, this monkey would respond by generating an eye movement to any of the white bars. Despite the presence of multiple targets in this situation, FEF neurons continue to show larger firing rates when targets fall in their receptive fields than when the single distractor falls within their receptive field.

In addition to FEF, other areas in prefrontal cortex participate in attentional selection. Many studies implicate dorsolateral prefrontal areas in selection; these studies examined search tasks in which the monkey first sees a cue object that depicts the target for which the monkey must search. Following the presentation of the cue, a display of objects appeared, and the monkey had to search for and remember the location of the target object. During the presentation of the search array, the activity of neurons in the dorsolateral prefrontal cortex was sensitive to the visual attributes of the target only; the distractors were effectively filtered out and did not influence the response of prefrontal neurons. Complementary studies have been performed in extrastriate regions such as the inferior temporal cortex with similar results. The selectivity to target attributes occurs earlier for prefrontal neurons than for inferotemporal neurons, suggesting that target selection first occurs in frontal areas and provides the top-down target template that guides selection in extrastriate areas.

II. EFFECTS OF VISUAL SPATIAL ATTENTION ON PERCEPTION

A. Types of Effects

Having previously discussed how spatial attention can be controlled to focus on an item, we now turn to the effects of attention: How is an attended stimulus processed differently from an ignored stimulus? For example, the representation of an attended item could be either enhanced or suppressed relative to distractor items. An attended item could also integrate all the visual attributes of the attended stimulus (e.g., the color, shape, and size of the stimulus).

1. Locus of Selection: Where Does Attention Have Its Effect?

Since the beginning of attention research, many studies and theories have examined whether attention operates at an early stage of processing (early selection) or at a late stage (late selection). The early selection account proposes that attention operates prior to stimulus identification. Thus, in a visual search task (Fig. 1), an item would be selected first by directing attention to its location and then fully identifying it (e.g., “black vertical line”). The late selection account proposes that attention operates after all stimuli have been identified to some degree; in visual search, all the items would be recognized in parallel and only the target item would be selected for storage in working memory and for control over behavior.

Under a biased competition account in which multiple forms of attentional selection occur, the early versus late debate has no absolute answer; some forms of attentional selection necessarily will occur earlier or later than others, allowing for both early and late selection. The main issue then becomes determining where effects occur for a given type of attention, such as spatial attention.

Numerous behavioral studies of spatial attention have supported an account in which items are selected at an early sensory level. If a spatial cue orients spatial attention to a region of space, targets appearing at that location (validly cued targets) are detected faster and more accurately than targets appearing elsewhere (invalidly cued targets). Using a signal detection theory approach, performance in such luminance detection tasks can be traced to changes in perceptual sensitivity, independent of changes in response bias. These changes in the sensitivity of perceptual processes also have implications for the second possible effect of spatial attention—that of sensory gain control.

2. Sensory Gain Control

One hypothesized effect of spatial attention is that it may control the gain or amplification of sensory information transmission. Sensory amplification may increase the signal-to-noise ratio between attended and unattended items. As with an early locus for attentional effects, behavioral evidence supports a sensory gain control effect of spatial attention. Because spatial
precues produce a change in perceptual sensitivity, it appears that spatial attention enhances or increases the gain of target items that appear at an attended location.

3. Binding the Attributes of Objects

Another potential effect of spatial attention is that it binds together the various attributes of a stimulus. In cluttered visual scenes that contain many objects (Fig. 1b), the presence of different attributes such as color and orientation is confusing: How does a viewer know that the color “black” belongs to a vertical line when both the color black and vertical lines are present? This question illustrates the binding problem: the difficulty of knowing which attributes belong together by virtue of being aspects of a single object.

Spatial attention may provide the “glue” that binds together the attributes of objects. The probability of binding errors (misconjunctions of feature attributes) can be increased by presenting brief displays while attention is broadly distributed. In such a situation, if a display contained a blue triangle and a red square, observers may occasionally report perceiving a red triangle or a blue square. If observers focus spatial attention on a region in response to a peripheral precue, illusory conjunctions are less likely for objects that appear at the cued location than for objects that appear at an uncued location. Focused spatial attention thus appears to bind together the features of objects.

B. Neuropsychological Evidence

Results from neuropsychological patients with damage to their parietal lobes support the role of spatial attention in solving the binding problem and conjointing the features of objects. In one representative study, an extinction patient was shown two letters in either the contralesional or ipsilesional visual field. One of the letters was a target (F or X) and the other was a distractor (O). The letters were colored, and the patient was instructed to name both the color and the identity of the target letter (i.e., was it F or X and what color was it?). In this task there are two types of errors. The first is a feature error, in which either letter name or color is reported incorrectly. For example, if the patient was presented with a blue F and a red O, reporting a yellow F would be a feature error. The second type of error is a conjunction error, in which a feature of the distractor letter O “migrates” to the target letter, forming an illusory conjunction. For example, if the patient was presented a blue F and a red O and reported a red F, the color of the red O was misconjoined with the target letter F. The extinction patient studied showed many conjunction errors in the contralesional field compared to the ipsilesional field. However, similar numbers of feature errors were made in the contralesional and ipsilesional fields, indicating that feature perception was similar in both fields. Presumably, the damaged parietal-based spatial attention system is unable to permit a correct conjunction of features such as color and shape; the individual features are represented, however, allowing for accurate reports of the features.

Other patients with damage to the parietal lobe attention areas show inabilitys to bind features correctly. Patients with bilateral damage to the parietal lobe have Balint’s syndrome, which is characterized by an inability to perceive multiple shapes simultaneously (simultanagnosia); Balint’s patients can perceive only one object at a time. Recent reports indicated that Balint’s patients may show higher than normal rates of illusory conjunctions. If shown a display containing a red X and a blue T and asked to report the name and color of the first letter seen, these patients may often report seeing a blue X and a red T. These misconjunctions even occur when the display is present for several seconds.

C. Physiological Evidence

Neurophysiological and electrophysiological studies have overwhelmingly supported the early locus of selection and sensory gain effects of spatial attention. An early locus for spatial attention has been demonstrated with event-related potential (ERP) studies in which the electroencephalogram is time locked to the appearance of a visual stimulus. The experimental paradigm used most often in these studies is illustrated in Fig. 3a. At the beginning of each trial block, observers are instructed to attend to either the left or the right visual field while maintaining fixation at the center of the screen. Stimuli are then presented rapidly and sequentially to the left and right visual fields, and observers are required to respond when they detect an infrequently occurring target stimulus in the attended field. By maintaining the same sequence of stimuli from trial block to trial block and varying whether the left or right field is attended, it is possible to compare
the response to the same physical stimulus when it is presented at an attended versus an ignored location.

As shown in Fig. 3b, the ERP waveform recorded over occipital scalp sites in this paradigm consists of a series of positive and negative peaks or components. The earliest component, which is called the “C1 wave” and is observed only under certain conditions, is typically unaffected by attention. Although it is usually difficult to determine the neuroanatomical site at which an ERP component is generated, it is known that the C1 wave is generated in primary visual cortex (area V1), and the finding that the C1 wave is unaffected by spatial attention indicates that the initial volley of V1 activity is not influenced by attention (although V1 activity appears to be modulated by attention at later time points, presumably due to feedback).

The C1 wave is followed by the P1 and N1 waves, both of which are typically larger in amplitude for attended location stimuli than for unattended location stimuli. The P1 effect typically begins before 100 msec poststimulus and combined PET/ERP studies have indicated that it is probably generated in the ventral extrastriate cortex. Moreover, this effect is present for target stimuli, nontarget stimuli, and completely task-irrelevant probe stimuli. Together, these factors indicate that the P1 modulation reflects an effect of attention on sensory processing, supporting early selection models of visual–spatial attention. The N1 effect appears to reflect a modulation of visual discrimination processes, although the precise nature of this effect and its neural origins are not clear.

This paradigm has also been modified for use with single-neuron recordings in monkeys, and a similar pattern of results was obtained (Fig. 3c). Attention had no effect on responses in area V1, but in area V4 (an intermediate visual processing region) attended location stimuli evoked higher rates of neural firing than did ignored location stimuli. Moreover, the effect of attention began at 60 msec poststimulus, which was the same time as the onset of stimulus-related activity in these neurons. However, spatial attention produces no changes in the tuning curves of the neurons. Thus, under certain conditions, attention acts as a preset filter that controls the amplitude of the sensory response in intermediate-level areas of visual cortex.

III. ATTENTION TO OBJECTS

A. Demonstrations of Object-Based Attention

In addition to selecting regions of space, recent research has demonstrated that objects can be attended and selected independently of their locations. Although some investigators have argued that attention is object-based instead of space-based, the emerging consensus is that space-based and object-based attentional systems coexist. A more subtle issue,
however, is whether the objects selected by attention are low-level retinotopically defined regions formed by gestalt grouping processes or higher level invariant objects formed by object representation processes. Again, the emerging consensus is that both types of object selection may exist.

1. Grouped Array Selection

One mechanism for object-based attention involves attending to perceptual objects that are defined in a spatial reference frame—a "grouped array." The grouped array is a spatiotopic map in which locations or features are grouped according to gestalt principles such as similarity (e.g., features similar in color group with one another), closure (e.g., features that form closed shapes group with one another), or figure-ground relations (e.g., figures are closer to the viewer and are more salient than grounds). Selection from a grouped array representation involves attending to the locations of items that are grouped together.

Results from several behavioral studies are consistent with grouped array selection. Two strategies have been used to study this form of object selection. One strategy is to manipulate whether stimulus objects, such as letters, are grouped together based on secondary features, such as a common color or direction of motion. For example, if observers are asked to attend and categorize a target letter presented at fixation, their responses are influenced by adjacent flanking letters. Flanking letters that are consistent with the response to the target decrease observers’ response times, and flanking letters that are inconsistent with the response to the target letter increase response times. The effect of flanks depends on object-grouping factors: Flanks that group with the target letter influence responses more strongly than flanks that do not group with the target (Fig. 4). Presumably, the gestalt grouping principles define a set of letters as a related group, and this group is attended as a single unit. The flankers within this single perceptual group then decrease or increase response times to the target letter. Grouping effects on targets and flankers have been reported with several gestalt principles, including similarity, common fate, connectedness, and good continuation.

A second strategy for studying object-based attention is to manipulate whether two attended features fall on the same object or on different objects or, alternatively, whether attention shifts within an object or across objects. One widely used paradigm is illustrated in Fig. 5. In this paradigm, observers view two rectangles oriented either horizontally or vertically. One end of one of the rectangles is precued with a brief flash, and this precue is followed by a target that requires a keypress response. The target usually appears at the cued location; when it appears at an uncued location, it may appear within the same object as the cued location or in the other object. Both of these uncued locations are the same spatial distance from the

Figure 4 Displays used to study the influence of gestalt organization on visual attention. Observers report whether the central letter is an H or a T. (a) Grouping via similarity; the nontarget Hs group with the target H. Because the flankers that group with the target are compatible with one another, observers would classify the target letter quickly. (b) Grouping via good continuation; the nontarget Ts group with the target H. Because the grouped flankers are incompatible with the target H, observers would classify the target letter slowly.

Figure 5 Spatial precuing task used to study object-based attention. Two rectangles appear, and the end of one is precued with a peripheral flash. After a delay, a target appears at one of three locations: a, a validly cued target; b, an invalidly cued target that appears in the cued object; c, an invalidly cued object that appears in the uncued object. Observers more quickly detect invalidly cued targets appearing in the cued rectangle faster than those appearing in the uncued rectangle.
precued region and the target is equally unlikely to appear at either of them, but observers are faster to respond to targets appearing in the uncued end of the cued rectangle than in either end of the uncued rectangle. Thus, attention appears to cover the entire cued rectangle even though only one end was cued. Similar results have been obtained with tasks that do not require spatial precues. In displays containing two rectangles that are overlapped to form an “X,” observers are faster to discriminate features on the same rectangle than on different rectangles even though the spatial distances are similar.

Note that spatial location is centrally important in selection from a grouped array because this representation is spatiotopic. A handful of studies have demonstrated the importance of location by manipulating both grouping principles and spatial position. These studies have demonstrated that both grouping principles and spatial position influence attentional selection. In the cued detection task depicted in Fig. 5, moving the rectangles closer to one another reduces the cost of switching attention from the cued rectangle to the uncued rectangle, although attention continues to shift faster within an object than between objects. On the basis of such results, it may be possible to explain many demonstrations of “object-based attention” as occurring within a spatially formatted representation.

2. Object-Centered Selection

A second mechanism for object-based attention involves attending to objects that are defined in an object-centered reference frame, which represents the parts and features of an object in relation to a reference point on the object. Coding parts and features in reference to the object allows the relative positions of the parts and features to be constant as the object changes spatial position and retinal size. A person’s head is above the torso irrespective of where the person appears (e.g., left or right visual field) or how distant the person is from the viewer.

Because an object-centered reference frame is relatively insensitive to spatial position, spatial manipulations should not influence this form of object-based selection. There is evidence for selection from a late, object-centered representation from a discrimination task that requires observers to focus attention on a single object or divide attention between two objects—a box and a line (Fig. 6). Observers report the values of two features, such as whether a gap is on the left or right side of a box. Sometimes, the two features are located on the same object (both features on the box) and sometimes on different objects (one feature on the box and one on the line). Performance is object-based in this task because features on the same object are reported more accurately than are features on different objects. However, unlike grouped array selection, performance in this task is not influenced by the spatial distance between the box and line, suggesting the objects are selected and not the locations occupied by the objects.

B. Neuropsychology of Object-Based Attention

1. Object-Centered Neglect

As with most neuropsychological studies of spatial attention, investigations of object-based selection have focused on patients with neglect following damage to the parietal lobe areas. Two key findings from neglect patients have implications for the neural basis of object selection. The first finding is that some of these patients exhibit object-centered neglect. The second finding is a hemispheric difference between object and spatial attention in patients with neglect.

Some patients with right parietal lobe damage (left neglect) neglect not only the left side of space but also the left side of an object, even when that object is located in the good (ipsilesional) visual field. Left neglect of objects can be observed when patients are asked to compare two novel objects and determine if they are the same or different. If the two objects are identical on their right sides but different on their left sides, neglect patients will incorrectly report that the objects are the same. Neglect patients continue to show this error when both objects are rotated 45° clockwise.
to place the differing feature in the good right visual field. If neglect occurred for spatial coordinates only, rotating part of the objects into the nonneglected visual field should have allowed the patients to notice the difference between the two objects. Because the neglected region of the object follows the object as it is rotated, the neglect must be defined relative to a reference point on the object, such as the object’s principal axis (i.e., midline).

Although object-centered neglect has been the focus of many recent studies, these effects are not present in all neglect patients, which raises two points. First, failure to find object-centered neglect in some patients may occur because visual neglect is not a unitary disorder. Second, and more interesting, object-centered neglect may be unobservable because of the stimulus objects used. Objects that do not possess a strong principal axis or do not have well-defined left and right sides (a “canonical handedness”) may not have a single object-centered reference point, which could prevent object-centered neglect. For example, a symmetric letter such as “A”, does not have a canonical handedness because the left and right sides are identical; there is no need for the visual system to represent the sides of a symmetric letter differently. Asymmetric letters (e.g., “F”) have a canonical handedness, and the visual system must represent the differences between the two sides. Accordingly, object-centered neglect is less likely for symmetric letters than for asymmetric letters, suggesting that the object’s handedness may influence the allocation of visual attention.

Finally, what type of object representation is involved in object-centered neglect—a grouped array or an object-centered representation? As noted previously, the common assumption is that object-centered neglect occurs within an object-centered reference frame. However, recent simulation results from connectionist models demonstrate that object-centered neglect could arise from a spatiotopic grouped array representation. These simulations indicate that perceptually organized input to a damaged attentional system may be sufficient to demonstrate object neglect; no object-centered coordinates, principle axis, or canonical handedness need to be computed to explain the findings from neglect patients.

2. Lateralization of Object and Spatial Attention

The second finding from neglect patients relevant to object attention is an apparent hemispheric difference between object-based attention and spatially based attention. Patients with damage to the right parietal lobe most often present with hemispatial neglect in which the left side of space is ignored. (Patients who demonstrate object-centered neglect also exhibit spatial neglect.) Left neglect can also be demonstrated in these patients by using object-based attention tasks. For example, in the task shown in Fig. 5, left neglect patients are slower to detect targets in the contralesional visual field than in the ipsilesional visual field. However, left neglect patients show preserved object-based attention: They detect targets in the cued rectangle faster than targets in the uncued rectangle, and this object-based effect is found in both the contralesional and ipsilesional visual fields. In contrast to patients with left neglect, patients with damage to the left parietal lobe (right neglect) appear to have deficits in object-based attention. Right neglect patients also show slower target detection in the contralesional visual field than in the ipsilesional field. However, these patients exhibit larger object attention effects in the contralesional field; it is more difficult for these patients to switch attention from the cued rectangle to the uncued rectangle in the contralesional field than in the ipsilesional field. These hemispheric differences between object-based and spatially based attention have been supported by research with a split-brain patient. In performing the cued detection task shown in Fig. 5, this patient had greater difficulty switching attention from the cued rectangle to the uncued rectangle when stimuli were presented in the right visual field (left hemisphere) than when stimuli were presented in the left visual field (right hemisphere).

3. Other Patient Groups

Finally, a few patient groups besides neglect patients have been studied to understand object-based attention. For example, studies with a visual form agnosic reported impaired object-based attention but intact spatial attention following diffuse damage to the occipital cortices. Patients with visual form agnosia fail to perceive objects because of damaged early level visual areas. Although these patients have intact sensory processes (e.g., acuity and color perception), they are unable to organize visual features using the gestalt principles. The damage to perceptual organization processes impairs the ability to form perceptual groups, which prevents any object-based component of visual selection. Despite having impaired object-based attention, spatial selection appears to be intact following diffuse occipital damage, suggesting that
object grouping processes appear to be dissociable from spatial selection processes. Thus, the parietal lobe attention system is not the only cortical system involved in mediating object selection.

C. Physiology of Object-Based Attention

In addition to the focus on parietal lobe involvement in neuropsychological studies of object selection, physiological studies have implicated other cortical areas in object attention. Multineuron recordings from macaque primary visual cortex (area V1) have implicated this area in object-based attention. Specifically, attending to one of two objects in a display results in enhanced firing for neurons whose receptive fields contain features of the attended object. Monkeys viewed scenes containing two objects (simple curves); one of the objects was connected to the fixation point, and monkeys were trained to attend to this object. The monkeys' task was to make an eye movement from the fixation point to the opposite end of the attended curve. Segments of the curves fell within receptive fields of V1 neurons. The neuronal responses were larger when a receptive field contained a segment of the attended curve than a segment of the unattended curve. This object-based attentional modulation in area V1 is important because previous studies of spatial attention were equivocal in finding V1 attentional modulation. Neurons in V1 exhibit attentional modulation when an object can act as the recipient or focus of attention; neurons in V1 do not appear to exhibit attentional modulation with blank displays or nonorganized cluttered displays. These neurophysiological findings are consistent with results from visual form agnosia, in which diffuse damage to early cortical visual areas (possibly V1) impaired object-based attention. Thus, there is growing evidence to support a central role for early cortical areas in perceptual organization and object attention.

Neurophysiological results have also suggested that object selection can occur in the oculomotor system as well as in purely sensory areas. Neurons in the supplementary eye field (SEF), located on the dorsomedial surface of the frontal lobes, appear to represent object-centered spatial selectivity for the direction of eye movements. That is, these neurons seem to code for spatial positions within an object, such as the left side of the object. Macaque monkeys were trained to make eye movements to the onset of a target spot. The target appeared in one of three conditions: alone in an otherwise blank display, at the left end of an object (a rectangle), or at the right end of an object. The absolute direction of the eye movement was identical in all three conditions; that is, the monkeys' eyes moved in exactly the same direction and same distance across these conditions. Although the eyes moved identically, a subset of SEF neurons fired at higher rates when eye movements were executed to a specific region of the object, regardless of its absolute spatial location. For example, some neurons responded vigorously to eye movements to the right side of the object; the same eye movement that landed on the left side of the object resulted in a smaller neuronal response. Thus, SEF neurons code for locations within an object; how these locations are coded—in a spatial reference frame such as the grouped array or in an object-centered coordinate frame—is unknown.

Finally, ERP studies with humans have investigated object-based selection. When viewing displays containing two superimposed surfaces (two transparent surfaces of different colored dots that rotate in opposite directions), observers can selectively attend to one of the two surfaces despite their spatial superimposition. If observers are instructed to attend to one of the surfaces, changes to the attended surface will produce evoked potential components with larger amplitudes than stimuli presented on the unattended surface. Specifically, changes on the attended surface generate larger P1 and N1 components compared to changes on the unattended surface. The similarity of these effects to the spatial attention effects described previously suggests that some object-based effects may be generated by neural processes shared with spatial attention. Attentional selection may be occurring from a grouped array in which motion segregation cues allow the two dot surfaces to be separated from one another in depth.

IV. ATTENTION TO OTHER MODALITIES

A. Selection beyond Vision

Beyond locations and objects in the visual modality, stimuli from other modalities can be selectively attended. This observation is evident from studies of selective attention in the 1950s and 1960s in which listeners attended one of two different speech signals arriving simultaneously in each ear. To determine how effectively attention could be restricted to one signal,
listeners were required to repeat ("shadow") the speech in the attended channel. This shadowing procedure was the main behavioral technique for studying selective attention for decades. Studies of auditory attention supported early selection of stimuli; words spoken into the unattended ear are effectively filtered out. For example, if listeners are instructed to tap a key when they hear the word "tap," they almost always tap when the word is presented to the attended ear and almost never tap when the word is presented to the unattended ear. Words presented to the unattended ear are filtered at an early level of processing prior to word identification; if filtering occurred later, after word identification, listeners should have tapped when the word tap was spoken in the unattended ear. However, the early attentional filter appears to be leaky in that salient material on the unattended channel, such as the listener's name, can deter attention from the attended channel.

An early locus for auditory selective attention has been confirmed with ERP studies. The general procedure is similar to that used to study spatial attention (described previously). Listeners hear a sequence of auditory tone pips, half presented to the left ear and half to the right ear. Listeners pay attention to the tones in one ear and press a button whenever an infrequent target tone is presented to the attended ear. Many studies using this procedure have found that the early ERP waves are larger for tones presented in the attended ear than in the ignored ear, consistent with a sensory gain effect of auditory attention. This enhancement of the voltage amplitude occurs temporally early, with the effect beginning as early as 20 msec after stimulus onset, well within the period of sensory-level processing. Moreover, the attentional enhancement was present for both targets and nontargets presented in the attended ear, indicating that selection occurred before the stimuli were identified. In addition, magnetoencephalographic studies have shown that these effects arise in or near primary auditory cortex. The results from auditory attention experiments are similar with results from visual attention experiments in suggesting an early selection account of attention in both modalities.

B. Cross-Modal Coordination of Attention

The existence of attentional selection in different modalities raises a basic question: Is there a single, supramodal attentional system that mediates selection across multiple modalities, or are there individual attentional systems for each modality that have some degree of cross talk with one another? Results from neuropsychological patients with neglect support a supramodal view of attention. Neglect patients have difficulty attending to both visual and auditory stimuli opposite the lesioned hemisphere, suggesting that parietal lobe attentional processes operate on a representation of space that codes both visual and auditory stimuli. Similar results have been reported from multimodal versions of the spatial precuing task. In the multimodal version of this task, neglect patients are asked to detect a lateralized visual stimulus. This visual target is preceded by a lateralized precue presented in either the visual or the auditory modality. Neglect patients show similar orienting behavior to both types of precues; specifically, neglect patients have difficulty disengaging attention from precues presented on the good (ipsilesional) side of peripheral space irrespective of the cue's modality. These results support a supramodal representation for parietal lobe attentional processes.

Further strengthening the supramodal view of attention, neglect patients also fail to attend to somatosensory stimuli presented on the bad (contralesional) side of peripheral space. However, somatosensory neglect could be explained by contralesional sensory deficits that accompany brain damage; inputs from the contralesional side of the body may be weaker than inputs from the ipsilesional side of the body. A convincing demonstration of somatosensory neglect was provided by testing neglect patients' ipsilesional hands, which have no sensory loss. The patients were touched simultaneously on the left and right sides of their right wrist and asked to report where they were touched. There were two key findings. First, left neglect patients failed to notice being touched on the left side of their right wrists, demonstrating that somatosensory neglect can occur in the absence of sensory deficits. Second, the attentional impairment for detecting contralesional touches occurred whether patients' hands were facing with the palm downward or facing with the palm upward. The neglect did not follow the rotation of the hands but instead remained fixed on the left side of the wrist. These results indicate that the attentional deficit did not occur in somatosensory coordinates, such as always neglecting the thumb side of the wrist or always neglecting the left side of the body. Instead, neglect occurred in abstract spatial coordinates that represent the left and right sides of a limb independent of that limb's orientation. This "limb-centered" somatosensory neglect bears a
striking similarity to the object-centered neglect observed in the visual modality: The neglected region is not necessarily defined by the patients' midline but by the midline of a stimulus (an object or a limb).

Finally, both behavioral and ERP studies with neurologically normal observers have extended the operation of selective attention across different modalities. There appear to be strong cross-modal links in spatial attention that allow observers to spatially attend a region and select stimuli occurring in different modalities. In behavioral studies, observers visually cued to one side of space detect more quickly both visual and auditory targets on the cued side of space than on the uncued side of space; this cued location advantage occurs when the modality of the target is unpredictable. Thus, spatial attention appears to operate across modalities. Behavioral studies have also attempted to decouple attentional shifts across modalities by varying the occurrences of auditory or visual targets. Can auditory spatial attention be allocated to a different region than visual spatial attention if an auditory target is expected at one location and a visual target is expected at another location? The answer to this question seems to be "no." If observers voluntarily shift auditory spatial attention to one region to detect a highly probable auditory target, visual spatial attention seems to follow. The same result holds for shifts of visual spatial attention; auditory attention will follow visual attention when visual attention is voluntarily shifted to a region to detect a highly probable visual target. ERP studies have reported similar results. For example, if observers are required to monitor a location for an infrequently occurring visual target, larger evoked responses are generated by both visual and auditory nontarget stimuli at the attended location than at the unattended location.

One caveat from the cross-modal studies of attention is that although visual and auditory attention appear to operate in concert, the effects across modalities are not equivalent to effects within a single modality. Larger attentional effects are found when the cue and target appear in the same modality than in different modalities. Such an observation cannot be explained with a strong supramodal account of spatial attention. The strong supramodal account would predict that each sensory modality could cause an equivalent shift of spatial attention, which would provide enhanced processing at the attended location across all modalities. However, cross-modal studies cannot distinguish between linked unimodal attention systems and a supramodal system that receives differentially weighted inputs from each modality. Furthermore, a supramodal system may be an emergent property of the connections that link modality-specific attentional systems. Consistent with the multiple attentional systems in the visual modality, there are likely to be both unimodal and supramodal attentional mechanisms for the coordination of attention across sensory modalities.

V. ATTENTION TO TASKS

A. Performing Multiple Tasks Simultaneously

In addition to coordinating the processing of sensory stimuli, attention must participate in the coordination of tasks. There are many situations in which humans must perform multiple tasks concurrently, as such having a conversation while driving. Performance is impaired when multiple tasks are performed concurrently, even when the tasks are highly practiced, as with driving and speaking. Attentional processes may be involved in selecting an individual task for current behavior, with a cost in performance occurring when attention is either divided or switched between multiple tasks.

The biased competition model we used to describe spatial attention can also be applied to performing multiple tasks such as the Stroop task, in which different tasks must be performed in different blocks of trials. In the Stroop task, observers view words that name colors (e.g., "red" or "blue") presented in different colors of ink. The words can be written in a compatible ink color ("red" written in red ink) or in incompatible colors ("red" written in blue ink). Observers perform one of two tasks—either reading the word or naming the ink color. Because word reading is more practiced than ink color naming, observers can read words with little effect of the ink color; observers can just as quickly read color words printed in a compatible ink color as color words printed in an incompatible ink color. In contrast, color naming is highly influenced by the word; observers are slower to name ink colors used to print an incompatible word ("red" printed in blue ink) than ink colors used to print a compatible word ("red" printed in red ink). In the Stroop task, the top-down task demands (i.e., the task observers are asked to perform) and the bottom-up stimulus features (the word and ink color) both guide behavior. The color naming task is difficult because the bottom-up inputs are stronger for words
than for ink colors. Thus, there is a stronger bias for word reading than for color naming, allowing the word reading task to compete more effectively for the control of behavior.

One difficulty in using the Stroop task to study attention to tasks is that one of the tasks, word reading, is much easier than the other. An attentional phenomenon that demonstrates competition between two equally difficult tasks is the "attentional blink." In the attentional blink task, observers view a stream of approximately 20 stimuli presented one at a time at a rate of about 10 stimuli per second; observers are asked to detect two targets from this stream. For example, the first target (T1) may be a number that observers must classify as even or odd, and the second target (T2) could be a letter that observers must classify as a consonant or vowel. Observers make both responses at the end of the stimulus stream. Observers often fail to identify T2 if it appears shortly after T1; if T2 appears somewhat later, observers more accurately report its identity. The temporary impairment in identifying T2 is referred to as the attentional blink because it is similar to the consequence of a T1-triggered eyeblink (i.e., a brief period during which subsequent targets cannot be detected).

The attentional blink does not appear to be caused by sensory-level interference between the two targets. Instead, the failure in reporting T2 is more central, resulting from a failure to store T2 in a durable form that can be reported at the end of the stimulus stream. In terms of a biased competition account, top-down task constraints related to the T1 task may bias this item to be coded into working memory. After T1 begins to be encoded into working memory, the task bias can begin to switch to the T2 task, but this reconfiguration takes time. Thus, if T2 appears soon after T1, it may not be efficiently encoded into working memory and may be overwritten by the next item in the input sequence. At the end of the stimulus sequence, reporting T2 is difficult because of this shallow encoding into working memory—T2 is identified but not reported, suggesting that selection may operate relatively late in the visual processing stream (i.e., after stimulus identification).

B. Neural Mechanisms

1. Attentional Blink and Neglect

As with almost every other type of attentional selection, the attentional blink appears to involve the parietal lobe attention system. Patients with damage to the right parietal lobe show a prolonged attentional blink. Compared to normal observers, these patients need longer intervals between T1 and T2 or T2 will be missed. This suggests that neglect is not only a disorder of visuospatial attention but also reflects more general attentional processes. Thus, the parietal lobe attention system may involve several types of attentional "gating," ranging from sensory gating to task gating, which allows the parietal lobes to participate in both early (sensory) selection and late (task) selection.

2. Human Electrophysiology of the Attentional Blink

Perhaps more than any other methodology, ERP studies of the attentional blink have elucidated the mechanisms of this form of selection. Recent ERP studies have demonstrated that the attentional blink occurs late in visual processing, after stimulus identification, consistent with the view that failure to recognize T2 is due to poor encoding of this item into working memory.

To determine if the attentional blink involves sensory-level attention processes, early ERP components were studied. Observers participated in a standard attentional blink task, but a task-irrelevant probe was presented simultaneously with T2. This irrelevant probe, a flashed visual stimulus, elicited the P1 and N1 components that are involved in spatial selection. If the attentional blink is due to suppressed sensory processing, P1 and N1 components should also be suppressed for irrelevant probes presented during the window of the attentional blink. However, no suppression of the P1 and N1 waves was observed, even though behavioral performance exhibited a strong attentional blink. There was no evidence for sensory suppression during the attentional blink period, indicating that the mechanisms of spatial attention are different from the mechanisms of the attentional blink.

Although early sensory processes measured by P1 and N1 are not responsible for the attentional blink, later perceptual processes may be. An additional experiment addressed whether the T2 item was recognized completely; complete recognition of the T2 item would indicate that the attentional blink was not due to any form of perceptual suppression, early or late. This study investigated the N400 ERP component. The N400 is typically elicited by words that mismatch a previously established semantic context. For example, an N400 would be generated by the last word in the sentence "The man drank his coffee with cream and
dog” because “dog” is inconsistent with the semantic meaning of the sentence. If an N400 is elicited by a word, then the word must have been identified; otherwise, a semantic comparison with the context would have been impossible.

In the N400 attentional blink study, the T2 stimulus was a word. Each trial began with a semantic context word, and the T2 word was either semantically related or unrelated to this semantic context word. When the T2 word semantically mismatched the context word, an N400 component was produced, even if the T2 word occurred during the window of the attentional blink such that observers could not report the word. This result indicates that the T2 word was identified during the attentional blink window, and the failure of observers to correctly report the word reflects a failure to store the word in working memory. Thus, the attentional blink occurs after identification, consistent with a late-selection account of attention.

VI. SUMMARY

Attention is necessary for eliminating sensory inputs or behavioral tasks that are irrelevant at a specified time. Although there may be multiple forms of attention, some neural sites, such as the parietal lobe, are involved in many aspects of attention. The control and effects of these multiple forms of selection are quite varied, however. The integration of top-down behavioral tasks or goals and bottom-up stimulus factors may allow the attentional system to be highly flexible and allow a small subset of components to have varied effects.

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