

Section I

## Structural and Functional Neuroanatomy

Chapter

# 8

## Attention

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The ability to effectively deal with the overwhelming amount of information present in the environment at any given time requires humans to focus on some things and ignore others. For example, imagine attempting to read a book in a crowded public place. This requires the reader to focus on the words on the page and ignore the sounds of conversations going on in the background, allowing an effective focus on the task at hand. The process by which people can both select relevant and suppress irrelevant environmental information refers to a number of processes collectively referred to as “attention.” From an information-processing standpoint, attention can be conceptualized as operating not as a single, monolithic process, but rather a group of more fragmented, domain-specific processes. For instance, in the example above, attention is required to select or suppress information across more than one sensory modality. In addition, attention can select information based on its location in space, its identity, or its relevance to current goals. For this reason, research in the cognitive and brain sciences has typically focused on specific subcomponents of attentional processing.

One broad distinction that has been made in the study of attention has been between the control of attention (i.e., how attention selects stimuli) and the subsequent effects of attention (i.e., what is the fate of stimuli once attended to). Within the domain of control, attentional selection can occur as the result of cognitive (top-down) or stimulus-driven (bottom-up) processes. In turn, these selection processes can bias the way in which information provided by the environment is interpreted. Since the majority of research on attention has focused on the visual system, the discussion of attention in this chapter will center primarily on the control of different aspects of visual attention.

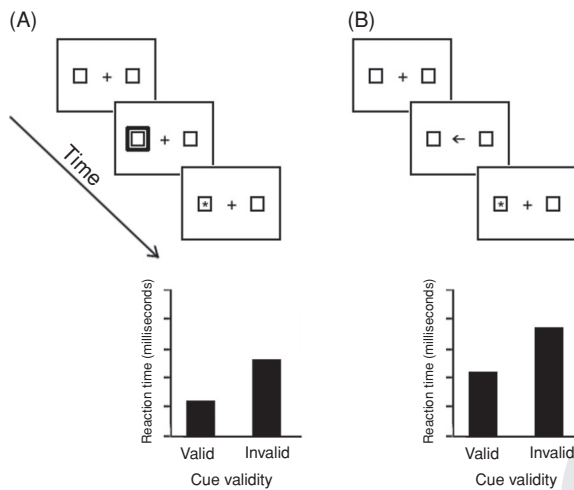
However, many of the principles discussed below hold true for the selection of information across other sensory domains. This chapter will outline relevant behavioral measures related to the control of attention, and functional theories of attention based on such measures. The major focus will be on the control of visual attention in both normal and neurologically impaired individuals, mapping functional theories of attention onto what is known about the cerebral structures subserving this process.

### Control of attention

One of the most important issues in attention research concerns how attention is controlled. At a basic level, attention can be considered a sensory gatekeeper, allowing humans to select and act upon only the subset of sensory information that is most relevant to carrying out specific goals. A familiar example illustrates this point. When conversing with a friend in a noisy room, one is able to carry on a normal conversation despite the milieu of irrelevant sensory information – in other words, to selectively attend to the conversation. However, if another friend shouts one’s name from across the room, attention is captured in a nearly automatic manner, putting on hold the conversation in which one was engaged.

This scenario highlights two ways in which attention can be controlled. On one hand, you are able to voluntarily attend to a conversation with your friend – an example in which you exercise “goal-directed,” or top-down, control of attention. However, this voluntary focus of attention can be overridden if a sufficiently important stimulus (in this case, the shouting of your name by another friend) is detected in the environment – a case of “stimulus-driven,” or bottom-up,

## Section I: Structural and Functional Neuroanatomy



**Figure 8.1.** The order of events in Posner's spatial cueing paradigm. Observers are asked to detect the appearance of a target that has been validly or invalidly pre-cued. (A) Peripheral pre-cue that automatically summons spatial attention to the cued region, and typical results. Note that in both cases, subjects respond more quickly to targets that have been validly cued. However, central pre-cues typically elicit a slower response to the target, reflecting the voluntary nature of the attentional orienting produced by such cues.

factors controlling the allocation of attention. This distinction between the bottom-up and top-down control of attention has served as an important concept informing the study of attention in both cognitive psychology and neuroscience. The following section will outline the concepts of bottom-up and top-down control of attention, their interaction, and their consequences for subsequent sensory processing.

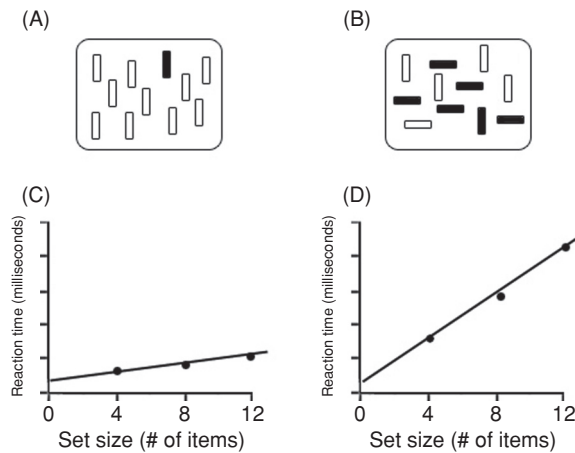
### Bottom-up vs. top-down selection: evidence from spatial cueing and visual search

Two experimental paradigms have contributed the most to the understanding of the control of visual attention: visual search and spatial cueing. In a spatial cueing paradigm, a stimulus or instruction precedes the presentation of a target stimulus. This stimulus or instruction is referred to as a "cue," and this cue typically either predicts or does not predict the location of a subsequently presented target stimulus. One widely used spatial cueing task is that developed by Posner [1]. In Posner's cueing task, depicted in Figure 8.1, each trial begins with a cue intended to orient an observer's

attention to one of several possible locations. The cue can take the form of either a peripherally presented "flicker" appearing in a location where a subsequent target may appear, or may appear as a centrally presented symbol such as an arrow, or a directionally related word ("left"). After a delay, a target is presented and observers indicate that they detect the target (e.g., by pressing a button as soon as the target appears) or they discriminate among several targets (e.g., reporting if the target is a "T" or an "L"). On "valid" trials, the cue correctly predicts the target's location; on "invalid" trials, the cue is misleading. Observers typically respond to valid trials fastest and invalid trials slowest, representing a "validity effect" of the cue.

Each of the cues mentioned above are designed to direct attention to locations in space, but each does so through different mechanisms. Specifically, peripherally presented cues tap bottom-up attentional control processes, whereas centrally presented cues recruit top-down processes. This distinction allows for the examination of bottom-up and top-down influences on attention independently of one another, and data from these types of cueing tasks have provided useful information regarding differences between these two types of attentional control:

- (1) Observers typically cannot ignore peripheral cues, and these cues attract attention to the cued location more or less automatically. However, observers can ignore central cues when instructed, demonstrating that central cues do not direct attention in a stimulus-driven manner and are instead under voluntary control.
- (2) Peripheral cues operate more quickly than central cues, with reaction time differences between validly and invalidly cued trials emerging sooner with peripheral cues. This phenomenon reflects greater processing time required to use central cues, indicating that these cues require voluntary and effortful cognitive control.
- (3) Peripheral cues have the capacity to interrupt attentional orienting produced by a central cue, but central cues exert little effect on orienting from peripheral cues. This observation indicates that peripheral cues attract attention more or less automatically, in a stimulus-driven manner.
- (4) Studies that use central cues tend to present more valid than invalid trials, in an effort to encourage observers to attend to locations predicted by the cue. For example when using central cues, 75% of



**Figure 8.2.** (A, B) Visual search displays and (C, D) typical results from a visual search task. Panel C shows an efficient search for a target that differs from distracters on a single feature dimension, such as color (A). D shows an inefficient search for a target that differs from distracters on two feature dimensions (B).

trials may include a valid cue, with only 25% of cues being invalid. By contrast, peripheral cues attract attention to a location regardless of validity, even if valid trials are less frequent than invalid (e.g., 25% valid, 75% invalid). Again, peripheral cues are shown to summon attention in an automatic manner.

The other paradigm that has provided insight into the control of visual attention is the visual search task (Figure 8.2). Visual search refers to the act of looking for a visual target among distracters – similar to the process encountered when trying to “find Waldo” in the popular book series. In a typical visual search task, the number of distracters, or “set size,” is varied across trials, and reaction time (RT) to detect a target item is measured as a function of the set size. An “efficient” visual search results in shallow search slopes (i.e., set size has little influence on an efficient search), and “inefficient” searches result in steep search slopes (i.e., set size affects the time taken to detect a target). These differences in search functions can be conceptualized as representing the differential recruitment of bottom-up, stimulus-driven attention mechanisms and top-down, goal-directed attention mechanisms.

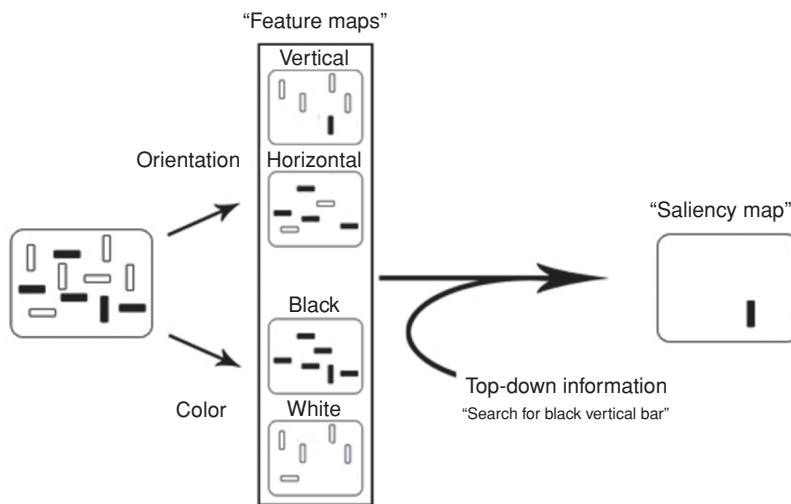
In the case of an efficient search, the target is typically perceptually distinct from the distracter items. An example of an efficient search would be a case

where observers are asked to search for a red bar among green distracters (Figure 8.2A). In this case, attention would be attracted more or less automatically to the target based on bottom-up factors – in this example, the bar’s distinctive color. Since the target is defined on the basis of a distinct perceptual attribute, this type of search would remain efficient regardless of the number of distracters present in the array, resulting in the characteristic shallow slope seen during efficient search. By contrast, in the case of an inefficient search, the target is typically less perceptually distinct from the distracter items. For instance, if an observer were asked to search for a target based on a conjunction of multiple features (i.e., a red vertical bar among red horizontal and green vertical distracters, Figure 8.2B), the observer would be forced to carry out a more effortful search, requiring a greater amount of cognitive control. In this case, bottom-up information is not sufficient to define a target, and observers are required to adopt a strategy in which each item in the display is treated as a possible target, with each item or a subset of items being examined until the target is identified.

## Functional models of attentional control

An early explanation for the differential efficiency during visual search was based on serial and parallel processing models, with efficient searches being classified as “parallel” and inefficient searches “serial.” This conceptualization of search being either serial or parallel is the core of Treisman and Gelade’s [2] feature integration theory of visual search. In their original model [2], these investigators proposed that during an efficient search, all items in the array are processed preattentively in parallel – all incoming visual sensory information is processed simultaneously, and the target is detected in a more or less automatic manner, “popping out” based on its bottom-up salience. This “parallel search” would lead to the shallow search slopes described during efficient search, since all items in the display could be processed simultaneously regardless of the number of distracters present. Conversely, a search in which bottom-up information alone is not sufficient to identify the target requires subjects to perform a more effortful “serial search.” It was hypothesized that during inefficient searches, observers are forced to direct attention to each item in the display, with attention to each item being required to “bind” the two features and identify the stimulus [3].

## Section I: Structural and Functional Neuroanatomy



**Figure 8.3.** An illustration of the visually guided search model of attentional allocation during visual search. In this model of attentional control, observers organize bottom-up information from the environment into “feature maps” that code for the identity and location of features in visual space. This information regarding stimulus features present in a scene is combined with top-down information based on the goals of the observer to create a “saliency map.” The saliency map then provides information on which areas of space are most likely to contain a particular stimulus in the environment, preferentially directing attention to these areas over others. This model allows the interaction of bottom-up and top-down information to bias the control of attention toward relevant visual stimuli.

Consequently, set size would have a large impact on target detection RTs, as increasing the number of serially searched items theoretically increases RTs with each distracter item added to the array.

Although this feature integration model of visual search provides a straightforward account of search slope differences between efficient and inefficient searches, it does not fully account for some findings in the visual search literature. Specifically, it has been shown that some “serial” looking processes can arise from parallel processing mechanisms. For instance, RT patterns that resemble those seen in serial search can be produced by limited capacity parallel search mechanisms.

To illustrate this point, imagine that multiple items in a display can be processed in parallel. However, due to capacity limitations not all items in the display can be processed at once. Since not all items in the display can be searched through in parallel, searching through many items (large set size) in a display takes longer than searching through only a few items (small set size), producing RT slopes that resemble those seen in “serial” searches. In addition, searches that would be deemed “serial” by feature integration theory can be surprisingly efficient, resulting in RT slopes that resemble parallel searches [4]. Therefore, search is typically discussed with respect to its efficiency, where efficient search leads to shallow search functions (slopes <10 ms/item) and inefficient search leads to steeper search functions (slopes >20 ms/item), rather than in terms of serial or conjunction search.

To account for results that appeared to be inconsistent with feature integration theory, Wolfe [4, 5] proposed a two-stage “guided search” model of attentional control (Figure 8.3). As with feature integration theory, the initial stage of processing is carried out preattentively and in parallel across the entire visual field. From this processing, independent parallel representations of items in the search array are created based on basic visual features such as color, shape, or orientation. These representations are termed “feature maps,” and code for all of the features that are present in a given visual scene. Importantly, these maps also code for the *location* that the different features occupy. For example, if a subject were asked to search for a red bar among green distracters, all items in the display would be preattentively processed in parallel. From this processing, a feature map for “color” would be generated that included representations for items that were both red and green (since both types of items are present in the display). In addition to this color information, the location at which this information was detected would be represented in the map, providing the observer with a spatial map of features present in the scene.

In contrast to feature integration theory, in the second stage of processing the bottom-up information represented in the feature map is combined with top-down information based on the goals of the observer. This combination, in turn, serves to bias attention toward particular elements of a visual scene [6]. In the case of the simple feature search described above, top-down information regarding target identity (i.e., the

target is red) is combined with bottom-up information regarding the location of red items in the display. This produces an “activation map” or “saliency map” that is used to direct the limited capacity resources of attention to a location or locations that are most likely to contain the target item.

The guided search model is important for three reasons. First, it clears up the serial vs. parallel issues that are not easily explained by feature integration theory, providing a more plausible explanation of the control of attention during search. Second, the underlying mechanisms of the model are made explicit and can be studied empirically. Third, and most importantly, the model is transparent at a neural level: although it is based on behavioral research and computer simulation, it maps well onto what is known about the structural organization of brain regions involved in attentional control (to be discussed in detail later). This point illustrates an important principle in neuroscientific research, which is that functional accounts of cognition should correspond with what is known about the anatomy of cognitive functions and vice versa. The following section will focus on the major forms of attention, and how functional accounts of these constructs map on to neuropsychological and neuroanatomical data.

## Major types of attention

Having considered how attention is controlled, it is now important to turn to the types of information that attention can select. In this section, four different classes of selection will be considered: (1) spatial attention, in which stimuli are selected based on their position in space; (2) object-based attention, in which stimuli are selected based on their identity; (3) attentional selection in visual working memory, in which attention selects items that will be remembered; and (4) executive attention, in which attention is involved in choosing which task or behavior an observer will perform.

### Spatial attention

Attention can be selectively directed toward different regions in space, a concept traditionally referred to as “spatial attention.” Spatial attention selects stimuli based on their location in space, allowing stimuli at a particular location to receive further processing. One of the first and most widely used paradigms

in the study of spatial attention is the spatial cueing task mentioned in the previous section. Recall that when observers are directed to a specific location in space, subsequent stimuli appearing in this location are detected or discriminated better than those appearing in other locations. This phenomenon suggests that once attention selects a location, stimuli appearing in that location receive processing benefits over other stimuli.

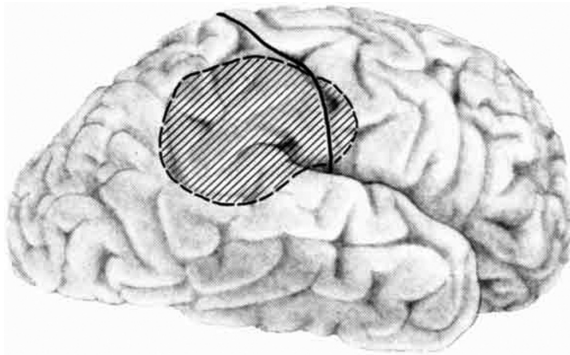
One way that spatial attention may exert an influence on stimulus processing at particular locations is by prioritizing these locations, so that stimuli located within a particular region are processed before those in other regions. In a standard spatial cueing task, the pre-cue draws attention to a particular location, putting stimuli falling within that region first in line for further processing. This sequence would result in the response time patterns seen in spatial cueing trials, with validly cued targets being detected or discriminated more quickly than those at invalidly cued locations based on the priority settings established by the cues.

Another way that spatial attention may exert an influence on stimulus processing at particular locations is by enhancing the perceptual representation of stimuli at those locations. Since there is a great deal of noise in the visual system, effective selection of incoming stimuli requires a mechanism that increases the signal-to-noise ratio in favor of relevant sensory information. At a neural level, this perceptual enhancement may be achieved through increased firing amplitude of neurons coding for stimuli at the selected location. In other words, attention acts as a sensory gain control that effectively “turns up” the neural representation of stimuli in an attended location versus those in unattended locations, causing these attended stimuli to stand out [7].

For example, spatial attention has been shown to change the appearance of items, actually making them more perceptible. Carrasco and colleagues [8] showed that directing attention to a location in a display effectively increased contrast for the item falling within the attended region, thus leading to increased performance on a visual discrimination task. From this observation it was concluded that attention intensified the sensory representation of the attended item, producing a stronger sensory impression of the stimulus. In this way, spatial attention can actually alter the phenomenological perception of objects occupying a particular location.



## Section I: Structural and Functional Neuroanatomy



**Figure 8.4.** Diagram indicating the region of the brain in which damage most commonly results in symptoms of visual neglect, the temporoparietal junction.

It has also been demonstrated that spatial attention can influence what information is allowed into visual working memory. If the appearance of multiple visual objects must be retained in working memory during a delay period, entry into visual working memory is necessary for these items to be remembered following the delay. If the location of one of the visual objects is cued either before or directly following its presentation, it is more easily remembered than other, uncued items [9]. Thus it appears that by directing attention to the location of one of the objects in a display, working memory is better able to encode the objects for later recall.

These effects of spatial attention are contingent on the ability of the attention system to effectively orient to particular locations in space. This process has been shown to be deficient in patients with focal cerebral damage, and these patients have enabled the study of spatial attention defects. More recently, these investigations have been complemented by functional imaging studies, shedding further light on the neural mechanisms responsible for the control of spatial attention.

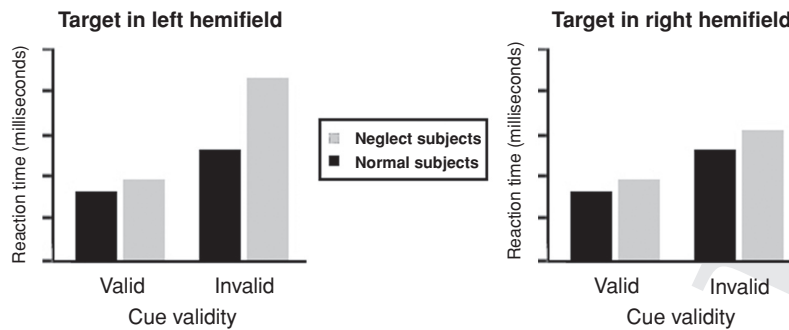
### The parietal lobes, spatial attention, and neglect

One of the most extensively studied cortical regions contributing to spatial attention processes is the posterior parietal lobe. Unilateral damage to the human parietal lobe, especially in the vicinity of the temporoparietal junction (or TPJ, see Figure 8.4), results in a profoundly disabling syndrome referred to as neglect or hemineglect [10, 11]. Because neglect

most often follows right parietal damage, clinical symptoms are most evident for the left side of extrapersonal space or the left side of the patient (i.e., left hemineglect). Neglect has been known to occur following focal lesions to areas other than the parietal lobes, such as the frontal lobes, but most studies of attention in patient populations have focused on damage to parietal lobe structures. Within the parietal lobe, there has been debate over what regions are most crucial to the control of attention. A number of studies have implicated damage to the TPJ in neglect, but others have associated symptoms of neglect with damage to the superior parietal lobe (SPL). Friedrich and colleagues [11] directly compared the effects of focal damage to either the TPJ or the SPL, and showed that patients with damage to the TPJ were more likely to display symptoms characteristic of neglect, supporting a central role of the TPJ in the control of spatial attention.

Patients with neglect typically fail to attend to stimuli falling within the region of space contralateral to the lesion (the contralesional side of space). In many cases, individuals with neglect will fail to read words on the left side of the page, eat food on the left side of the plate, or shave the left side of the face. Importantly, this failure to attend to stimuli in the hemifield opposite to the lesion is not the result of visual sensory deficits such as scotoma or hemianopia. Patients with sensory disturbances alone are aware of their defects, and therefore will orient to a contralesional hemifield stimulus in order to compensate for their impairment. However, patients with hemineglect are generally unaware of their deficit, and if confronted with a defect on the impaired side (such as a hemiparesis) may even deny it, a phenomenon known as anosognosia.

Insights into the nature of the attentional impairments seen in neglect have come from studies using the attention paradigms discussed above. Posner and colleagues [12] were among the first to study patients with right parietal lobe damage using the guidance of an explicit cognitive theory of attention. Using a spatial cueing task, they found asymmetries in attentional orienting in patients with right parietal lobe damage, who were slower to detect invalidly cued targets presented in the contralesional field. In other words, patients with right parietal damage were slower to detect targets appearing in the left hemifield following an invalid cue in the right hemifield than they were to detect targets



**Figure 8.5.** Hypothetical data depicting a typical “disengage” pattern of results on a spatial cueing task. Compared with normal subjects, patients with parietal lobe damage show slightly slower overall reaction times to targets. Importantly, these patients show a disproportionate slowing in their reaction time to invalidly cued targets following cues presented in their intact hemifield (note the disproportionate cost of invalid cues when the subsequent target appeared in the damaged hemifield). These results have been taken as evidence for a role of the parietal lobe in the disengagement of attention.

appearing in their right hemifield following an invalid cue in the left hemifield (Figure 8.5). However, these patients were nearly as fast to detect validly cued targets in their contralateral hemifield as they were to detect targets in their ipsilesional hemifield, suggesting a disproportionate cost for reorienting attention following invalid cues in the ipsilesional hemifield. Based on this response asymmetry, Posner and colleagues [12] suggested that the parietal lobes allow disengagement of attention and that right parietal lesions cause a “disengage deficit,” that hinders disengagement from the ipsilesional visual field. Thus, when a cue appears in the ipsilesional field and a target follows in the contralesional field, a right parietal lobe patient would have difficulties detecting the target.

This interpretation would predict that patients with damage to both the left and right parietal lobes would be equally likely to show symptoms of neglect. However, as discussed above, this is not the case, and severe or lasting neglect typically results only from damage to the right parietal lobe. Therefore, alternative theories of the deficits present in neglect have emphasized competitive interactions between left and right parietal regions and how this competition affects the control of attention.

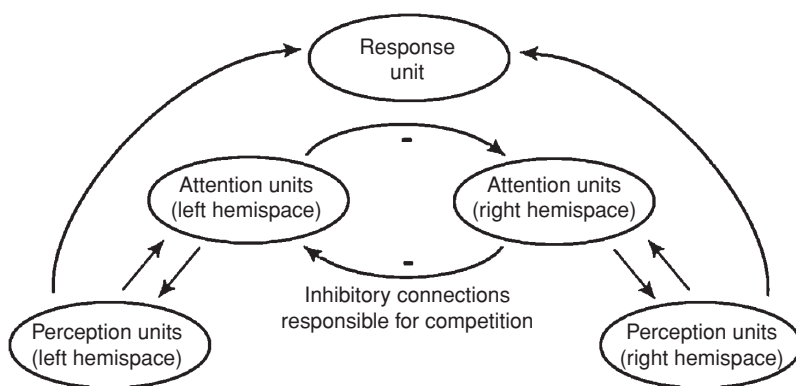
For example, Cohen and colleagues [13] presented a neural network model as an alternative explanation of the disengage deficit (Figure 8.6). In their model [13], neural representations of each visual hemifield compete with each other for attentional selection. If the representation of the left field is damaged, it competes less effectively with the representation of

the right field. As a consequence, when attention is directed to the right (good) field, a target appearing in the left (damaged) field is at a competitive disadvantage. Thus, detecting an invalidly cued target appearing in the left field would be difficult. In contrast, when attention is directed to the disordered left field, a target appearing in the intact right field could compete effectively for attention, allowing this target to be detected relatively quickly. Under this account, no mention of “attentional disengaging” is required. Patients’ behavior appears as though there is a disengagement of attention, but the mechanism underlying the patients’ behavior is based on competition between damaged and intact representations of space, not on an “attentional disengager.”

Effects of right parietal damage on visual search are consistent with results from spatial cueing paradigms. Egly and colleagues [14] asked patients with parietal damage to perform a conjunction search (e.g., color and shape, see Figure 8.2B) across a number of set sizes. The patients were much slower to detect target items when the distracters appeared in the ipsilesional field compared with when they appeared in the contralesional field. In the context of Cohen and colleagues’ model, the presence of ipsilesional distracters may have prevented the contralesional representation of the target from competing effectively for attention.

Taken together, these data suggest that the attention deficits seen following parietal lobe damage are the result of impaired processing of bottom-up inputs to the attention system. This interpretation does not necessarily mean that neglect is an elemental sensory

## Section I: Structural and Functional Neuroanatomy



**Figure 8.6.** An illustration based on the neural network that simulates the “disengage deficit” seen in patients with damage to the parietal lobe by performing a simulated version of Posner’s spatial cueing task. The perception units provide parallel input to both attention units and a response unit. Spatial cues and targets are presented as input to the model by “turning on” one of the perception units. This activation propagates through the network and activates the attention and response units. Thus, if a target is then presented to the right perception unit – an invalidly cued target – the model takes a long time to respond because the right pool of attention units has been inhibited. This model shows a disengage-like pattern of results because damage to one of the attentional pools impairs these units’ ability to compete with the intact pool of attentional units. If the right pool of attention units is damaged (e.g., in parietal damage) a spatial cue on the left (which activates the left pool of attention units) is able to inhibit the right pool of attention units more than if the model was undamaged.

deficit, but rather that it may involve an inability of the attention system to effectively use bottom-up sensory information in the allocation of attention. Recall Wolfe’s guided search model, where bottom-up and top-down inputs are combined to create a salience map of the visual environment. If the attention system is less able to use bottom-up information from contralesional space, salient items in that portion of the visual environment would be less able to compete for attentional selection. As a result, these items would not be readily detected and it would take the observer with neglect longer to respond to them, resulting in the types of search and detection deficits outlined above. Therefore, rather than conceptualizing the posterior parietal lobe as an “attentional disengager,” it may be more accurate to think of this region as being responsible for detecting salient aspects of the environment, allowing the attention system to reorient toward them.

### Frontal lobe influences on spatial attention

Although neglect has typically been studied in patients with parietal lobe damage, neglect can also occur in patients with damage to areas of the frontal lobes. Specifically, damage to the regions of the dorsolateral prefrontal cortex (DLPFC) has been implicated in neglect [15, 16]. Husain and Kennard [17] performed a lesion overlap analysis on lesion information from

patients with focal frontal lobe damage who showed symptoms of neglect. The region of greatest overlap in this analysis was located in a specific area of the DLPFC, the frontal eye field (FEF). This region has been implicated in both overt attentional orienting (attention requiring eye movements) and covert orienting (attentional orienting that does not require eye movements).

Many studies of damage to the FEF have focused on the ability of patients with lesions to this region to overtly direct attention in space. Typically, directing the eyes to a region of space is preceded by directing covert spatial attention to the target region [18], and lesions to the FEF seem to disrupt particular types of eye movements. In a study by Henik and colleagues [19], performance on a spatial cueing task was compared between a group of patients with damage to the FEF and a group of patients with frontal lobe damage that did not include the FEF. In one portion of the experiment, patients performed a “saccade task” in which they were instructed to make eye movements to a peripheral location, indicated by either a central cue (an arrow) or a peripheral cue (a brief peripherally located flicker). In another portion of the experiment, patients performed a detection task in which they were told to respond to a target by pressing a particular key, without making saccades. As in the first task, subjects were presented with either a central arrow cue



or a peripheral flicker cue, which in this task was followed by the presentation of a target, which observers responded to with a button press. In both tasks, half of the cues (central and peripheral) were valid and half were neutral; there were no invalid cues.

It was shown that FEF lesions disrupted eye movements to peripheral locations, but not all eye movements were disrupted equally [19]. The FEF patients were slower to make eye movements into the contralesional field than into the ipsilesional field following central cues. Conversely, following peripheral cues, the patients with frontal damage that included the FEF made faster eye movements into the contralesional field than into the ipsilesional field. However, frontal lobe patients with an intact FEF made eye movements into the contra- and ipsilesional field approximately equally following both central and peripheral cues. The results from the FEF patients indicate that overt, voluntary orienting to central cues is impaired in this group, as these patients are only slowed in directing eye movements to the contralesional field following the symbolic arrow cue. Thus the FEF appears to play a role in the voluntary, or top-down, orienting of attention.

Further evidence implicating the frontal lobes in the voluntary orienting of attention comes from a study by Vecera and Rizzo [20]. In this study patient E.V.R., a well-known patient with bilateral frontal lobe damage, performed two spatial cueing tasks. In both tasks, E.V.R. was instructed to press a key as quickly as possible in response to the detection of a target appearing on either the left or right side of the screen. In one task, peripheral cues were used to direct attention to the location of the target, on either the left or right side of the display. In the other task, central word cues (left, right) were used to direct attention to the target location. It was shown that E.V.R. could use peripheral cues, as evidenced by quicker reaction times to validly vs. invalidly cued target locations. However, performance in the central cue task did not reflect any reaction time differences between validly and invalidly cued trials, indicating that E.V.R. could not use the directional information provided by the central cue. These results suggest that regions of the frontal lobes are critical for voluntary, top-down attentional control, with the FEFs being particularly important.

### Functional imaging of spatial attention

As already mentioned, top-down or “goal-directed” attentional processes are those that rely on an

observer’s knowledge about the environment to guide attention. This knowledge can include previously learned information (e.g., looking for a friend’s face in a crowd) or can be based on a particular goal state (e.g., searching for an empty chair in a crowded auditorium). Conversely, bottom-up, “stimulus-driven” attentional processes rely on the properties of the stimuli present in a scene and attract attention on the basis of some unique visual quality rather than any cognitive factors. Whereas the patient studies discussed above provided early insights into brain regions involved in the control of attention, a number of recent functional imaging investigations have attempted to more precisely elucidate the mechanisms involved in both stimulus-driven and goal-directed attentional orienting.

In an early event-related functional magnetic resonance imaging (fMRI) study by Hopfinger and colleagues [21], hemodynamic responses of observers were recorded while they performed a cueing task that used a central cue. In this study, observers were presented with a central arrow cue that always indicated the location of the target to-be-discriminated. By using a predictive central cue, it was possible to isolate the activation of brain structures involved in voluntary allocation of attention in space. Analyses of hemodynamic responses to these stimuli revealed that a number of discrete regions of parietal and frontal cortex were differentially active during attentional orienting and response. Specifically, regions in superior frontal and parietal cortex showed increased activity in response to the presentation of the central cue. This increased activity was greatest for the FEF and intraparietal sulcus (IPs), suggesting that these regions were linked in controlling the voluntary orienting of attention to locations indicated by the cue. In contrast to the more dorsal activation in response to the top-down information provided by cue, ventral regions of the prefrontal and parietal cortex showed greater activation in response to the presentation of the target. In particular, the inferior frontal gyrus (IFG) and inferior parietal lobule (IPL) showed greater activity during target presentation, indicating that these regions may be involved in the selective processing of stimuli and subsequent response processes rather than attentional orienting in general.

Further evidence for a dorsal-ventral distinction between structures supporting voluntary attentional orienting and stimulus detection comes from a study in which the neural activity in response to

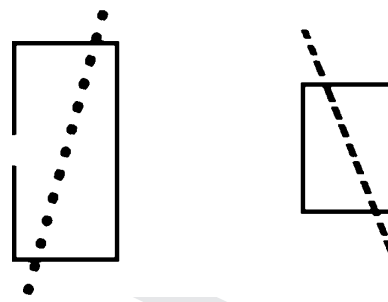
## Section I: Structural and Functional Neuroanatomy

peripheral and central cues was directly compared. Kincaid and colleagues [22] used a spatial cueing task in which observers monitored a display for a target letter appearing on either the left or right side of the display, responding to the identity of the letter once presented. Before target presentation, a spatial cue was presented that could be either valid or invalid with respect to the subsequent target presentation. Critically, across blocks of trials the cue could be peripheral, central, or neutral (no cue), allowing for a comparison between cues that relied on voluntary and stimulus-driven shifts of attention. When central cues were used to direct attention, there was significantly higher activation in bilateral areas of the FEF and IPs than in conditions where either peripheral or neutral cues were presented, consistent with previously discussed findings. Moreover, these same dorsal regions showed greater activation in response to peripheral cues as well, suggesting that this dorsal frontoparietal network mediates both stimulus-driven (bottom-up) and goal-directed (top-down) allocation of attention.

### Object-based attention

To this point, our discussion has focused on the control of attention in space. However, attention also may be directed toward objects. In particular situations, object selection can take place regardless of where the object appears, suggesting that object-based and space-based attention are dissociable processes. When studying object-based attention, it is important to use designs that rule out selection by spatial attention, since by necessity objects occupy locations in space. For this reason, most studies of object-based attention have used experimental designs that eliminate or hold constant the spatial separation between objects.

Although a number of object-based attention paradigms have been employed in the attention literature, this discussion will be limited to two of the most widely used tasks. In the “object attribute” task developed by Duncan [23], observers view a stimulus which includes two overlapping objects: a box and a line (Figure 8.7). Each object has two features: the box can be tall or short, and has a gap on either the left or the right side; the line can be either dashed or dotted, and can be tilted either to the left or the right. A box/line stimulus is presented briefly (~100 ms) and followed by a masking stimulus that disrupts perception. Observers are asked to report two of the



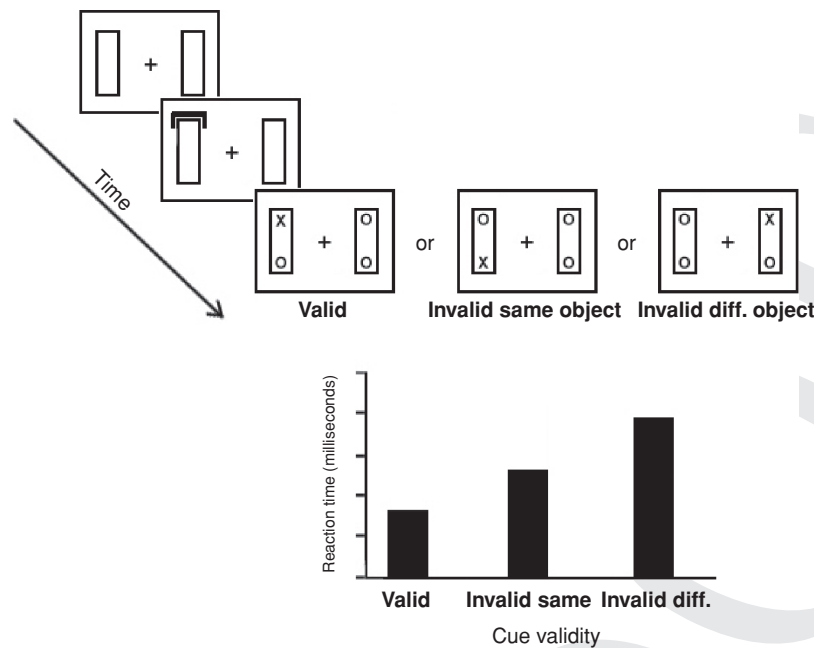
**Figure 8.7.** An illustration of stimuli used to study object-based attention. Participants report features from the same object (e.g., box height and side of gap) or from different objects (e.g., box height and line tilt).

four features mentioned above, and the features can come from the same object (e.g., box height and side of gap) or from different objects (e.g., box height and type of line). Observers are typically more accurate when reporting two features from the same objects than when reporting two features from different objects.

A second paradigm developed for studies of object-based attention uses an adaptation of the spatial cueing method already discussed. In a task developed by Egly and colleagues [24], observers view two rectangles, and the end of one of the rectangles is cued with a brief flash (i.e., a peripheral cue), followed by a target item (Figure 8.8). On most trials, the cue is valid and the target appears in the same location as the cue. Critically, on some trials the target appears at an uncued location, either within the same object that was cued or in another, uncued object. Even when uncued targets appear at the same distance from the cued region of the rectangle, observers are faster to respond to targets appearing in the uncued end of the cued rectangle than at any location in the uncued rectangle. This seems to suggest that attention automatically spreads across an entire object, conferring the benefits of attention to any region located within an attended object.

Results from these studies suggest that space- and object-based attention can be dissociated from one another at the behavioral level. A number of patient and functional imaging studies seem to support this dissociation, although it appears that portions of the same attention system responsible for carrying out space-based attention are recruited during object-based attention. The next section reviews relevant data from patient populations and functional imaging studies regarding the neural mechanisms of object-based selection.

## Chapter 8: Attention



**Figure 8.8.** An illustration of the object cueing paradigm and typical results. Following a pre-cue, a target appears at either the cued location (left), at an uncued location in the same (cued) object (center), or at an uncued location in the other (uncued) object (right). Response times are faster to targets that appear in the cued object (Invalid Same) than in the uncued object (Invalid Different [Diff.]), even though these two locations are the same spatial distance from the cued region.

### Object-based attention in neglect

As discussed above, patients with neglect due to parietal lobe damage often fail to attend to stimuli falling within the region of space contralateral to the lesion, neglecting to read words on the left side of the page or eat food on the left side of the plate. In addition to deficits in spatial attention, patients with neglect may also show deficits in object-based attention. Although it is possible that some object-based attention deficits in neglect patients arise as a secondary effect of their spatial attention deficits, a number of studies have shown that these deficits can be dissociated in these patients.

An early study of object-based attention in parietal patients was carried out by Egly and colleagues [24], as a portion of the study described above. In their study, patients were placed into two groups based on the laterality of their parietal lobe lesion; one group consisted of patients with damage to the left parietal lobe, and the other group had damage to the right parietal lobe. With the use of a cued detection task identical to that described above (see Figure 8.8), object-based attention effects were measured between the two groups. Results showed that the two groups exhibited different types of attentional impairment in the task. Both groups showed evidence of impaired disengagement following invalid cues, which would be expected

based on the site of their lesions. However, the two groups differed in their object-based results. Patients with damage to the right parietal lobe showed a typical object effect, responding faster to invalid targets appearing in the cued object than those appearing in the uncued object. In contrast, patients with damage to the left parietal lobe showed a larger object effect in their contralesional field than in their ipsilesional field, indicating that they had trouble shifting attention between objects when the objects fell within their contralesional field. The authors suggested that the performance differences between patients with damage to left and right parietal lobes was due to differential recruitment of left and right parietal lobes during object-based attentional selection. Specifically, it was hypothesized that the right parietal lobe may be more involved in spatial attention processes (since damage here results in space- but not object-based attention effects), whereas the left parietal lobe may be more involved in object-based attention processes.

### Functional imaging of object-based attention

The neural mechanisms underlying object-based attention effects have received a great deal of study using functional imaging in recent years. In many of these studies, locations of to-be-attended items are held constant, as described above, allowing the control

## Section I: Structural and Functional Neuroanatomy

processes responsible for attention to objects to be isolated from those involved in attention to spatial locations. In a functional imaging study reported by Serences and colleagues [25], observers viewed a continuous stream of superimposed houses and faces, presented in the same location at the center of the display. Observers were asked to selectively attend to either the house stream or the face stream, monitoring the streams for one of four possible targets (two houses, two faces). One of the face or house targets signaled that attention should remain on the current stream of objects (the “hold” condition), and the other target signaled that attention should be shifted to the other object stream (the “shift” condition). By comparing activations in the hold and shift conditions, it was possible to isolate regions involved in object-based shifts of attention. It was shown that relative to the hold condition, there was increased activity in bilateral regions of the superior parietal lobule (SPL) during trials that required a shift of attention between object streams. The authors concluded that this response reflected a transient signal that indicated an object-based shift of attention.

Further support for the involvement of the SPL in object-based shifts of attention comes from another study using an object-based cueing task similar to that in Figure 8.8 [26]. Observers viewed two rectangles oriented perpendicular to each other, with a color patch located in both ends of each rectangle, and were initially instructed to attend to a single color patch. The color patches changed in color synchronously every 250 ms, and observers were asked to monitor the stream for one of three particular target colors. One color indicated that observers should hold attention on the current patch, another indicated that they should shift attention to the color patch at the other end of the same object, and another indicated that they should shift attention to the color patch at the same end of the other object. Overall, activation in bilateral SPL regions was greater for shift trials versus hold trials, consistent with the results of Serences and colleagues [25]. In addition, activation in the left SPL showed object-based modulation; in trials that required within object shifts, left SPL activations were increased relative to trials requiring between-object shifts. These data indicate that regions of the left SPL may be specifically involved in object-based shifts of attention, a finding consistent with that reported

in Egly and colleagues’ [24] study of object-based attention in a patient with left parietal lobe damage. Taken together, these results show that some parietal regions involved in spatial attention processes may also be responsible for mediating object-based attention. Additionally, there appears to be a bias toward regions in the left SPL in mediating the control of attention to objects.

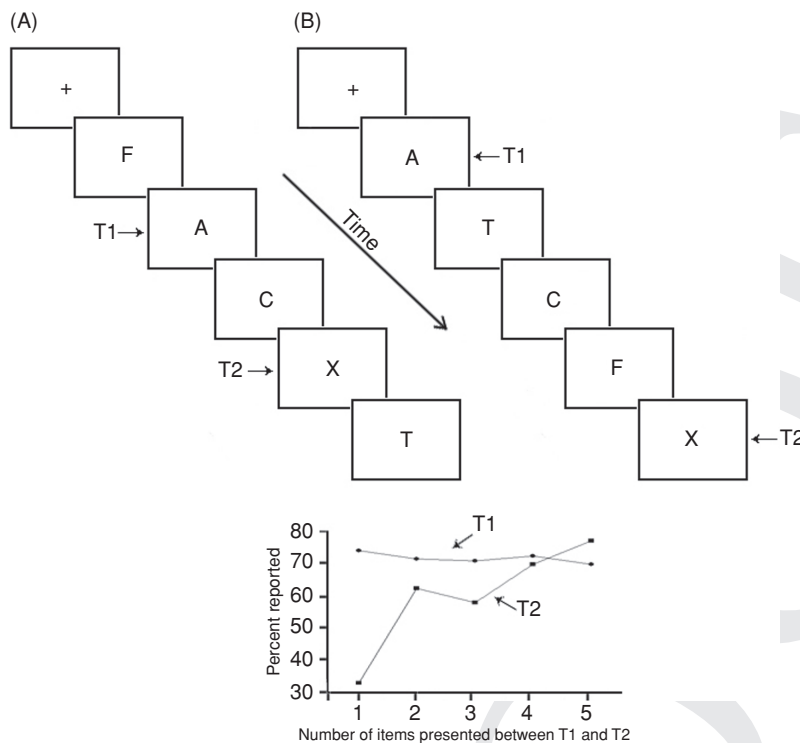
## Attention and visual working memory

Both spatial and object attention involve selection of perceptual characteristics that do not persist beyond the duration of the attentional operation. Visual working memory provides a mechanism for the storage of three to four objects in a more durable form over a longer period of time [9]. Recent research suggests that attention is vital for allowing information to enter into visual working memory, gating incoming sensory information, and keeping the working memory system from becoming overloaded.

Evidence for this function of attention – as a gatekeeper for working memory – comes from studies of an event referred to as the “attentional blink.” In a typical attentional blink task, observers are presented with a rapid serial visual presentation (RSVP) of stimuli in which they are asked to detect two targets from the stream, responding at the end of the stream [27]. Figure 8.9 depicts a typical attentional blink task. In this example, observers are asked to identify two letters within a stream of numbers, with letter one being target one (T1) and letter two being target two (T2). There is a window of time following the detection of target one where observers fail to detect the presentation of a second target (see Figure 8.9A). However, if T2 is presented a sufficient time after T1, observers typically have little problem detecting the target (see Figure 8.9B). The period of time following the presentation of T1 where subjects are unable to detect T2 is referred to as the attentional blink because, as in an eyeblink, there is a brief period during which targets cannot be detected. Typical results from an attentional blink task are shown in Figure 8.9C. Note that the recognition of T2 depends upon the occurrence of T1. If no T1 target appears, observers are accurate at reporting T2, and there is no attentional blink.

These results suggest that the attentional blink arises from an inability to store T2 in visual working

## Chapter 8: Attention



**Figure 8.9.** Attentional blink paradigm and typical results from this paradigm. In this example, subjects are asked to monitor the stream of letters and respond to two targets – the letters A and X. (A) shows a rapid serial visual presentation (RSVP) stream of letters and numbers, with T1 and T2 separated by a single item. (B) shows the same RSVP task, but T1 and T2 are separated by a greater number of intervening letters. The bottom panel shows a typical attentional blink result: After identifying the first target digit (T1), observers fail to correctly identify the second target digit (T2) when it appears shortly after T1, as in A. However, if T2 is presented sufficiently long after T1, as in B, observers can correctly identify both targets.

memory. This incapacity is due to the fact that attending to T1 delays the allocation of attention to the second target for a short period of time. Therefore, if the second target is presented soon after the first, it cannot be immediately processed and decays before being stored in working memory. However, as the time between T1 and T2 increases, processing of T1 is more likely to be completed by the time T2 appears, allowing attention resources to be allocated to T2 and resulting in detection of the second target.

The attentional blink paradigm has been used in patient populations to shed light on the neural structures responsible for the type of memory-based attention outlined above. For example, Husain and colleagues [17] showed that an increased attentional blink can accompany visual neglect. Eight subjects with a mean age of 64 years were studied one month (on average) after a right hemisphere stroke affecting IPL, ventral frontal cortex (VFC), or the basal ganglia. All had clinically defined visual neglect and performed an attentional blink task similar to that in Figure 8.9. It was shown that the neglect patients could not identify the second target

in the visual stream until 1.4 s had elapsed after the identification of the first target, an attentional blink that was nearly twice that of non-brain-damaged subjects (540 ms). Based on these results, the authors concluded that visual neglect is a disorder that affects the patient's ability to direct attention in time as well as space. Furthermore, this study implicated the same cortical regions involved in attention in space and attention to objects in higher-level memory-based attention.

However, Rizzo and colleagues [28] provided further details in 13 subjects with chronic focal brain lesions on MRI and nine control subjects without neurological impairments performing an RSVP task that used letters as targets. The results showed that an abnormal attentional blink could occur with lesions in either hemisphere and persist for years. The abnormality affected both length and magnitude of the attentional blink; did not require a lesion in the parietal lobe, frontal lobe, or basal ganglia; occurred independently of spatial neglect, and persisted after spatial neglect resolved. The authors concluded that an increased attentional blink has no special status



## Section I: Structural and Functional Neuroanatomy

in neglect, and that the neural mechanisms of spatial attention that are disrupted in the visual hemineglect syndrome differ from the neural mechanisms that underlie the attentional blink. Elucidation of the neural structures responsible for the type of temporal selection seen during the attentional blink is an active area of research, with a number of recent functional imaging studies providing insights into the neural correlates of memory-based attentional control [29].

### Executive attention and task selection

The last form of attentional selection to be discussed is the selection of one task from among many possible ones, which also implicates the coordination of multiple tasks [30, 31]. In all of the paradigms discussed above, observers perform the same attention task throughout, yet in real life, humans often perform different tasks concurrently or in series, such as rehearsing a phone number that was looked up, dialing the phone number, and conversing with the person just called. In general, executive functions control the focus of attention [32] and the executive system permits the awareness of marked changes in an object or a scene.

The failure of executive control over attention has important real-world implications for noticing changes in the environment, particularly when information load is high. For example, automobile drivers navigating through complex driving environments with high traffic and visual clutter would be required to use the executive system to recognize and cope with changes in the driving environment [33, 34]. Driver errors occur when attention is focused away from a critical roadway event in which vehicles, traffic signals, and signs are seen but not acted upon, or are missed altogether [35]. Sometimes eye gaze is captured by irrelevant distracters [36] that may prevent a driver from seeing a critical event [37], such as an incurring vehicle or a child chasing a ball. Drivers with cerebral lesions disrupting the executive system are liable to be “looking but not seeing” despite low information load [38, 39].

Considering the multiple tasks involved in a complex task such as driving, executive control is needed to switch the focus of attention between various critical tasks such as tracking the road terrain, monitoring the changing locations of neighboring vehicles,

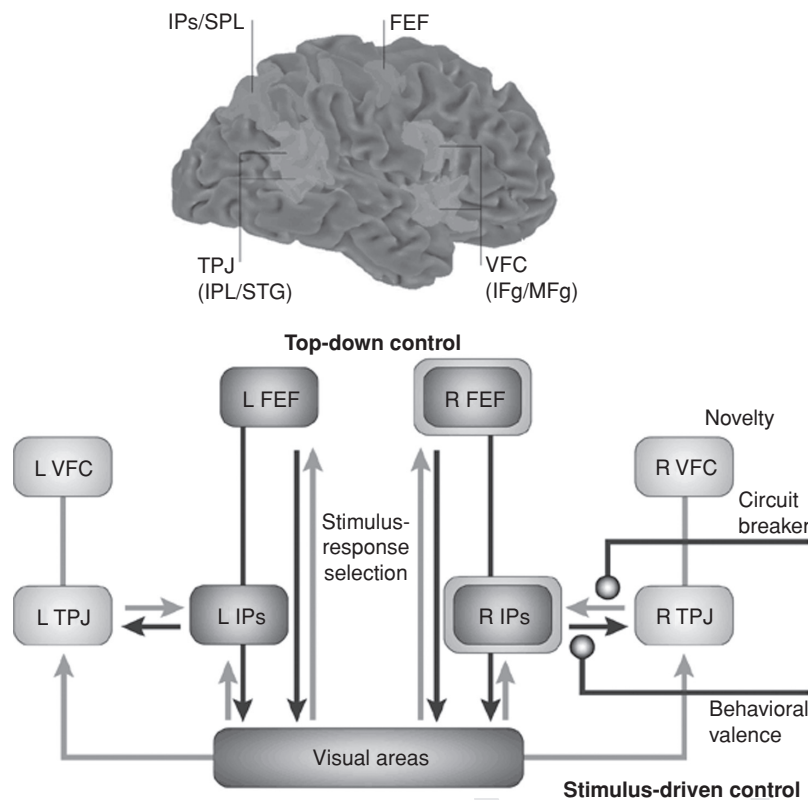
reading signs, maps, traffic signals, and dashboard displays, and checking the mirrors. This requires switching attention between disparate spatial locations, local and global object details, and different visual tasks. Drivers must also switch attention between modalities when they drive while conversing with other vehicle occupants, listening to the radio, using a mobile phone, and interacting with in-vehicle devices [40]. These attentional abilities can fail in drivers with visual processing impairments caused by cerebral lesions or fatigue [32, 41].

### Neural systems involved in the control of attention

Before the advent of functional imaging techniques, research on patients with focal brain damage provided a great deal of evidence for brain regions involved in the control of attention. From this work, a number of cortical areas involved in attentive processing were revealed, allowing an early classification of the neural systems involved in the control of attention [12, 42]. These theories paved the way for functional imaging studies that attempted to classify the large-scale operations of attention systems involved in the performance of specific attention-demanding tasks. To this point, the account has focused on distinct regions of the brain that play a role in the control of attention. This section will center on the relationships between these various regions, describing how specific brain areas directly interact to form large-scale neural systems responsible for the control of attention.

A useful organizing concept is Corbetta and Shulman's [43] model of selective attention, which was developed by synthesizing large amounts of data from patient and functional imaging studies, as well as information from early models of attentional selection. Based on this information, Corbetta and colleagues have developed a theoretical framework for the neural mechanisms of attentional selection. In their model, two separate attentional systems are posited that rely on differential frontoparietal connectivity, each system being involved in a different aspect of attentional control. The bilateral dorsal frontoparietal system is hypothesized to be involved in the overall control of attention, and consists of the IPs-FEF network shown to be responsible for the voluntary orienting of attention in response to relevant top-down information. This system is complemented by a right-lateralized

Chapter 8: Attention



**Figure 8.10.** Illustration of a neuroanatomic model of attentional control. Top: diagram indicating brain regions involved in the control of attention. Bottom: Schematic of the mechanisms of a model of attentional control [43]. The dorsal network (IPs-FEF), indicated by the black arrows, is involved in the top-down, or “goal-directed,” control of attention. The ventral network (TPJ-VFC), indicated by the gray arrows, is involved in bottom-up, or “stimulus-driven,” control of attention. The dorsal system is also modulated by bottom-up information, with the TPJ communicating with the IPs and acting as a “circuit breaker” allowing salient bottom-up information to interrupt voluntary, top-down orienting, in turn reorienting attention to salient aspects of the environment. Abbreviations: IPs: intraparietal sulcus; SPL: superior parietal lobule; FEF: frontal eye field; TPJ: temporoparietal junction; IPL: inferior parietal lobule; STG: superior temporal gyrus; VFC: ventral frontal cortex; IFg: inferior frontal gyrus; MFg: middle frontal gyrus; L: left; R: right. Adapted from Corbetta M, Shulman GL. Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci.* 2002;3(3):201–15, with permission from Macmillan Publishers Ltd. This figure is presented in color in the color plate section.

ventral-frontoparietal system that includes regions of VFC and the TPJ. The ventral-frontoparietal system is involved in the detection of salient or novel bottom-up information, especially with regard to behaviorally relevant stimuli, and can act as a circuit breaker for the dorsal system. Specifically, it is hypothesized that the right TPJ is involved in detecting task-relevant or salient stimuli outside of the focus of processing, and through interactions with the IPs in the dorsal system can cause attention to re-orient in response to these stimuli (Figure 8.10).

To illustrate this model, consider another familiar example. Imagine searching the night sky for a particular constellation. In an example such as this, one

uses previously learned information such as the constellation’s location or the way that it typically appears to guide one’s search. At a neural level, this process would rely on structures in the dorsal-frontoparietal circuit. Now imagine that, suddenly, a shooting star appears in the corner of one’s eye, capturing attention. This event would be detected by structures in the ventral-frontoparietal circuit, and a signal would be sent to the IPs to re-orient attention toward the shooting star. By this account, the dorsal attention system is responsible for the overall control of attention, but the ventral-frontoparietal system acts as an environmental sensor that picks up on relevant bottom-up information.

## Section I: Structural and Functional Neuroanatomy

An appealing feature of this neural model of attentional control is that it maps well onto Wolfe's guided search model of attentional control during visual search [4, 5]. Recall that according to guided search theory, salient bottom-up information from the visual field is represented by category-specific feature maps, with separate maps for features such as color and orientation. In addition, these maps include not only information about physical features present in the visual field, but also for the locations of these features, marking possible areas of interest for the allocation of attention. This information is combined with top-down information regarding current goals or previous knowledge, forming an overall saliency map of the entire visual scene. This saliency map is then used to guide attention to regions of a scene most likely to include stimuli of interest.

In the context of Corbetta and Shulman's model, the ventral frontoparietal system may act as a saliency detector that, through reciprocal connections with visual and association cortices, uses bottom-up information to alert the dorsal system to salient aspects of the environment. This arrangement would allow the ventral system to direct attention in a stimulus-driven manner to highly salient stimuli in the visual field through its interactions with the dorsal system. Based on the functional imaging findings discussed above, Kincade and colleagues [22] hypothesized that the dorsal frontoparietal system is an ideal candidate for the saliency map described in guided search theory. Through interactions with the ventral system, this map receives bottom-up information from the environment. In addition, its involvement in goal-directed attentional control indicates that it directly uses top-down information to direct attention. Therefore, in the context of guided search components, the dorsal system (especially the FEF) appears to be a candidate region responsible for overall saliency coding, representing a possible neural correlate of the saliency map [44].

### Dorsal and ventral attention systems and neglect

As we have already described in detail, damage to regions of the parietal lobe, particularly on the right, results in profound neglect of contralesional space. How does Corbetta and Shulman's model of attention map onto the deficits seen in patients with neglect?

Mesulam [45] has hypothesized that the deficits seen in neglect result from damage to regions that control the deployment of attention in response to top-down signals, which in the context of Corbetta and Shulman's model would imply that neglect arises following damage to the FEF or IPs, or the dorsal attention system. However, data previously discussed show that neglect is most often the result of damage to the TPJ [11], a component of the ventral attention system. Therefore, Corbetta and Shulman have suggested that neglect more likely reflects damage to the ventral TPJ-VFC system, an assertion based on the following findings from neglect studies:

- (1) Neglect most often arises following damage to regions of the TPJ, which is part of the ventral attention circuit [11, 46].
- (2) Neglect is more frequent, severe, and lasting following right parietal lesions. Recall that the functions of the ventral TPJ-VFC system are right lateralized, whereas the functions of the dorsal system are bilateral. The stronger association of neglect with right parietal damage is consistent with ventral-system damage.
- (3) Neglect patients show impaired inability to effectively use bottom-up information in the control of attention, as evidenced by the "disengage" deficits described above – a function attributed to the ventral system. However, they retain the ability to effectively use top-down information to guide attention, indicating an intact dorsal attention system [47].

Although this model fits many of the data regarding the deficits seen during neglect, one point of divergence from the literature should be noted. In this model the ventral frontoparietal system is hypothesized to be right lateralized, with no homologous function attributed to the TPJ-VFC system in the left hemisphere. Therefore, damage to this system would predict bilateral deficits in attentional orienting to salient bottom-up sensory information by the dorsal IPs-FEF system.

However, this is not typically the case: there is a disproportionate deficit in directing attention to stimuli appearing in contralesional space, with a relative sparing of the ability to orient to stimuli in the ipsilesional field. It is possible that damage to the right TPJ or underlying white matter could impair communication between the ventral saliency detector and dorsal

orienting system, resulting in a functional inactivation of the right dorsal IPS-FEF system. This would lead to the same types of “disengage” deficits described above, with the intact left dorsal attention system more effectively competing for attentional resources. Although Corbetta and Shulman’s model is tentative, it provides an intuitive framework for understanding the allocation of attention in response to bottom-up and top-down information. Importantly, this model maps well onto a widely accepted functional theory of attention, and is supported by a large amount of converging evidence from patient and functional imaging studies.

## Conclusion

Attention is required for focusing on relevant information in the environment, simultaneously suppressing irrelevant information. By restricting what stimuli are and are not processed, attention acts as a gating system that allows us to function efficiently in a highly complex, ever-changing environment. Although the term attention has traditionally been considered to represent a single, monolithic process, it is clear that attention can and does operate across a number of different functionally defined levels. Whereas it is evident from the above discussion that many forms of attention have been defined, further research is needed to better understand both the functional and anatomic mechanisms involved in the control of these processes.

Using behavioral techniques provided by cognitive psychology, the processes of attention can be studied rigorously across these multiple domains. By using well-defined behavioral measures in conjunction with neuropsychological and neurophysiological techniques, it is also possible to study the multiple components of attention at a structural level, providing further insights into how the brain carries out attentive processing. This chapter has provided evidence for a number of cerebral sites that appear to be involved in the overall control of attention. Understanding how these sites interact and how they relate to functional theories of attentional control will greatly increase our understanding of normal and disordered attentional control processes.

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Chapter 8: Attention

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