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CHAPTER SEVEN

Neurophysiology of Selective Attention

Steven J. Luck
University of Iowa, USA

INTRODUCTION

Why Neurophysiology?

At any given moment, the human brain is confronted with a multitude of inputs: sounds from many sources; tactile sensations from the entire surface of the body; visual inputs from a huge array of retinal receptors; a variety of smells and tastes; and internally generated thoughts, emotions, memories, and images. Most of these inputs are irrelevant at any given moment, however, and it is therefore more efficient to focus our limited cognitive processing resources on a subset of the available information and ignore the rest; this is the primary role of selective attention in information processing. Although this selection process is usually conceptualized as a cognitive phenomenon that falls exclusively within the domain of psychology, neuroscientists have also become interested in the topic of selective attention in recent years. Before I begin describing their discoveries, however, I would like to consider why neuroscientists have become interested in attention and why psychologists are becoming interested in neurophysiological studies of attention.

To understand the recent interest of neuroscientists in attention, it is useful first to review some important developments in the areas of sensory anatomy and physiology. During the past 20 years, scientists have discovered over 30 separate areas of primate visual cortex that contribute to different aspects of visual perception, including depth perception, motion discrimination, spatial frequency analysis, color processing, and face recognition. As shown in Fig. 7.1a, visual information enters the nervous system in the retina, travels through a relay station called the lateral geniculate nucleus (LGN), and enters the cerebral cortex at the back of the head in an area named V1 (also known as "striate cortex" because of a prominent striation [stripe] that demarcates this area). From this starting point, information branches off and travels forward into the many specialized visual areas that are located in the posterior half of the brain (called "extrastriate" visual areas). As the information travels forward from striate cortex into extrastriate cortex, the features coded by single neurons change from simple bars and edges to more complex attributes of object identity (see Fig. 7.1b).

At the same time that neurophysiologists were discovering this posterior-to-anterior flow of visual information, neuroanatomists were mapping the connections between visual areas, and they discovered something unexpected: wherever a forward connection existed from a lower-level area to a higher-level area, there was also an extensive backward connection from the higher-level area back to the lower-level area (see Rockland, Saleem, & Tanaka, 1994; Rockland & Van Hoesen, 1994; Van Essen, 1985). If visual processing consists of the transformation of simple representations in posterior visual areas into complex representations in anterior visual areas, then what could explain the ubiquitous anterior-to-posterior connections that were so obvious in the anatomy? One likely answer is that these backward "feedback" connections allow top-down cognitive processes like attention to exert control over visual processing. Indeed, computational models of the visual system have frequently relied on top-down processing to solve certain computational problems that arise in simple feedforward systems (e.g. McClelland & Rumelhart, 1981; Mozer, 1991). Unfortunately, however, most studies of visual physiology are conducted with anesthetized animals in whom many of these top-down processes are shut down, potentially eliminating half of the inputs into each visual area. Several neurophysiologists have therefore developed methods to measure neural activity in awake monkeys so that the important effects of attention and other top-down factors can be assessed, as will be discussed later.

There are two other aspects of visual anatomy and physiology that have also led neuroscientists to become interested in attention. First, many studies have shown that the different features of a stimulus, such as its color and its shape, may be coded by different neurons, and these neurons may be located in very different areas of visual cortex. This form of stimulus coding is very efficient, allowing the brain to form representations of many different types of stimuli without devoting a different set of neurons to each combination of features that might be encountered. However, this coding scheme requires a mechanism for linking together the different features that

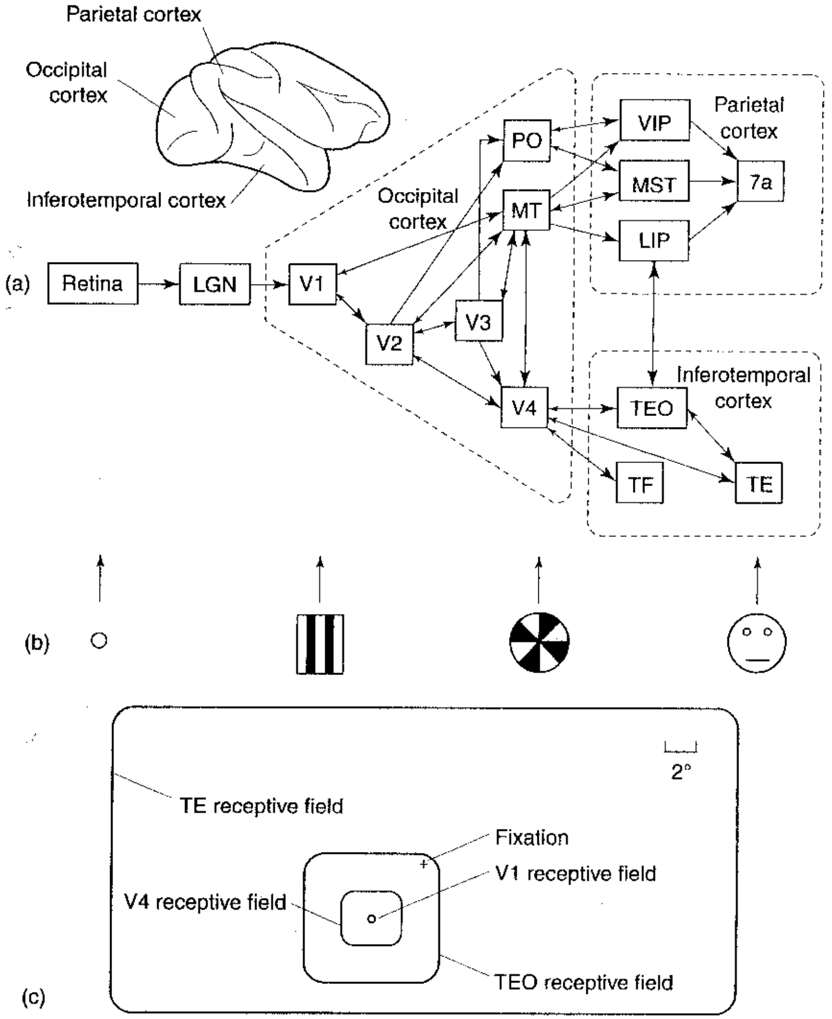

FIG. 7.1. (a) Diagram of several of the major visual areas and their interconnections in the macaque monkey (adapted from Desimone & Ungerleider, 1989). Large arrowheads represent feedforward connections and small arrowheads represent feedback connections. Information enters the retina, passes through the lateral geniculate nucleus (LGN) of the thalamus, and enters cortex in area V1. From area V1, the information diverges into an upper pathway that travels into the parietal lobes and a lower pathway that travels into the ventral portion of the temporal lobes. This diagram shows only a subset of the known areas and connections; for a more complete listing, see Felleman and Van Essen (1991). (b) Examples of the stimuli to which neurons in the various visual areas are sensitive. Neurons in the retina will produce large responses to simple spots of light and neurons in area V1 typically respond well to bars and gratings, whereas neurons in areas V4 and TE are selective for progressively more complex stimuli. (c) Typical receptive field sizes in several visual areas in the object recognition pathway (based on data from Boussaoud, Desimone, & Ungerleider, 1991; Desimone & Schein, 1987). Each outlined region represents the area in which an appropriate stimulus will elicit responses from a typical neuron in a given part of the visual system. In area V1, for example, a neuron

define a single object, and many researchers have proposed that attentional processes are responsible for solving this "binding problem" (Crick & Koch, 1990; Desimone, Wessinger, Thomas, & Schneider, 1990; Mozer, 1991; Niebur, Koch, & Rosin, 1993; Treisman & Gelade, 1980). A related characteristic of the visual system is the progressive increase in receptive field sizes that is observed as information flows forward through the visual system (see Fig. 7.1c). The receptive field of a neuron is the area of space to which the neuron is sensitive: an individual neuron in the initial cortical visual area (V1), for example, will respond only to stimuli presented within a very restricted area, whereas an individual neuron in the final area of visual cortex (TE) will respond to stimuli presented almost anywhere within the central region of visual space. The large receptive fields that are present in anterior visual areas also help the brain to code stimuli efficiently, because separate neurons are not needed to indicate the presence of a given stimulus at each possible location. Unfortunately, large receptive fields can lead to ambiguous responses because most natural scenes are likely to contain multiple objects within a single large receptive field. For example, if a neuron that codes blue stimuli is presented with a blue object and a red object simultaneously within its receptive field, its response will indicate that a blue object is present but it cannot indicate which of the two objects is blue. This is really just another form of the binding problem, and may also be solved by means of attentional mechanisms.

In addition to answering questions concerning the role of attention in neural processing, neurophysiological studies of attention have also provided a useful source of information about how attention operates at the psychological level. In particular, neurophysiological techniques provide an alternative means of measuring the effects of attention on perceptual processing. Many questions in the study of attention address the nature of the processing that is allocated to attended versus unattended stimuli, but behavioral responses such as button presses or verbal reports have two major limitations when questions of this nature are addressed. First, in order to compare the processing of attended and unattended stimuli with behavioral measures, it is often necessary to require responses for both attended and unattended stimuli; requiring a response for an unattended stimulus may make it impossible for subjects to ignore these stimuli fully. Second, behavioral responses occur only after a long series of perceptual, decision, and motor processes, and attention-related changes in overt responses may be difficult to attribute to a particular process within that series. For example, if subjects are unable to report the identity of an unattended stimulus, how can we tell whether they failed to perceive this stimulus or whether they perceived it but simply failed to store it in memory for later report? Neurophysiological techniques can be used to provide measurements of the individual processes between a stimulus and a response, and can therefore provide a relatively direct means of assessing the effects of attention on specific perceptual processes.

Neurophysiological Techniques for Studying Attention

Most neurophysiological studies of attention have employed one of three methodologies: (1) direct electrical recordings of individual neurons in monkeys; (2) indirect electrical recordings of large groups of neurons in humans; or (3) noninvasive measurements of regional cerebral blood flow in humans. The first of these, the single-unit recording technique, is conceptually the simplest but is probably the most difficult in practice. With this technique, it is possible to record the output of a neuron, which is a momentary voltage impulse or "spike" that begins in the cell body and travels down the length of the axon to the terminals, where neurotransmitter chemicals are released to pass the signal on to other neurons. The voltage spikes can be recorded by inserting a tiny electrode into the brain until the tip of the electrode is near enough to a neuron's body to pick up its spikes; this is called an "extracellular" recording, because the electrode remains outside the neuron. Fortunately, there are no pain receptors within the brain, so the electrode can be inserted without any anesthesia.

When an appropriate visual stimulus is presented, a neuron in visual cortex will respond with a burst of spikes, and the so-called "firing rate" during this burst (the number of spikes per second) is used as a measure of extent to which the stimulus is registered by the neuron. For example, some neurons prefer blue stimuli and will fire vigorously when a blue stimulus is presented, but may give no response to a red stimulus. Because the responses of a given neuron may vary from trial to trial, the average response over a large number of trials is typically computed in the form of a poststimulus histogram, as shown in Fig. 7.2a. This histogram shows how the average firing rate varies over time during the interval following stimulus onset, and provides a convenient means of displaying the time course of sensory processing within a single neuron.

It is not usually possible to insert electrodes into the human brain,[1] but there are alternative techniques that can be used to record the electro-

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[1] Intracranial recordings are sometimes obtained from epilepsy patients who are undergoing evaluation for surgical removal of the epileptic focus. In this procedure, strips of electrodes may be placed on the cortical surface or depth electrodes may be inserted directly into the cortex. The electrodes may be left in place for several days, during which they are used to find the epileptic focus so that it can be removed, and to identify critical areas of cortex (e.g. language areas) so that they can be avoided. In some cases, the patients also agree to participate in experiments designed to assess the electrophysiology of cognition (e.g. Allison et al., 1993; McCarthy, Wood, Williamson, & Spencer, 1989; Nobre, Allison, & McCarthy, 1994), but these experiments are necessarily limited by the condition and availability of the patients.

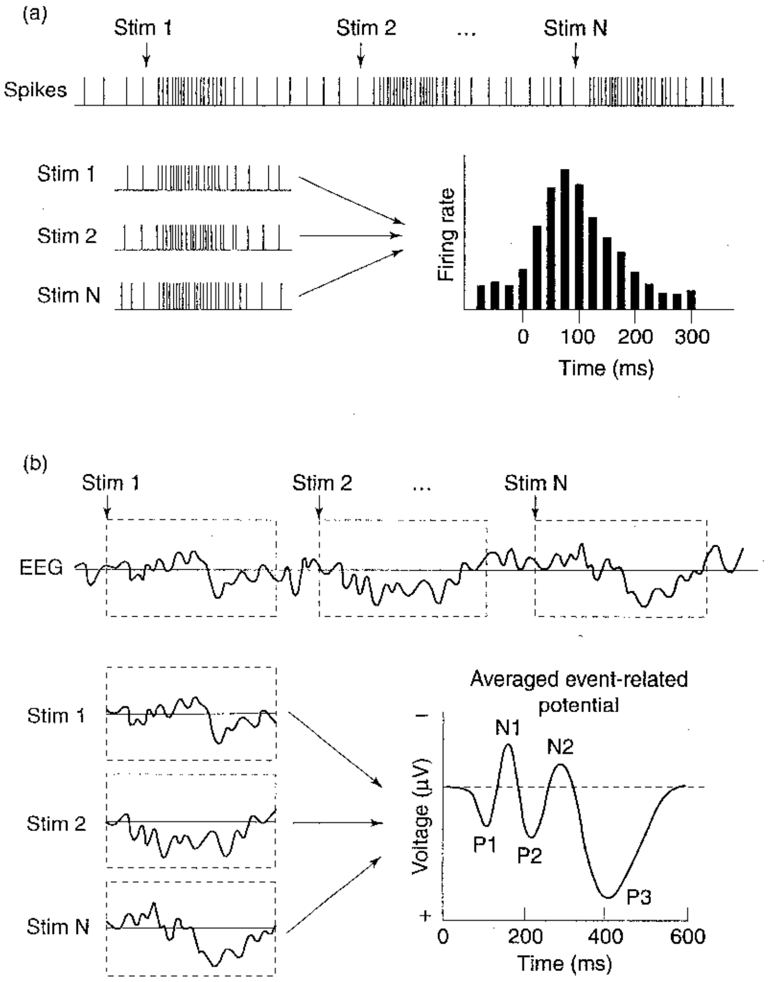

FIG. 7.2. (a) Data obtained in recordings of single-unit activity. In single-unit recordings, a train of spikes is recorded from a single neuron while stimuli are presented (the spikes are represented as vertical lines in this diagram). If the stimuli are effective in stimulating the neuron, the neuron's firing rate increases for a brief period following stimulus onset. The neuron's average response can be visualized by computing a poststimulus histogram, which plots the average number of spikes in each successive time bin following stimulus onset. (b) Data from the ERP technique. In these recordings, the electroencephalogram (EEG) is recorded from the surface of the scalp while stimuli are presented. Each stimulus evokes a sequence of voltage fluctuations (i.e. an ERP), but these fluctuations are normally obscured by the much larger EEG. To visualize the small ERP response, a signal-averaging technique is used: the EEG segments following individual stimuli are extracted from the incoming data, lined up with respect to stimulus onset, and then averaged together. Any voltage fluctuations that are consistently elicited by the stimulus will remain in this average, whereas any random voltage fluctuations will be eliminated if enough trials are averaged together. The resulting waveform consists of a set of positive and negative peaks that follow the onset of the stimulus (represented as time zero on the X-axis). Note that, by convention, negative is plotted upward and positive is plotted downward.

physiological activity non invasively from humans. In particular, if an electrode is placed on the scalp, the well-known electroencephalogram (EEG) can be recorded as a sequence of voltage fluctuations. The EEG consists of the sum of many different sources of electrical activity within the brain, and much of it is unrelated to the processing of specific stimuli. However, some of the activity within the EEG does reflect the brain's response to individual sensory, cognitive, or motor events, and these specific responses are known as event-related potentials or ERPs. Unlike single-unit spikes that reflect the output of a neuron, ERPs arise from the electrical potentials that are produced when a neuron receives input in the form of neurotransmitters. When a large number of neurons receive inputs at the same time, the resulting electrical potentials sum together and spread through the conductive media of the brain, the skull, and the scalp, where they contribute to the overall EEG. These potentials are very small, both in absolute terms and in relation to the overall EEG, but it is possible to measure them with high precision by means of a process called signal averaging, which is shown in Fig 7.2b. In this procedure, many individual stimuli are presented, and the segment of EEG following each stimulus is extracted and lined up with respect to the moment of stimulus onset. The EEG segments are then simply averaged together into a single waveform. Any activity that is consistently time-locked to stimulus onset across trials will remain in this average, whereas any activity that is unrelated to the stimulus will be random from trial to trial and will therefore average out (given a sufficient number of trials). This procedure is analogous to the creation of poststimulus histograms in single-unit recordings, as shown in Fig. 7.2a.

The result of the averaging process is an average ERP waveform, which is typically displayed as a plot of voltage over time (note that, by convention, negative is plotted upward and positive is plotted downward in plots of ERP waveforms). The ERP waveform consists of a number of positive and negative voltage deflections or "components", each of which is named for its polarity (P for positive or N for negative) and its position within the waveform (for example, "P1" for the first positive component or "P105" to indicate the exact time of the peak). Each component reflects activity from a different set of brain areas, and a large number of different components can be observed under different conditions (see Donchin et al. 1986; Hillyard & Kutas, 1983; Hillyard & Picton, 1987). Because the time course of a component indicates the period during which the corresponding brain area is active, the early components reflect sensory processing and the later components reflect higher cognitive processes and motor-related activity. In addition, the distribution of voltage over the surface of the head for a component is related to the anatomical location of its generator source (i.e the area of cortex in which the component was initially generated); the measured scalp distribution of a component can therefore be used to compute a rough estimate of its intracerebral source. Thus, ERPs can be used as a continuous measure of processing between a stimulus and a response, providing information about the time course and neuroanatomical substrates of cognitive processing.

In the past few years, new techniques have been developed for measuring neural activity in humans that provide much greater neuroanatomical precision than the ERP technique, although with a concomitant loss in information about the time course of activation. These techniques are based on a phenomenon first described by Roy and Sherrington in the 1890s: when neurons in a brain region are stimulated and start firing at an increased rate, there is an increase in blood flow to that region. By measuring localized changes in cerebral blood flow, therefore, it is possible to infer the presence of changes in neural firing. Until recently, the best technique for measuring changes in local blood flow was positron emission tomography (PET). In a PET scan, a small amount of a radioactively labeled marker (usually water) is injected into the bloodstream and travels to the brain, where it flows into different regions in proportion to the local blood flow. Specialized detectors are then used to measure the radiation emitted from each area, which allows the creation of 2- or 3-dimensional images of blood flow. By subtracting a scan obtained during a resting state from a scan obtained during a task, the brain regions that are activated during that task can be visualized, as shown in Fig. 7.3. Recently, a new blood flow measurement technique has been developed that has better spatial resolution than PET and does not require the injection of radioactive isotopes. This technique is based on the magnetic resonance imaging (MRI) method that has been used for many years to create static images of brain structure; because the new technique is used to study function as well as structure, it has been named functional magnetic resonance imaging (fMRI). The physics of this technique are quite complex, but in essence it uses differences in the magnetic properties of oxygenated and deoxygenated hemoglobin molecules to detect changes in blood flow that can be localized to areas as small as one cubic millimeter.

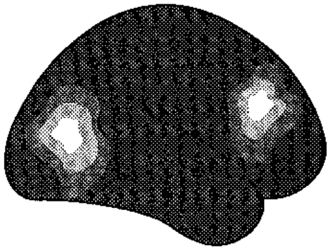

FIG. 7.3. Example of the type of data acquired in a positron emission tomography (PET) experiment. In these experiments, blood flow is measured during a baseline condition and an active condition. For example, subjects may passively view a stream of visual stimuli in the baseline condition and actively look for targets in the same stimulus stream in the active condition. The blood flow image obtained during the passive condition is then subtracted from the blood flow image obtained during the active condition, and the resulting image shows the increase in blood flow in specific brain areas during the active condition. In this figure, brain areas that did not exhibit significant increases in blood flow are shown in dark gray and areas that exhibited significant increases are shown in lighter shades of gray, with progressively lighter values indicating larger increases in blood flow during the active condition.

Although PET and fMRI scans allow very precise localization of changes in neural activity, they provide little information about the time course of activation because changes in blood flow are relatively slow (in the range of 5–10 seconds compared to a few milliseconds for changes in neural firing rates). They also require extremely complex scanners and, in the case of PET, a cyclotron to create radioactive isotopes, and are therefore very expensive. In contrast, the ERP technique provides temporal resolution in the millisecond range and is relatively inexpensive, but lacks the anatomical precision of PET and fMRI. Single-unit recordings allow both high temporal resolution and precise anatomical localization, but these recordings are typically limited to nonhuman animals, who require months of training to learn tasks that humans find trivial and whose visual systems may operate somewhat differently from the human visual system. In addition, recording from awake, behaving monkeys is technically very challenging and requires expensive animal care and surgical facilities. It is also impractical to record from more than a single electrode in most cases, making it difficult to study a large number of brain areas. Thus, each of the major methods used for studying the neurophysiology of attention has both benefits and limitations, and different techniques are therefore appropriate for answering different questions.

We now turn to the application of these techniques to questions about selective attention.

THE LOCUS OF SELECTION

Initial Behavioral Evidence

Most cognitive psychologists agree that selective attention is used to filter out irrelevant information, allowing cognitive processing resources and behavioral outputs to be concentrated on a small number of relevant sources of information. Although there is widespread agreement about this general view of attention, there has been a great deal of debate about which cognitive processes are limited and the stage at which attention selects the relevant inputs. Some early theorists, such as Broadbent (1958) and Treisman (1969), proposed that attention operates at an early stage of processing, allowing only selected inputs to be perceived and recognized.

Others, however, argued that all incoming sensory events receive equal perceptual processing, and proposed that attention operates at a late stage of processing to regulate the flow of information into decision processes, memory, and behavioral output systems (Deutsch & Deutsch, 1963; Norman, 1968). In the subsequent decades, many other scientists have addressed this issue of the "locus of selection," and some debate continues today.

Many of the early experiments on selective attention were related to the "cocktail-party effect," the common phenomenon of being unable to understand anything in a room full of people speaking unless attention is focused on one speaker at a time. A particularly provocative investigation of this phenomenon was reported by Moray (1959), who played passages of prose into one ear and required subjects to "shadow" (verbally repeat) these passages. While subjects shadowed the information in one ear, irrelevant verbal information was also presented in the other ear. When tested on their ability to recall or recognize the irrelevant information 30 seconds later, subjects showed no evidence of having heard anything in the ignored ear. The experiment was replicated with several different types of irrelevant material, including numbers and simple words, but subjects were unable to recall material from the ignored ear even if it was repeated many times. Moray found one exception, however: if a subject's own name was presented in the ignored ear, this stimulus was very likely to be detected, just as one is likely to detect one's own name being mentioned in an unattended conversation at a cocktail party. Thus, Moray provided evidence that information from an irrelevant source may be recalled under some conditions but not others, depending on its intrinsic value to the subject.

Results such as these have been used as evidence for "late-selection" models of attention, which propose that stimuli are identified in both the attended and ignored ears, followed by the selection of important stimuli for decision, memory, and action. Normally, only the to-be-shadowed information is considered important, and this is the information that is typically remembered. However, the subject's own name may also be intrinsically interesting, and will be remembered even if it is presented in the ignored ear. According to this view, the failure of subjects to recall words or numbers from the ignored ear is the result of selective storage of attended information in memory and not a result of selective perception. However, these findings are also compatible with "early-selection" models, in which attention is presumed to suppress the perceptual processing of ignored stimuli. According to these models, the poor memory performance for words in the ignored ear occurs because of degraded perceptual processing for stimuli in that ear. The recognition of the subject's own name in the face of this perceptual suppression can be explained by experiments showing that one's own name can be recognized more easily than other words when presented at low intensities relative to the background noise (Howarth & Ellis, 1961). In other words, perceptual processing is suppressed for all unattended information, but subjects can still identify easily perceived stimuli such as their names.

In the decades following these early experiments, a large number of psychological experiments have been conducted to test the early- and late-selection models of attention, and virtually everyone now agrees that attentional selection may occur at late processing stages, at least under some conditions. However, many researchers believe that attention also operates at an early stage in certain circumstances (e.g. under conditions of high perceptual load; see Lavie, 1995), but this has been difficult to establish unequivocally: for almost every behavioral finding that has been used as evidence for early selection, an alternative late-selection explanation has been proposed (see, for example, Duncan, 1980; Duncan & Humphreys, 1992; Luck et al., 1996). In part, this is due to the fact that behavioral responses reflect the product of both early and late stages of processing, making it difficult to demonstrate that a change in behavioral output is due to a change in processing at a particular stage.

As discussed previously, neurophysiological measures can be particularly useful for determining the stage at which an experimental manipulation affects processing, and these measures are therefore very appropriate for distinguishing between early and late selection. If attention operates at an early stage to attenuate the processing of irrelevant information, then the initial physiological responses in sensory cortical areas should be smaller for ignored stimuli than for attended stimuli. Conversely, if relevant information is selected only after perceptual processing is complete, then the initial sensory-evoked responses should be the same for attended and ignored stimuli.

Auditory ERP Experiments

During the 1960s and early 1970s, several experiments were conducted to determine whether selective attention affects the early sensory ERP components, but these experiments had various methodological shortcomings that made their results difficult to interpret. In 1973, however, Steve Hillyard and his colleagues developed an experimental design that allowed an unambiguous assessment of the effects of selective attention on auditory ERPs (Hillyard, Hink, Schwent, & Picton, 1973). In this experiment, which is diagrammed in Fig. 7.4, subjects were instructed to attend to the left ear in some trial blocks and the right ear in others. A rapid sequence of tone pips was presented, with half of the stimuli presented in each ear; to make the discrimination between the two ears even easier, the tones were presented at a different pitch in each ear. Subjects were instructed to monitor the attended ear and press a button whenever a slightly higher-pitched target

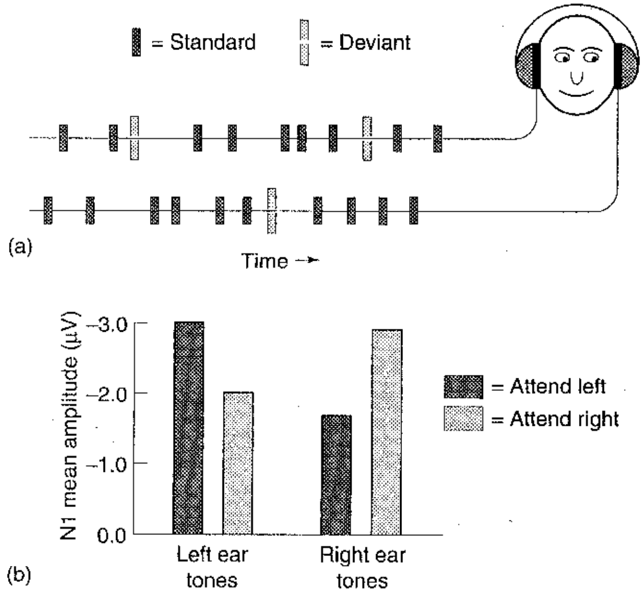

FIG. 7.4. Experimental paradigm (a) and results (b) from the study of Hillyard et al. (1973). Subjects listened to streams of tone pips in the left ear and right ear. Most of the tones were a standard frequency (800 Hz in the left ear and 1500 Hz in the right ear), but occasional deviant tones were presented at a slightly higher frequency (840 Hz left; 1560 Hz right). Subjects were instructed to attend to the left ear for some trial blocks and to the right ear for others, and counted the number of deviant tones in the attended ear. The average N1 amplitude was measured for the standard tones and used as an index of sensory processing. Left ear tones elicited a larger N1 wave when attention was directed to the left ear than when attention was directed to the right ear; conversely, right ear tones elicited a larger N1 wave when attention was directed to the right ear than when attention was directed to the left ear.

tone was detected in that ear, which occurred infrequently and unpredictably. Higher-pitched tones were also presented occasionally in the ignored ear, but subjects were instructed not to respond to these "unattended deviants."

In some prior ERP experiments, subjects were required to respond to all attended stimuli and withhold responses to all unattended stimuli. As a result, any differences in the ERPs evoked by attended and unattended stimuli could have been due to motor-related activity that was present for the attended ERPs but absent for unattended ERPs. Hillyard et al. (1973) avoided this problem by presenting nontarget stimuli in both the attended and unattended ears and focusing their analyses on these nontargets. Because the target and nontarget stimuli presented in the attended ear were difficult to discriminate from each other, but easy to discriminate from stimuli in the ignored ear, subjects focused attention on all of the stimuli

within the to-be-attended ear and ignored all stimuli within the other ear. As a result, it was presumed that the same initial selection processes would be applied to both targets and nontargets in the attended ear. The main experimental question was therefore whether the early sensory ERP components evoked by a nontarget stimulus presented in the attended ear would be larger than those evoked by a nontarget stimulus presented in the unattended ear.

The sensory ERP components are highly sensitive to the physical characteristics of the evoking stimulus. As a result, one cannot legitimately compare the ERP evoked by an attended tone in the left ear with an unattended tone in the right ear: any differences between these ERPs could be due to differences between the two ears that have nothing to do with attention. The design employed by Hillyard et al. (1973) circumvents this problem by allowing the ERP elicited by the same physical stimulus to be compared under different psychological conditions. For example, the ERP evoked by a left nontarget during attend-left blocks can be compared with the ERP evoked by the same left nontarget during attend-right blocks. Because the same stimulus is used in both cases, any differences in the ERPs between the attend-left and attend-right conditions must be due to differences in attentional processing.

In many attention experiments, the investigators compare an "active" condition in which the subject responds to the stimuli with a "passive" condition in which the subject completely ignores the stimuli and engages in a distracting activity such as reading a book. Frequently, however, the task in the active condition is much more demanding than the distraction task in the passive condition, leading to greater overall arousal during the active condition. If we compare the ERPs in the two conditions, any differences might be due to these global arousal differences rather than selective changes in stimulus processing. Although this might be interesting, arousal-related changes in ERPs tell us little about *selective* attention. To ensure that differences in global arousal would not interfere with their study, Hillyard et al. (1973) compared ERPs evoked during equally difficult attend-left and attend-right conditions rather than active and passive conditions.

Now that we have discussed the logic behind the study of Hillyard et al. (1973), let us consider the results. As shown in Fig.7.4b, the N1 component was found to be larger for attended stimuli than for unattended stimuli. Specifically, the N1 elicited by left-ear tones was larger when the left ear was attended than when the right ear was attended, and the N1 elicited by right-ear tones was larger when the right ear was attended than when the left ear was attended. These effects began approximately 60–70 ms after stimulus onset and peaked at approximately 100 ms poststimulus, clearly within the time period of sensory processing. In addition, this early modulation of sensory activity was observed for both target and nontarget stimuli, indicating that stimuli from the attended ear were selected for enhanced processing before they were fully identified. On the basis of these findings, Hillyard and colleagues concluded that attention was operating at an early stage of processing to enhance the sensory processing of stimuli presented in the attended ear. Thus, this study provided strong evidence for the early-selection hypothesis.

More detailed information about the time course and neural origins of auditory selective attention has been provided in a series of recent studies by Woldorff and colleagues (Woldorff, Hansen, & Hillyard, 1987; Woldorff & Hillyard, 1991; Woldorff et al., 1993), who used a slightly modified version of the paradigm developed by Hillyard et al. (1973). These experiments were designed to optimize the focusing of attention and to provide extremely precise ERP recordings, thus allowing the investigators to determine the earliest time point at which attention can influence sensory processing. To optimize the focusing of attention, Woldorff used very fast trains of stimuli, analogous to the high information rates found in human speech, thus overloading the auditory system so that subjects were forced to "tune out" information from the unattended ear. In addition, the difficulty of the target/nontarget discrimination (a loudness discrimination) was carefully adjusted to provide uniformly high levels of difficulty for all subjects. Finally, a combination of fast stimulation rates and long recording sessions allowed the collection of many thousands of trials, providing a very high signal-to-noise ratio in the ERP recordings.

The very first ERP components evoked by an auditory stimulus can be seen within 10 ms of stimulus onset and are called the "brainstem evoked responses" because they are generated in the auditory relay stations of the brainstem. As shown in Fig.7.5a, Woldorff and colleagues found that these initial sensory responses were completely unaffected by attention, which indicates that the selection of information from the attended ear occurs sometime after the earliest stages of sensory transmission. When the same ERPs are plotted on a longer time base, the later ERP components can be observed. As in the study of Hillyard et al. (1973), the N1 component was larger for stimuli presented in the attended ear than for stimuli presented in the unattended ear (see Fig.7.5c). This was not the earliest effect, however. In the range of the so-called "midlatency" components (20–50 ms post-stimulus), the attended-stimulus ERPs contained a more positive voltage deflection than the unattended-stimulus ERPs (see Fig.7.5b). The midlatency components appear to reflect the initial activation of auditory cortex, and so this effect in the 20–50 ms time range suggests that selective attention modulates either the very first cortical responses or the transmission of auditory information from the thalamus to the cortex (see Woldorff et al., 1993, for a detailed analysis of the generator sources of the midlatency and N1 attention effects).

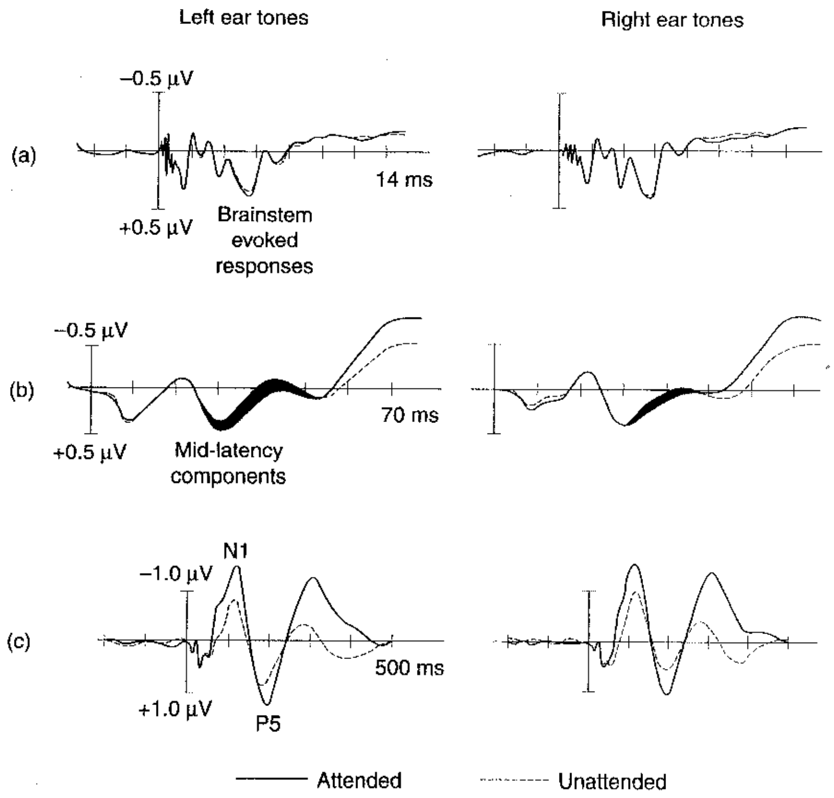

FIG. 7.5. ERP waveforms elicited by left ear and right ear tones in the experiments of Woldorff and colleagues (Woldorff et al., 1987; Woldorff & Hillyard, 1991). The three rows of this figure show data from the same trials, but recorded on different time scales and with different filters to show different ERP components: (a) the brainstem evoked responses on a scale of 2 ms per time division; (b) the midlatency components on a scale of 10 ms per time division; and (c) the long latency components on a scale of 100 ms per time division. The brainstem responses were virtually identical when attention was directed toward or away from the ear to which the tone was presented. For the midlatency components, however, the amplitude was more positive from approximately 20–50 ms (shaded region) when attention was directed toward the ear of the stimulus. The N1 and P2 components were also enhanced by attention, as in the study of Hillyard et al. (1973). Adapted with permission from Woldorff et al. (1987) and Woldorff and Hillyard (1991). Reprinted with kind permission from Elsevier Science Ireland Ltd, Bay 15K, Shannon Industrial Estate, Co. Clare, Ireland.

To summarize, the studies of Hillyard, Woldorff, and others have shown that attending to information in one ear and ignoring information in the other causes a difference in the sensory ERP responses evoked by the attended and ignored stimuli (Giard, Perrin, Pernier, & Peronnet, 1988; Hillyard, et al., 1973; Woldorff, et al., 1987; Woldorff & Hillyard, 1991;

Woldorff et al., 1993; Woods & Clayworth, 1987). Specifically, attention modulates sensory-evoked activity beginning around 20 ms after stimulus onset, probably in primary auditory cortex, and also modulates the amplitude of later components such as the N1 wave. These results provide clear support for early-selection theories of attention, which propose that attention is used to select relevant sources of input at an early stage in order to enhance perceptual processing.

Visual ERP, PET, and Single-unit Experiments

The locus-of-selection issue has also been addressed in the visual modality with the ERP technique, and many of these experiments have used a visual version of the paradigm developed by Hillyard et al. (1973) for studying auditory attention. In the visual attention paradigm, which is shown in Fig.7.6a, subjects fixate a central point and direct attention either to the left visual field (LVF) or the right visual field (RVF). Streams of bars are flashed in the LVF and RVF, and most of these bars are a standard size. Smaller deviant bars are presented occasionally, and subjects are required to press a button when they detect a deviant bar in the attended visual field. As in the auditory attention paradigm, the ERPs elicited by the standard stimuli are examined instead of the ERPs elicited by the targets in order to avoid contamination by any motor-related ERP components. In order to make sure than any changes in the ERP components are due to internal attentional mechanisms rather than external shifts in eye position toward the attended location, subjects are required to fixate a central point during these experiments, and trials contaminated by eye movements are excluded from the ERP averages.

Many experiments of this type have been conducted by the Hillyard group and by other investigators (e.g. Eason, Harter, & White, 1969; Mangun & Hillyard, 1988, 1990; Mangun, Hillyard, & Luck, 1993; Neville & Lawson, 1987; Rugg, Milner, Lines, & Phalp, 1987; Van Voorhis & Hillyard, 1977), and the typical results are presented in Fig.7.6b. Attended stimuli elicit larger sensory-evoked ERP waves than unattended stimuli beginning with the first major visual ERP component, the P1 wave, which typically onsets between 60 and 90 ms poststimulus and peaks between 100 and 130 ms poststimulus.[2] Visual information typically reaches primary

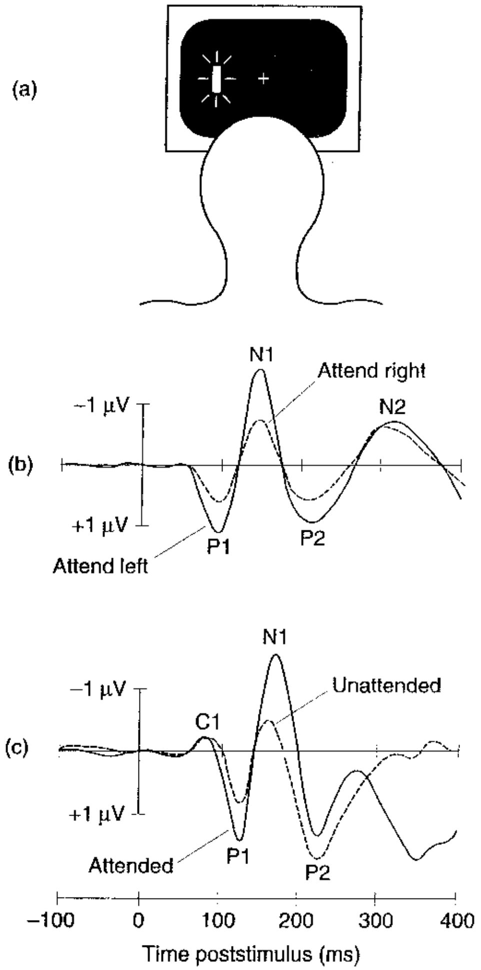

FIG. 7.6. Stimuli and results from a typical visual ERP attention paradigm. (a) Streams of bars are presented at locations in the left and right visual fields; most of these bars are a standard size, but smaller deviant bars are occasionally presented. Subjects fixate a central point and direct attention to the left location on some trial blocks and to the right location on others. Subjects are instructed to press a button whenever a deviant bar is detected on the attended side. (b) Idealized responses to a standard bar in the left visual field. The P1, N1, and P2 components elicited by this left stimulus are larger when attention is directed to the left than when attention is directed to the right (a complementary pattern is observed for stimuli in the right visual field). (c) Results from the study of Gomez Gonzales et al. (1994), in which the C1 component—which appears to be generated in primary visual cortex—could be observed. Although the P1 and N1 components were strongly modulated by attention, there were no significant attention effects for the C1 component, indicating that spatial selective attention operates after the arrival of information into primary visual cortex. Adapted from Luck (1995).

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[2] It is important to note that similar naming conventions are used for both auditory and visual ERP components, and both types of waveforms therefore have components with the same names. These names are purely descriptive, and ERP components from different modalities with the same name are not necessarily the same component in any physiological or psychological sense. For example, the first major negative component is named "N1" in both auditory and visual ERP waveforms, but the auditory and visual N1 components arise from different areas of the brain and reflect different neurophysiological processes.

visual cortex (area V1) approximately 40–60 ms after stimulus onset, and the time course of the P1 attention effect therefore indicates that attention begins to influence stimulus analysis during the early stages of cortical processing.

Under certain conditions, it is possible to record an ERP component that precedes the P1 wave and appears to be generated in primary visual cortex (area V1). The effects of attention on this component, which is called the "C1" wave, have been examined in two recent experiments (Gomez Gonzales et al., 1994; Mangun et al., 1993). As shown in Fig.7.6c, the amplitude of this component is the same for attended and unattended stimuli, whereas the later P1 and N1 components are larger for attended stimuli than for unattended stimuli. Thus, although the P1 and N1 effects indicate that visual attention operates at a *relatively* early stage of processing (i.e. within 150 ms of stimulus onset), the effects of attention in the visual modality do not begin until after information from a stimulus has passed through primary visual cortex. This contrasts with the auditory modality, where attention appears to influence processing beginning as early as primary auditory cortex.

Although it is clear that the P1 and N1 components do not arise from primary visual cortex (Clark, Fan, & Hillyard, 1995; Mangun et al., 1993), it has been difficult to determine exactly where they are generated and thereby assess the precise neuroanatomical locus of selection in the visual modality. Unfortunately, it is generally quite difficult to localize the generators of ERP components, especially components arising from visual cortex, which contains more than 30 separate visual processing areas and has a very complex 3-dimensional organization. To provide more precise neuroanatomical localization, Heinze and his colleagues recently conducted an experiment in which they obtained both ERP and PET data using a paradigm similar to that shown in Fig.7.6a (Heinze et al., 1994). When subjects attended to the stimuli, there was an increase in blood flow in an area of visual cortex on the base of the occipital lobe, and this effect was larger in the hemisphere that received direct inputs from the side of the display that was attended (i.e. the contralateral hemisphere). A P1 attention effect was also observed in the ERP recordings, and the estimated generator of this effect was quite close to the locus of the PET attention effect (see Fig. 7.7). Although it is currently impossible to prove that these PET and ERP attention effects reflect the same neurophysiological events, these results provide reasonably convincing evidence that visual attention influences sensory processing in extrastriate visual cortex within 100 ms of stimulus onset, consistent with early-selection models of attention.

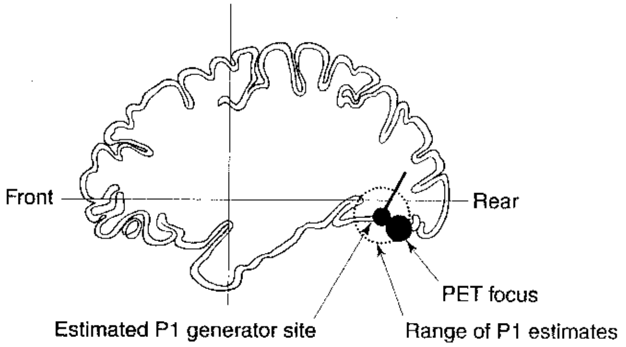


FIG. 7.7. Location of the PET attention effect and estimated location of the P1 attention effect in the study of Heinze et al. (1994). The small dark circle represents the best estimate of the P1 generator location, and the line extending from this circle represents the orientation of the estimated current dipole. The broken circle surrounding this generator shows the range of generator solutions that were compatible with the observed data. The larger dark circle represents the location of the PET attention effect. Although the PET and P1 effects were not identical in location, the PET effect was within the error range of the P1 effect. These results are therefore consistent with the proposal that the P1 attention effect is generated in the extrastriate visual areas located on the ventral surface of the occipital lobe.

Although Heinze et al. (1994) were able to identify a precise neuroanatomical site where attention influences sensory processing, their results reveal relatively little about the specific changes in processing produced at that site by attention. For example, it is important to know what sorts of processes are normally conducted in the attention-sensitive brain region and exactly how these processes are changed by attention. Most of our knowledge of the specific sensory processes carried out in the different visual areas has been obtained from macaque monkeys, however, and we are just beginning to be able to determine which areas of the human brain are homologous to specific areas within macaque visual cortex. As a result, it is difficult to combine our detailed knowledge of the visual processes carried out in specific areas of macaque visual cortex with our initial mapping of the areas that are affected by attention in humans. Although future technical improvements may allow these two sets of data to be combined more directly, at present single-unit recordings provide the only technique for measuring the precise effects of attention in well-characterized areas of visual cortex.

Several single-unit studies of visual attention have been conducted in the last decade (Chelazzi, Miller, Duncan, & Desimone, 1993; Moran & Desimone, 1985; Motter, 1993; Wurtz, Richmond, & Newsome, 1984), and one of these studies was adapted directly from the paradigm used in the ERP and PET studies described earlier (Luck, Chelazzi, Hillyard, & Desimone, 1997). In this study, recordings were obtained from V1, V2, and V4 in macaque monkeys; these areas are primarily responsible for the early and intermediate stages of visual object recognition and process features such as color, orientation, and spatial frequency (for more information on these areas, see Desimone & Ungerleider, 1989; Felleman & Van Essen, 1991; Maunsell & Newsome, 1987; Van Essen, 1985). Consistent with the ERP and PET results, no consistent effects of attention were observed in area V1. In areas V2 and V4, however, significant attention effects were observed for many neurons, as shown in Fig. 7.8. In these neurons, the response to a stimulus was larger when it was attended than when attention was directed to another location, just as the P1 component in previous ERP experiments was larger for attended stimuli than for unattended stimuli. In addition, this effect was present immediately at the onset of sensory-evoked activity (c. 60 ms poststimulus in area V4), and appeared to consist of a simple increase in the size of the sensory response, which is also similar to the P1 effects observed in ERP experiments. These results demonstrate that attended-location information is selected for preferential processing during the processing of basic stimulus features such as color and orientation.

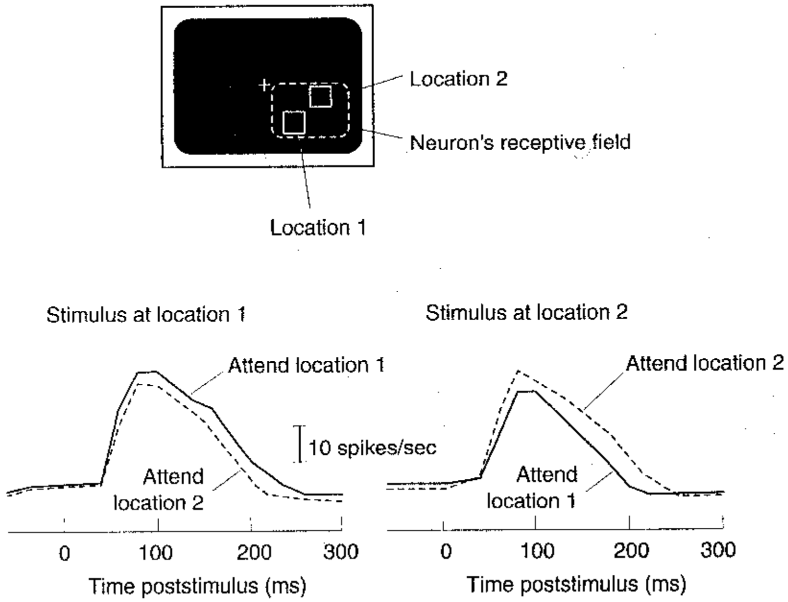


FIG. 7.8. Single-unit attention effects from area V4 (Luck et al., 1997). The monkey fixated the central cross and attended either to location 1 or location 2, which were positioned so that they were both inside the receptive field of the cell being recorded. The poststimulus histograms shown in this figure represent an average of 28 neurons that showed significant effects of attention. Note that the response to a stimulus at location 1 was larger when location 1 was attended than when location 2 was attended, and the response to a stimulus at location 2 was larger when location 2 was attended than when location 1 was attended. These effects were absent when only one of the two locations was inside the receptive field.

Although the single-unit data were largely consistent with the ERP and PET studies, there was one important difference. In the single-unit study, attention modulated the size of the sensory response only when both the attended and unattended locations were inside the receptive field of the neuron being recorded; no sensory modulation was observed if one location was inside the receptive field and the other was outside. In addition, these effects were much stronger when the attended and unattended stimuli were presented simultaneously rather than sequentially. This pattern of results was considered surprising by many researchers, but it is not really so surprising when one considers the ambiguous nature of the information coded by individual neurons. Specifically, when two stimuli are simultaneously presented inside a neuron's receptive field, the neuron's output could reflect either the attended stimulus or the unattended stimulus (this is the same "binding problem" that was discussed earlier). As a result, it is computationally useful to suppress information arising from the unattended location so that it is not confused with attended information. When only one location is inside the receptive field, however, the neuron's output clearly reflects information arising from that one location and no suppression is necessary. This pattern of results is quite different from the pattern observed in ERP experiments, however, in which P1 and N1 attention effects have been observed with stimulus locations that were too far apart to fall within a single V2 or V4 receptive field. One possible explanation for this discrepancy is that the ERP attention effects may reflect activity in a part of the human brain that is homologous to macaque inferotemporal cortex, where neurons have very large receptive fields and are strongly influenced by attention (Chelazzi et al., 1993; Moran & Desimone, 1985).

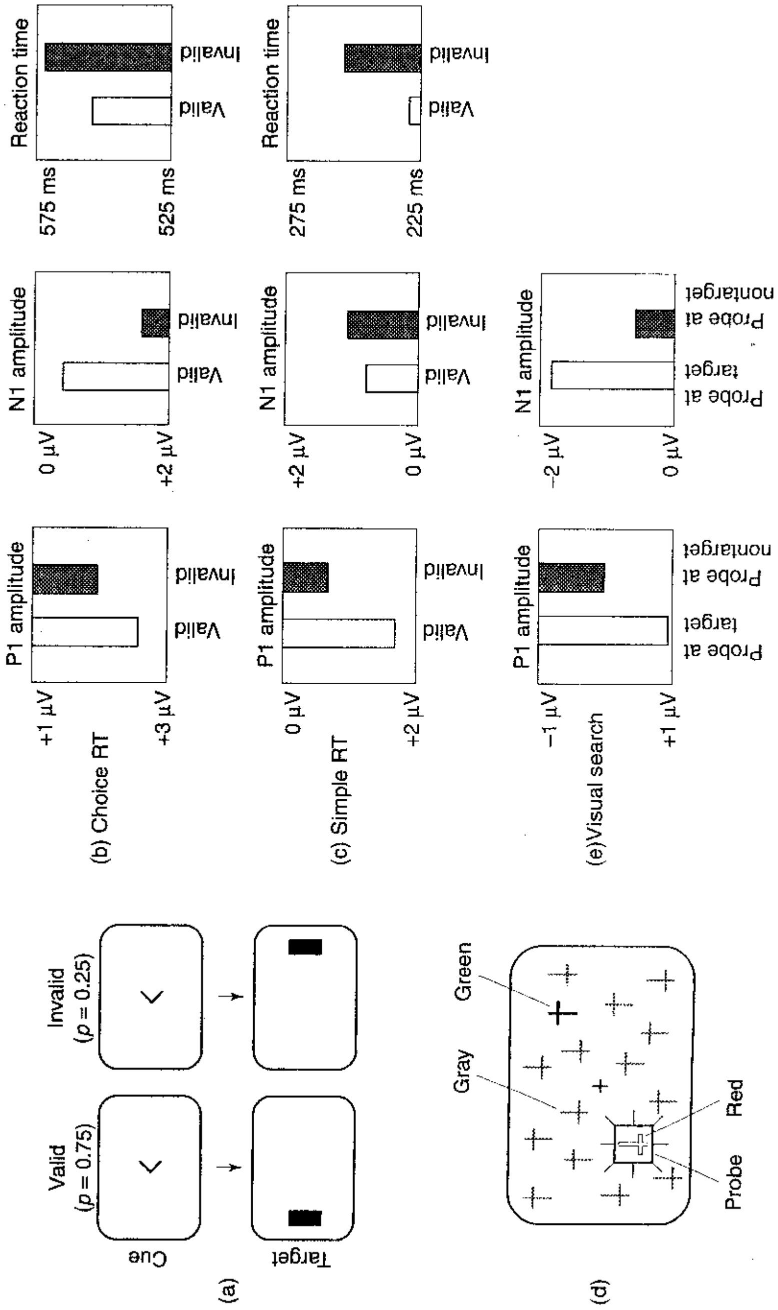
To summarize, the locus-of-selection issue has been addressed in the visual modality using the ERP, PET, and single-unit methodologies, and although it can be difficult to compare results directly across techniques, these studies have yielded converging evidence that attention begins to select visual information at a relatively early time (c. 60 ms poststimulus) and a relatively early neuroanatomical locus (extrastriate visual cortex; see, however, Motter, 1993), consistent with a mechanism that selects information during the intermediate stages of object recognition. Selection appears to occur at a somewhat later time in the visual modality than in the auditory modality, but this difference may simply reflect the greater amount of time required for the initial sensory transduction and integration in the retina. In any case, these neurophysiological studies of attention provide clear support for the early-selection hypothesis in both the auditory and visual modalities.

NEUROPHYSIOLOGICAL STUDIES OF CUING AND SEARCH

Although the experimental paradigm used in the experiments described earlier has been very useful for studying the neural substrates of attention, it is substantially different from the paradigms typically used by cognitive psychologists to study attention. In recent years, however, neurophysiologists have begun to explore the two paradigms used most commonly in psychological studies of attention, namely spatial cuing and visual search (Chelazzi et al., 1993; Eimer, 1994a; Luck, Fan, & Hillyard, 1993b; Luck & Hillyard, 1994, 1995; Luck et al. 1994b; Mangun & Hillyard, 1991). As will be described next, these studies have provided new information about the mechanisms of attention that are used by the visual system when performing these tasks. Before discussing these findings, however, it is necessary to describe the cuing and search paradigms as they have been used by psychologists.

In the spatial cuing paradigm, each trial consists of a cue stimulus followed by a target stimulus, and the subject is required to respond to the target (see Fig. 7.9a). The cue indicates the probable location of the target, allowing subjects to focus attention on this location before the onset of the target (the cue typically precedes the target by several hundred milliseconds). On the majority of trials (called "valid" trials), the target appears at the location indicated by the cue; responses to these targets are typically fast and accurate because the target falls inside the focus of attention. On a small percentage of trials (called "invalid" trials), the target appears at an uncued location; responses to these targets are typically slow and inaccurate

FIG. 7.9. Opposite. (a) Examples of cue and target stimuli in the spatial cuing study of Mangun and Hillyard (1991). Each trial began with a cue arrow presented at fixation, and this was followed after an 800-ms delay by a target bar that appeared either at the location indicated by the cue (valid trial) or at the opposite location (invalid trial). In one experiment, subjects pressed one of two buttons to indicate whether the target bar was tall or short (choice RT). In a second experiment, subjects simply pressed a single button as soon as a bar appeared (simple RT). (b) Results from the choice RT experiment. RTs were faster and the P1 and N1 were larger on valid trials than on invalid trials (note that negative voltages are plotted upward). (c) Results from the simple RT experiment. The same RT and P1 effects were observed in this experiment, but there was no significant N1 difference between valid and invalid trials. (d) Stimuli used in the visual search study of Luck et al. (1993). Subjects attended to red on some runs and green on other runs, and pressed one of two buttons to indicate whether the item drawn in the attended color (the target) was an upright T or an inverted T. A small, white, outline square was presented as a probe stimulus 250 ms after the onset of the search array, and this probe was completely task-irrelevant. (e) ERP results from the search experiment. As in the choice RT cuing experiment, both the P1 and N1 components were larger for probes presented within the focus of attention (at the location of the target) than for probes presented outside the focus of attention (at the location of a nontarget). Adapted from Mangun and Hillyard (1991), and Luck (1995).



because the target falls outside the focus of attention. Thus, this task provides a direct technique for measuring perceptual processing inside and outside the focus of attention (for more information, see Cheal, Lyon, & Gottlob, 1994; Hawkins et al. 1990; Jonides, 1981; Posner, 1980).

The visual search paradigm provides a somewhat less direct means of comparing the processing of attended and ignored stimuli, but it is much more similar to the tasks that the visual system must perform in natural settings. In this paradigm, subjects are presented with arrays containing multiple stimulus elements, and they must indicate whether or not a target item is present within the array, much like the task of looking for a friend in a crowd. In many cases, the amount of time required to detect the target item increases as the number of elements in the array increases. This is usually taken as evidence that attention moves in a series of shifts from one item to the next until the target is found, at which point a response is made; this is called a "serial search" process. During a serial search, the number of distractor items that are examined before the target is found typically increases as the number of items in the array increases, and this explains the finding that reaction times (RTs) increase as the number of items in the array increases.[3] Under certain conditions, however, subjects can detect the target quickly no matter how many distractors are present, which indicates that an item-by-item search is not necessary; this is called a "parallel search" process. An enormous number of visual search experiments have been conducted in the last 15 years, and a great deal has been discovered about the conditions under which search proceeds in serial or in parallel (summarized by Wolfe, this volume; see also Duncan & Humphreys, 1989; Enns & Rensink, 1991; Treisman & Gelade, 1980; Treisman & Souther, 1985; Wolfe, 1994).

One of the most basic questions addressed by neurophysiological studies of cuing and search is whether the visual system uses the same or different mechanisms of attention in these very different tasks. Although cuing and search are the most commonly used paradigms in the study of visual attention, there have been surprisingly few studies aimed at determining whether they actually tap into the same mechanisms of attention. One reason for this is that it is difficult to determine from behavioral performance data whether the same mechanisms of attention operate in different tasks. For example, even if both tasks lead to some particular change in performance, this change might arise from different mechanisms in the two paradigms. With neurophysiological measures, however, it is possible to measure individual sensory processes in relative isolation, making it possible to determine whether attention influences the same specific processes across paradigms. For example, if attention affects the same set of ERP components in both spatial cuing and visual search, then this would provide good evidence that similar attentional mechanisms operate in both paradigms. In addition, neurophysiological measures can also be used to determine whether the same attentional control structures are active across paradigms, which would provide additional evidence for a common set of mechanisms. Let us now consider some recent pieces of evidence indicating that the same sensory processes are modulated by attention and the same attentional control structures are active in both the spatial cuing and visual search paradigms.

Attention Effects in the Spatial Cuing Paradigm

Mangun and Hillyard (1991) recorded ERPs in a set of spatial cuing experiments to determine whether early-selection mechanisms operate in this paradigm. In their first experiment, subjects were cued to the left or right visual field by means of an arrow and were then required to press a button to indicate whether a subsequent target stimulus was a tall bar or a short bar (see Fig. 7.9a). This is called a "choice reaction time" or "choice RT" task because subjects must choose between multiple target alternatives and then make a speeded response. The target bar appeared at the cued location on 75% of trials and at the uncued location on 25% of trials. Consistent with previous studies, shorter reaction times were observed on valid trials than on invalid trials (see Fig. 7.9b). Although many investigators have explained such results by postulating increased sensory efficiency at the cued location (e.g. Bashinski & Bacharach, 1980; Hawkins et al., 1990; Posner, Snyder, & Davidson, 1980), proponents of the late-selection hypothesis have shown that such results can also be explained by changes in postsensory decision or motor processes (Duncan, 1980; Shaw, 1984; Sperling & Dosher, 1986). If these results were caused by an attentional modulation of sensory processes, then larger sensory-evoked ERP components would be expected on valid trials than on invalid trials. This is exactly the pattern that Mangun and Hillyard found. As shown in Fig. 7.9b, both the P1 and N1 components were larger for targets appearing at the cued location than for targets appearing at the uncued location, indicating that the faster responses observed on valid trials were due, at least in part, to facilitated sensory processing.

Mangun and Hillyard (1991) also conducted a second experiment in which all of the target bars were identical and subjects simply pressed a single button upon detecting a bar (a "simple RT" task). As shown in Fig. 7.9c, responses were again faster on valid trials than on invalid trials in this experiment. In addition, the P1 component was again larger on valid trials

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[3] Although many investigators assume that results of this nature indicate that subjects are performing a serial search of the array, there are other search mechanisms that could produce this same pattern of results (Bundesen, 1990; Mordkoff, Yantis, & Egeth, 1990; Townsend, 1990).

than on invalid trials, consistent with an early locus of selection. However, the N1 component was not significantly different on valid and invalid trials in this experiment. This difference between the P1 and N1 components has two implications. First, the P1 and N1 attention effects appear to reflect separate mechanisms of attention that can be activated independently rather than being two different manifestations of a single early change in sensory processing. Second, the absence of the N1 attention effect in the simple RT experiment suggests that the attentional process reflected by the N1 component may be involved in discriminative processing at the attended location. We will return to these issues later.

Attention Effects in the Visual Search Paradigm

To determine whether the same mechanisms of attention operate across paradigms, Luck et al. (1993) recorded ERPs during a visual search task. In order to measure the P1 and N1 components at the attended (target) and unattended (distractor) locations during visual search, however, this experiment had to overcome two methodological obstacles. First, stimuli in the spatial cuing task are presented at the attended and unattended locations on separate trials and therefore elicit separate ERP waveforms, whereas the targets and distractors are presented simultaneously during visual search and elicit a single ERP waveform containing contributions from both attended and unattended items. To provide separate waveforms corresponding to the target and distractor locations, task-irrelevant "probe" stimuli were presented at the locations of individual items within the visual search arrays (see Fig. 7.9d). The ERPs elicited by these probe stimuli were used as measures of sensory processing at the probed location, which was the location of the target on some trials and the location of a distractor on other trials. A second problem with the search paradigm is that it is difficult to determine where attention is focused at any given moment during a serial search; to solve this problem, the targets in this experiment were presented in a unique color that could be localized immediately. To ensure that attention would be focused on the target item once it was localized, subjects were required to discriminate the shape of the target item, which was a highly demanding task. Thus, although subjects were not explicitly cued to a particular location, the demands of the task implicitly required subjects to focus attention on the target item. After the search array was displayed for 250 ms—providing subjects with sufficient time to find the target—the probe stimulus was presented either at the target location or at the location of a distractor item on the other side of the array. Trials on which the probe was presented at the location of the target item were analogous to valid trials in a cuing experiment, because the ERP-eliciting stimulus was presented within the focus of attention; trials on which the probe was presented at a distractor location were analogous to invalid trials, because the ERP-eliciting stimulus was presented outside the focus of attention.

As discussed earlier, one cannot legitimately compare the ERPs elicited by two different physical stimuli in an attention experiment, because any differences in the waveforms could be explained by the physical stimulus differences rather than the effects of attention. One cannot, therefore, compare the ERP elicited by a probe presented at the location of a uniquely colored target item with the ERP elicited by a probe presented at the location of one of many identically colored distractor items. To provide a well-controlled comparison, two uniquely colored items were presented within each array (a red item and a green item) and different colors served to define the target on different runs (i.e. the red item was the target for some runs and the green item was the target for others). This design allowed a comparison between the ERP elicited by a probe at the location of the red item when attention was directed to that red item and the ERP elicited by a probe at the location of the same red item when attention was directed to the green item on the opposite side of the array (and vice versa for probes presented at the location of the green item).

Figure 7.9e displays the results from this experiment, and shows that both the P1 and N1 components were larger for probes presented at the location of the target item than for probes presented at the location of the nontarget item on the opposite side of the array. These results are very similar to the results obtained by Mangun and Hillyard (1991) during the choice RT spatial cuing task, and this similarity indicates that attention influences the same sensory processes during both visual search and spatial cuing. This is an important conclusion, because it indicates that we can legitimately integrate the results from cuing and search experiments into a single theory of attention (see also Briand & Klein, 1987; Prinzmetal, Presti, & Posner, 1986; Treisman, 1985).

Suppression and Facilitation in Cuing and Search

Although the studies just described indicate that attention modulates the same sensory processes in both the cuing and search paradigms, it is possible that these similar effects are actually caused by different mechanisms of attention in the two paradigms. One way to provide additional evidence that both paradigms employ the same mechanisms would be to show that the finer details of the attentional modulations are also similar across paradigms. Evidence of this nature was provided recently by studies that examined whether attention operates by facilitating processing at the attended location or by suppressing processing at the unattended location.

The P1 and N1 attention effects discussed earlier have typically been described as reflections of facilitated processing at the attended location, but they could just as easily represent a suppression of processing at the unattended location. Recently, Luck et al. (1994b) provided evidence indicating that although the N1 attention effect does reflect attended-location facilitation, the P1 effect actually reflects unattended-location suppression. This conclusion was reached on the basis of a cuing experiment that included neutral trials as well as valid and invalid trials. On the valid and invalid trials, an arrow cue was used to direct attention to one of four possible target locations, where the target was likely to occur. On neutral trials, four arrows appeared (pointing at all four locations), indicating that the target could occur with equal probability at any of these locations. These trials provided a baseline condition in which attention was presumably unfocused or diffusely focused over the entire set of locations. As shown in Fig. 7.10a, the P1 was suppressed on invalid trials compared to these neutral trials, but no P1 facilitation was observed on valid trials compared to neutral trials. Conversely, the N1 component was enhanced on valid trials compared to neutral trials, but no N1 suppression was observed on invalid trials. Thus, the P1 attention effect appears to reflect a specific suppression of processing at the unattended locations whereas the N1 attention effect appears to reflect a specific facilitation of processing at the attended location.

To test whether this same pattern of suppression and facilitation is also present in the visual search paradigm, Luck and Hillyard (1995) conducted a visual search study that was very similar to the search experiment just described (Luck et al., 1993b), but also included trials that were analogous to neutral trials. In this experiment, the two uniquely colored items in the search arrays were selected at random on each trial from a set of four possible colors (red, green, blue, and purple). When an item of the attended color was present, subjects pressed a button to indicate its shape, as in the previous experiment; when the attended color was absent from the display, no response was required. On target-absent trials, attention was presumably unfocused or diffusely focused, making these trials comparable to the neutral trials of the cuing experiment. These trials were used as a baseline for comparison with trials on which the probe was presented at the location of the target (analogous to valid trials) or trials on which the probe was presented at the location of a distractor item on the opposite side of the array from the target (analogous to invalid trials). As in the cuing experiment, the P1 was suppressed for probes presented on the opposite side of the array from the target compared to the neutral-like target-absent trials, but was not enhanced for probes presented at the target location (see Fig. 7.10b). The N1, in contrast, was enhanced for probes presented at the target location compared to target-absent trials, but was not suppressed for probes presented on the opposite side of the array from the target. These results are extremely similar to the results from the cuing experiment, and this similarity provides additional evidence that the same mechanisms of attention operate during both cuing and search.

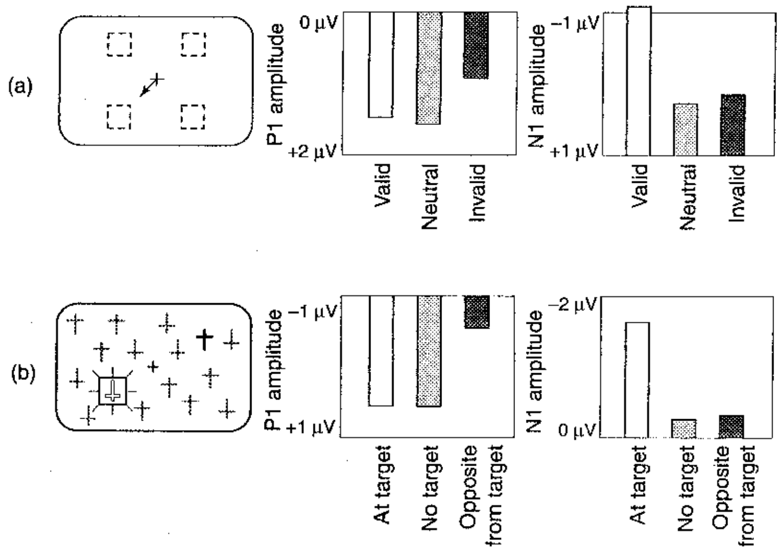


FIG. 7.10. (a) Stimuli and results from the spatial cuing study of Luck et al. (1994b). Each trial began with a cue presented at fixation, and this was followed after a 200–500-ms delay by a masked luminance target. The cue pointed to a single location on most trials, indicating the most likely location for the subsequent target. On neutral trials, however, the cue pointed to all four locations, indicating that the target could occur equiprobably at any of the locations. The P1 component was suppressed on invalid trials compared to neutral trials, but was not facilitated on valid trials compared to neutral trials. The N1 component, in contrast, was facilitated on valid trials but was not suppressed on invalid trials. (b) Results from the visual search experiment of Luck and Hillyard (1995). This experiment was identical to the search experiment of Luck et al. (1993b), except that the two colored items within the search array were selected at random from a set of four possible colors. Subjects attended to one of the four colors, and pressed a button to indicate the orientation of the item presented in this color when the attended color was present in the array. When the attended color was absent, subjects made no response. The same pattern of P1 suppression and N1 facilitation was observed in this experiment. Adapted from Luck (1995).

Attentional Control Structures in Cuing and Search

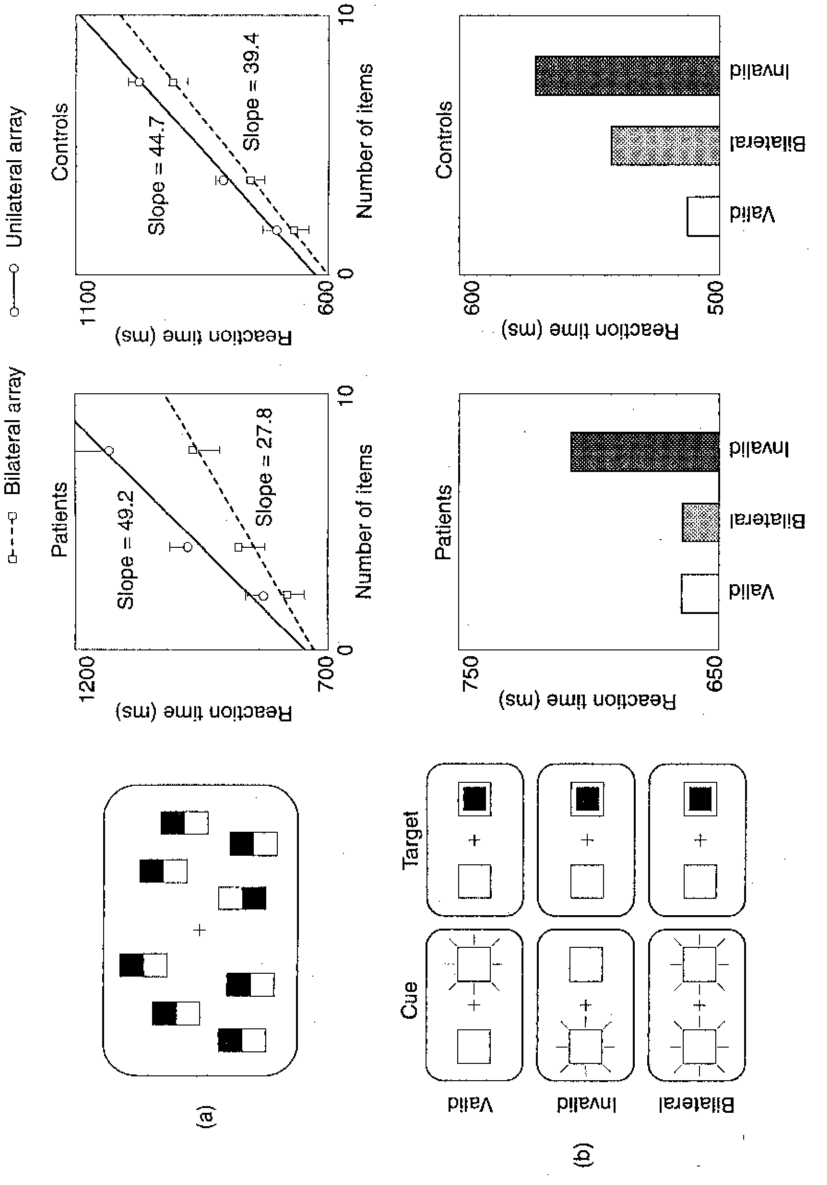
Evidence for a shared set of attentional mechanisms in the cuing and search paradigms has also been provided by studies of the brain structures that are responsible for controlling the focus of attention (see also Driver, this volume). One of the most important of these control structures is the parietal lobe: stroke patients with damage to this area often show impairments in directing attention to the side of space represented by the damaged hemisphere (the "contralesional" side of space). This disorder is called "hemispatial neglect" because the patients may totally neglect all information arising from one side of space. Posner and his colleagues have examined the performance of these neglect patients in spatial cuing experiments (Posner, Cohen, & Rafal, 1982; Posner, Walker, Friedrich, & Rafal, 1984), and have shown that these patients are specifically impaired when they are cued to the intact visual field but the target appears in the impaired field. This result suggests that the parietal lobe is involved in disengaging attention: when the parietal lobe in one hemisphere is damaged, it becomes difficult to disengage from the intact side of space in order to detect targets presented on the impaired side (for a somewhat different interpretation, see Kinsbourne, 1987).

A very similar pattern of results has also been reported in a visual search task (Eglin, Robertson, & Knight, 1989). When neglect patients perform a serial search, their performance is comparable to normal control subjects as long as the target is placed in the intact visual field: as the number of elements in the intact field increases, reaction time increases at a normal rate. Patients also show fairly normal performance for targets placed in the contralesional visual field as long as there are no distractors in the intact field. When distractors are present in the intact field, however, the detection of targets in the impaired field shows two striking abnormalities. First, reaction times are several seconds longer for targets in the impaired field than for targets in the intact field when distractors are present in both fields. Second, responses to targets in the impaired field become increasingly slow as more distractor items are added to the intact field. These results suggest that the patients are unable to disengage attention from the intact field, and search through the intact field several times before finally orienting attention to the impaired field. Because it takes longer to search the intact field when there are more distractors in that field, reaction times for targets in the impaired field are strongly affected by the number of distractors in the intact field. These results show that the hemispatial neglect syndrome produced by damage to the parietal lobes has comparable effects in both the spatial cuing and visual search paradigms.

Another important attentional control structure is the corpus callosum, the long belt of nerve fibers that connects the left and right hemispheres, and recent studies have shown that damage to this structure also has comparable effects in the cuing and search paradigms. These experiments utilized "split-brain" patients who had previously undergone surgical transection of the corpus callosum for the purpose of treating epilepsy. After this operation, the left and right hemispheres become largely independent, and can communicate only indirectly via their connections with subcortical structures. Because of this separation, split-brain patients are commonly used to examine differences in function between the left and right hemispheres. However, they are also very useful for assessing the extent to which subcortical structures are involved in cognitive processes. If a cognitive process is exclusively cortical, then the two hemispheres in a split-brain patient should be able to perform that process independently. If a process involves subcortical structures, however, then the two hemispheres may compete for access to those structures, leading to interference between the hemispheres. This line of reasoning was used to examine the role of subcortical structures in attentional processing.

The left hemisphere receives direct inputs from the right visual field and the right hemisphere receives direct inputs from the left visual field. In most people, information from a given hemifield can eventually reach both hemispheres by traveling through the corpus callosum, but the information remains in a single hemisphere in split-brain patients. As a result, each hemisphere of a split-brain patient should be able to search its own visual field independently of the other hemisphere if attention is controlled by cortical mechanisms. This is exactly what was found when split-brain patients performed a serial search task, as shown in Fig. 7.11a. In this experiment (Luck, Hillyard, Mangun, & Gazzaniga, 1994a), the search items were divided between the left and right visual fields on some trials (bilateral arrays) and were located entirely within a single visual field on others (unilateral arrays). Reaction times increased for both the split-brain patients and normal control subjects as more items were added to a given field, and for normal subjects the rate of increase was the same for both unilateral and bilateral arrays. For split-brain patients, however, the rate of increase was approximately twice as great for unilateral arrays as for bilateral arrays, indicating that they could search twice as fast when the stimuli were divided between the two hemispheres. This result suggests that the two separated hemispheres of the split-brain patients were able to search the bilateral arrays independently, resulting in a more efficient search than was possible when the stimuli were restricted to a single hemisphere. These findings indicate that attention is coordinated across the two hemispheres in normal subjects by means of the corpus callosum.

A similar set of findings was also obtained from split-brain patients in a study of spatial cuing (Mangun et al., 1994). If the separated hemispheres of split-brain patients have their own independent attentional systems, as indicated by the aforementioned search experiment, then it should be possible to cue each hemisphere to its own visual field without any interference from the other hemisphere. This proposal was tested by presenting split-brain patients with a target stimulus that was preceded by either a cue in the left visual field, a cue in the right visual field, or a bilateral cue in both fields (see Fig. 7.11b). In both normal and split-brain subjects, responses on single-cue trials were faster when the cue was valid than when it was invalid.



On bilateral-cue trials, normal subjects exhibited intermediate reaction times, presumably because the two visual fields were competing for attention. Split-brain patients, in contrast, were just as fast on bilateral-cue trials as they were on valid single-cue trials, indicating that they were able to attend to both visual fields simultaneously. These results provide yet another example of similarities between the neural systems involved in cuing and search.

These split-brain studies provide evidence that the coordination of attentional processing between the left and right hemispheres is controlled by the direct callosal connections between the hemispheres rather than subcortical structures. However, this does not imply that subcortical structures are not important in the control of attention within a given hemisphere. Indeed, there is substantial evidence indicating that two specific subcortical structures—the superior colliculus and the pulvinar—play important roles in attention. The superior colliculus is best known for its role in the programming of saccadic eye movements, and given the important links between eye movements and attention, it is not surprising that this structure also plays a role in attention. Specifically, the superior colliculus appears to be involved in automatically orienting attention when a new stimulus suddenly appears. The pulvinar is a nucleus within the thalamus, but does not serve as a simple sensory gateway like the better-known thalamic nuclei. Instead, it appears to receive both cortical and subcortical inputs and has outputs projecting widely throughout the cortex; these outputs appear to be important for the suppression of ignored information that can be observed in the cortex. These roles of the superior colliculus and the pulvinar in attention have recently been described in great detail by LaBerge (1995).

FIG. 7.11. Opposite. (a) Stimuli and results from the visual search study of Luck et al. (1994a). The distractor items in the search arrays were blue-over-red rectangles and the target was a red-over-blue rectangle. Each array consisted of two, four, or eight items, and these were either distributed evenly across both visual fields (bilateral arrays) or concentrated in a single hemifield (unilateral arrays). Subjects pressed a left-hand button if the target was present in the left visual field, pressed a right-hand button if the target was present in the right visual field, and made no response if the target was absent. Average reaction times for detecting the target are presented for a group of four split-brain patients and a group of six normal control subjects. (b) Stimuli and results from the spatial cuing study of Mangun et al. (1994). Two boxes and a fixation point were continuously present on the display. On each trial, one or both of the boxes flashed briefly, which cued the subject to the probable location of the subsequent target stimulus. The target was filled square, and subjects pressed one of two buttons to indicate the color of this square. The data shown here reflect responses made with the hand controlled by the hemisphere that directly received the target information, and are averages from three split-brain patients and ten control subjects. Adapted from Luck et al. (1994a) and Mangun et al. (1994).

CONCLUSIONS

This chapter has discussed two key issues within the study of attention that have been addressed in detail by neurophysiologists, namely the locus of selection and the relationship between the visual search and spatial cuing paradigms. Studies of the locus of selection—especially those using variants on the paradigm developed by Hillyard et al. (1973)—have provided strong evidence that attention may operate at an early, sensory stage to select relevant inputs for preferential processing. This selection may occur in the primary sensory cortex as early as 20 ms poststimulus in the auditory modality, and may occur in secondary sensory cortical areas as early as 60 ms poststimulus in the visual modality. In both modalities, intermediate-level perceptual processes are conducted at these times and in these cortical locations, so these attentional modulations clearly reflect early-selection mechanisms. It is important to remember, however, that the existence of early-selection mechanisms does not preclude the existence of late-selection mechanisms: early selection may be limited to conditions of information overload, in which efficient perceptual processing requires a reduction in the amount of sensory information being processed.

Although the most detailed neurophysiological evidence for early selection has been obtained using the paradigm developed by Hillyard et al. (1973), the same early-selection mechanisms observed in that paradigm also appear to operate in paradigms used more commonly by cognitive psychologists, such as visual search and spatial cuing. The conclusion that the same attentional mechanisms operate across these very different paradigms is heartening, because it indicates that theories of attention can validly draw on evidence obtained from both paradigms. However, the findings on which this conclusion is based also add a complication to theories of attention, because they also indicate that both tasks use multiple mechanisms of attention. This conclusion is based primarily on the dissociations that have been observed between the P1 and N1 attention effects. Specifically, the N1 attention effect appears to reflect a facilitation of processing of attended information and is present only when subjects must perform a discrimination, whereas the P1 attention effect appears to reflect a suppression of unattended information and is present in both detection and discrimination tasks. There are additional dissociations between these attention effects as well (reviewed by Luck, 1995), and it now seems clear that these two ERP attention effects reflect independent mechanisms of attention that are used under different conditions and have different effects on sensory processing. Because neurophysiological techniques allow the subcomponents of sensory processing to be recorded in relative isolation, they lead quite naturally to the differentiation of a seemingly unitary process such as attention into a set of separable component mechanisms. The challenge for the future will be to

integrate these neurophysiological findings into theories of attention at the cognitive level.

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