

THE ATTENTION SYSTEM OF THE HUMAN BRAIN

Michael I. Posner

Department of Psychology, University of Oregon, Eugene, Oregon 97403

Steven E. Petersen

Department of Neurology and Neurological Surgery,
Washington University, School of Medicine, St. Louis, Missouri 63110

INTRODUCTION

The concept of attention as central to human performance extends back to the start of experimental psychology (James 1890), yet even a few years ago, it would not have been possible to outline in even a preliminary form a functional anatomy of the human attentional system. New developments in neuroscience (Hillyard & Picton 1987, Raichle 1983, Wurtz et al 1980) have opened the study of higher cognition to physiological analysis, and have revealed a system of anatomical areas that appear to be basic to the selection of information for focal (conscious) processing.

The importance of attention is its unique role in connecting the mental level of description of processes used in cognitive science with the anatomical level common in neuroscience. Sperry (1988, p. 609) describes the central role that mental concepts play in understanding brain function as follows:

Control from below upward is retained but is claimed to not furnish the whole story. The full explanation requires that one take into account new, previously nonexistent, emergent properties, including the mental, that interact causally at their own higher level and also exert causal control from above downward.

If there is hope of exploring causal control of brain systems by mental states, it must lie through an understanding of how voluntary control is exerted over more automatic brain systems. We argue that this can be

approached through understanding the human attentional system at the levels of both cognitive operations and neuronal activity.

As is the case for sensory and motor systems of the brain, our knowledge of the anatomy of attention is incomplete. Nevertheless, we can now begin to identify some principles of organization that allow attention to function as a unified system for the control of mental processing. Although many of our points are still speculative and controversial, we believe they constitute a basis for more detailed studies of attention from a cognitive-neuroscience viewpoint. Perhaps even more important for furthering future studies, multiple methods of mental chronometry, brain lesions, electrophysiology, and several types of neuroimaging have converged on common findings.

Three fundamental findings are basic to this chapter. First, the attention system of the brain is anatomically separate from the data processing systems that perform operations on specific inputs even when attention is oriented elsewhere. In this sense, the attention system is like other sensory and motor systems. It interacts with other parts of the brain, but maintains its own identity. Second, attention is carried out by a network of anatomical areas. It is neither the property of a single center, nor a general function of the brain operating as a whole (Mesulam 1981, Rizzolatti et al 1985). Third, the areas involved in attention carry out different functions, and these specific computations can be specified in cognitive terms (Posner et al 1988).

To illustrate these principles, it is important to divide the attention system into subsystems that perform different but interrelated functions. In this chapter, we consider three major functions that have been prominent in cognitive accounts of attention (Kahneman 1973, Posner & Boies 1971): (a) orienting to sensory events; (b) detecting signals for focal (conscious) processing, and (c) maintaining a vigilant or alert state.

For each of these subsystems, we adopt an approach that organizes the known information around a particular example. For orienting, we use visual locations as the model, because of the large amount of work done with this system. For detecting, we focus on reporting the presence of a target event. We think this system is a general one that is important for detection of information from sensory processing systems as well as information stored in memory. The extant data, however, concern primarily the detection of visual locations and processing of auditory and visual words. For alerting, we discuss situations in which one is required to prepare for processing of high priority target events (Posner 1978).

For the subsystems of orienting, detecting, and alerting, we review the known anatomy, the operations performed, and the relationship of attention to data processing systems (e.g. visual word forms, semantic

memory) upon which that attentional subsystem is thought to operate. Thus, for orienting, we review the visual attention system in relationship to the data processing systems of the ventral occipital lobe. For detecting, we examine an anterior attention system in relationship to networks that subservise semantic associations. For alerting, we examine arousal systems in relationship to the selective aspects of attention. Insofar as possible, we draw together evidence from a wide variety of methods, rather than arguing for the primacy of a particular method.

ORIENTING

Visual Locations

Visual orienting is usually defined in terms of the foveation of a stimulus (overt). Foveating a stimulus improves efficiency of processing targets in terms of acuity, but it is also possible to change the priority given a stimulus by attending to its location covertly without any change in eye or head position (Posner 1988).

If a person or monkey attends to a location, events occurring at that location are responded to more rapidly (Eriksen & Hoffman 1972, Posner 1988), give rise to enhanced scalp electrical activity (Mangoun & Hillyard 1987), and can be reported at a lower threshold (Bashinski & Bachrach 1984, Downing 1988). This improvement in efficiency is found within the first 150 ms after an event occurs at the attended location. Similarly, if people are asked to move their eyes to a target, an improvement in efficiency at the target location begins well before the eyes move (Remington 1980). This covert shift of attention appears to function as a way of guiding the eye to an appropriate area of the visual field (Fischer & Breitmeyer 1987, Posner & Cohen 1984).

The sensory responses of neurons in several areas of the brain have been shown to have a greater discharge rate when a monkey attends to the location of the stimulus than when the monkey attends to some other spatial location. Three areas particularly identified with this enhancement effect are the posterior parietal lobe (Mountcastle 1978, Wurtz et al 1980), the lateral pulvinar nucleus of the postereolateral thalamus (Petersen et al 1987), and the superior colliculus. Similar effects in the parietal cortex have been shown in normal humans with positron emission tomography (Petersen et al 1988a).

Although brain injuries to any of these three areas in human subjects will cause a reduction in the ability to shift attention covertly (Posner 1988), each area seems to produce a somewhat different type of deficit. Damage to the posterior parietal lobe has its greatest effect on the ability

to disengage from an attentional focus to a target located in a direction opposite to the side of the lesion (Posner et al 1984).

Patients with a progressive deterioration in the superior colliculus and/or surrounding areas also show a deficit in the ability to shift attention. In this case, the shift is slowed whether or not attention is first engaged elsewhere. This finding suggests that a computation involved in moving attention to the target is impaired. Patients with this damage also return to former target locations as readily as to fresh locations that have not recently been attended. Normal subjects and patients with parietal and other cortical lesions have a reduced probability of returning attention to already examined locations (Posner 1988, Posner & Cohen 1984). These two deficits appear to be those most closely tied to the mechanisms involved with saccadic eye movements.

Patients with lesions of the thalamus and monkeys with chemical injections into the lateral pulvinar also show difficulty in covert orienting (Petersen et al 1987, Posner 1988). This difficulty appears to be in engaging attention on a target on the side opposite the lesion so as to avoid being distracted by events at other locations. A study of patients with unilateral thalamic lesions showed slowing of responses to a cued target on the side opposite the lesion even when the subject had plenty of time to orient there. This contrasted with the results found with parietal and midbrain lesions, where responses are nearly normal on both sides once attention has been cued to that location. Alert monkeys with chemical lesions of this area made faster than normal responses when cued to the side opposite the lesion and given a target on the side of the lesion, as though the contralateral cue was not effective in engaging their attention (Petersen et al 1987). They were also worse than normal when given a target on the side opposite the lesion, irrespective of the side of the cue. It appears difficult for thalamic-lesioned animals to respond to a contralateral target when another competing event is also present in the ipsilateral field (R. Desimone, personal communication). Data from normal human subjects required to filter out irrelevancies, showed selective metabolic increases in the pulvinar contralateral to the field required to do the filtering (LaBerge & Buchsbaum 1988). Thalamic lesions appear to give problems in engaging the target location in a way that allows responding to be fully selective.

These findings make two important points. First, they confirm the idea that anatomical areas carry out quite specific cognitive operations. Second, they suggest a hypothesis about the circuitry involved in covert visual attention shifts to spatial locations. The parietal lobe first disengages attention from its present focus, then the midbrain area acts to move the index of attention to the area of the target, and the pulvinar is involved

in reading out data from the indexed locations. Further studies of alert monkeys should provide ways of testing and modifying this hypothesis.

Hemispheric Differences

The most accepted form of cognitive localization, resulting from studies of split brain patients (Gazzaniga 1970), is the view that the two hemispheres perform different functions. Unfortunately, in the absence of methods to study more detailed localization, the literature has tended to divide cognition into various dichotomies, assigning one to each hemisphere. As we develop a better understanding of how cognitive systems (e.g. attention) are localized, hemispheric dominance may be treated in a more differentiated manner.

Just as we can attend to locations in visual space, it is also possible to concentrate attention on a narrow area or to spread it over a wider area (Eriksen & Yeh 1985). To study this issue, Navon (1987) formed large letters out of smaller ones. It has been found in many studies that one can concentrate attention on either the small or large letters and that the attended stimulus controls the output even though the unattended letter still influences performance. The use of small and large letters as a method of directing local and global attention turns out to be related to allocation of visual channels to different spatial frequencies. Shulman & Wilson (1987) showed that when attending to the large letters, subjects are relatively more accurate in the perception of probe grating of low spatial frequency, and this reverses when attending to the small letters.

There is evidence from the study of patients that the right hemisphere is biased toward global processing (low spatial frequencies) and the left for local processing (high spatial frequencies) (Robertson & Delis 1986, Sergent 1982). Right-hemisphere patients may copy the small letters but miss the overall form, while those with left hemisphere lesions copy the overall form but miscopy the constituent small letters. Detailed chronometric studies of parietal patients reveal difficulties in attentional allocation so that right-hemisphere patients attend poorly to the global aspects and left-hemisphere patients to the local aspects (Robertson et al 1988).

These studies support a form of hemispheric specialization within the overall structure of the attention system. The left and right hemispheres both carry out the operations needed for shifts of attention in the contralateral direction, but they have more specialized functions in the level of detail to which attention is allocated. There is controversy over the existence (Grabowska et al 1989) and the nature (Kosslyn 1988) of these lateralization effects. It seems likely that these hemispheric specializations are neither absolute nor innate, but may instead develop over time, perhaps in conjunction with the development of literacy. Although the role of

literacy in lateralization is not clear, there is some evidence that the degree of lateralization found in nonliterate normals and patients differs from that found in literate populations (Lecours et al 1988).

The general anatomy of the attention system that we have been describing lies in the dorsal visual pathway that has its primary cortical projection area in V1 and extends into the parietal lobe. The black areas on the lateral surface of Figure 1 indicate the parietal projection of this posterior attention system as shown in PET studies (Petersen et al 1988a). The parietal PET activation during visual orienting fits well with the lesion and single cell recording results discussed above. PET studies of blood flow also reveal prestriate areas related to visual word processing. For example, an area of the left ventral occipital lobe (gray area in Figure 1) is active during processing of visual words but not for letter-like forms (Snyder et al 1989). The posterior attention system is thought to operate upon the

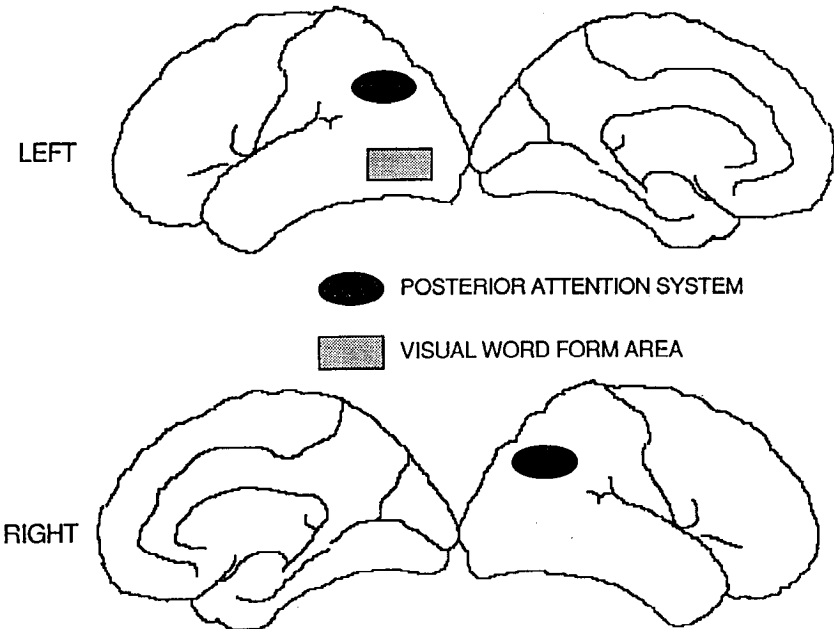


Figure 1 The posterior attention system. The upper two drawings are the lateral (left) and medial (right) surfaces of the left hemisphere. The lower two drawings are the medial (left) and lateral (right) surfaces of the right hemisphere. The location of the posterior visual spatial attention system is shown on the lateral surface of each hemisphere as determined by blood flow studies (Petersen et al 1988a). The location of the visual word form area on the lateral surface of the left hemisphere is from Snyder et al (1989).

ventral pathway during tasks requiring detailed processing of objects (e.g. during the visual search tasks discussed in the next section).

A major aspect of the study of attention is to see how attention could influence the operations of other cognitive systems such as those involved in the recognition of visual patterns. The visual pattern recognition system is thought to involve a ventral pathway, stretching from V1 to the infra-temporal cortex. Anatomically, these two areas of the brain can be coordinated through the thalamus (pulvinar) (Petersen et al 1987), or through other pathways (Zeki & Shipp 1988). Functionally, attention might be involved in various levels of pattern recognition, from the initial registration of the features to the storage of new visual patterns.

Pattern Recognition

VISUAL SEARCH All neurons are selective in the range of activation to which they will respond. The role of the attention system is to modulate this selection for those types of stimuli that might be most important at a given moment. To understand how this form of modulation operates, it is important to know how a stimulus would be processed without the special effects of attention. In cognition, unattended processing is called “automatic” to distinguish it from the special processing that becomes available with attention.

We have learned quite a bit about the automatic processing that occurs in humans along the ventral pathway during recognition of visual objects (Posner 1988, Treisman & Gormican 1988). Treisman has shown that search of complex visual displays for single features can take place in parallel with relatively little effect of the number of distractors. When a target is defined as a conjunction of attributes (e.g. red triangle) and appears in a background of nontargets that are similar to the target (e.g. red squares and blue triangles), the search process becomes slow, attention demanding, and serial (Duncan & Humphreys 1989).

We know from cognitive studies (LaBerge & Brown 1989, Treisman & Gormican 1988) that cueing people to locations influences a number of aspects of visual perception. Treisman has shown that subjects use attention when attempting to conjoin features, and it has also been shown that spreading focal attention among several objects leads to a tendency for misconjoining features within those objects, regardless of the physical distance between them (Cohen & Ivry 1989). Thus, attention not only provides a high priority to attended features, but does so in a way that overrides even the physical distance between objects in a display.

While these reaction time results are by no means definitive markers of attention, there is also evidence from studies with brain lesioned patients that support a role of the visual spatial attention system. These clinical

studies examine the ability of patients to bisect lines (Riddoch & Humphreys 1983), search complex visual patterns (Riddoch & Humphreys 1987), or report strings of letters (Friedrich et al 1985, Sieroff et al 1988). Damage to the posterior parietal lobe appears to have specific influences on these tasks. Patients with right parietal lesions frequently bisect lines too far to the right and fail to report the left-most letters of a random letter string (Sieroff et al 1988). However, these effects are attentional not in the recognition process itself. Evidence for this is that they can frequently be corrected by cueing the person to attend covertly to the neglected side (Riddoch & Humphreys 1983, Sieroff et al 1988). The cues appear to provide time for the damaged parietal lobe to disengage attention and thus compensates for the damage. It is also possible to compensate by substituting a word for a random letter string. Patients who fail to report the left-most letters of a random string will often report correctly when the letters make a word. If cues work by directing attention, they should also influence normal performance. Cues presented prior to a letter string do improve the performance of normals for nearby letters, but cues have little or no influence on the report of letters making words (Sieroff & Posner 1988). Blood flow studies of normal humans show that an area of the left ventral occipital lobe is unique to strings of letters that are either words or orthographically regular nonwords (Snyder et al 1989). This visual word form area (see gray area of Figure 1) appears to operate without attention, and this confirms other data that recognition of a word may be so automated as not to require spatial attention, whereas the related tasks of searching for a single letter, forming a conjunction, or reporting letters from a random string do appear to rely upon attention.

Studies of recording from individual cells in alert monkeys confirm that attention can play a role in the operation of the ventral pattern recognition system (Wise & Desimone 1988). It appears likely that the pathway by which the posterior attention system interacts with the pattern recognition system is through the thalamus (Petersen et al 1987). This interaction appears to require about 90 ms, since cells in V4 begin to respond to unattended items within their receptive field but shut these unattended areas off after 90 ms (Wise & Desimone 1988). Detailed models of the nature of the interaction between attention and pattern recognition are just beginning to appear (Crick 1984, LaBerge & Brown 1989).

IMAGERY In most studies of pattern recognition, the sensory event begins the process. However, it is possible to instruct human subjects to take information from their long-term memories and construct a visual representation (image) that they might then inspect (Kosslyn 1988). This

higher level visual function is called imagery. The importance of imagery as a means of studying mechanisms of high-level vision has not been well recognized in neuroscience. Imagery, when employed as a means of studying vision, allows more direct access to the higher levels of information processing without contamination from lower levels. There is by now considerable evidence that some of the same anatomical mechanisms are used in imagery as are involved in some aspects of pattern recognition (Farah 1988, Kosslyn 1988). Patients with right parietal lesions, who show deficits in visual orienting of the type that we have described above, also fail to report the contralesional side of visual images (Bisiach et al 1981). When asked to imagine a familiar scene, they make elaborate reports of the right side but not the left. The parts of the image that are reported when the patient is facing in one direction are neglected when facing in the other. This suggests that the deficit arises at the time of scanning the image.

When normal subjects imagine themselves walking on a familiar route, blood flow studies show activation of the superior parietal lobe on both sides (Roland 1985). Although many other areas of the brain are also active in this study, most of them are common to other verbal and arithmetical thoughts, but activation of the superior parietal lobe seems more unique to imagery. As discussed above, the parietal lobe seems to be central to spatial attention to external locations. Thus, it appears likely that the neural systems involved in attending to an external location are closely related to those used when subjects scan a visual image.

TARGET DETECTION

In her paper on the topography of cognition, Goldman-Rakic (1988) describes the strong connections between the posterior parietal lobe and areas of the lateral and medial frontal cortex. This anatomical organization is appealing as a basis for relating what has been called involuntary orienting by Luria (1973), and what we have called the posterior attention system, to focal or conscious attention.

Cognitive studies of attention have often shown that detecting a target produces widespread interference with most other cognitive operations (Posner 1978). It has been shown that monitoring many spatial locations or modalities produces little or no interference over monitoring a single modality, unless a target occurs (Duncan 1980). This finding supports the distinction between a general alert state and one in which attention is clearly oriented and engaged in processing information. In the alert but disengaged state, any target of sufficient intensity has little trouble in

summoning the mechanisms that produce detection. Thus monitoring multiple modalities or locations produces only small amounts of interference. The importance of engaging the focal attention system in the production of widespread interference between signals supports the idea that there is a unified system involved in detection of signals regardless of their source. As a consequence of detection of a signal by this system, we can produce a wide range of arbitrary responses to it. We take this ability to produce arbitrary responses as evidence that the person is aware of the signal.

Evidence that there are attentional systems common to spatial orienting as well as orienting to language comes from studies of cerebral blood flow during cognitive tasks. Roland (1985) has reported a lateral superior frontal area that is active both during tasks involving language and in spatial imagery tasks. However, these studies do not provide any clear evidence that such common areas are part of an attentional system. More compelling is evidence that midline frontal areas, including the anterior cingulate gyrus and the supplementary motor area, are active during semantic processing of words (Petersen et al 1988b), and that the degree of blood flow in the anterior cingulate increases as the number of targets to be detected increases (Posner et al 1988). Thus, the anterior cingulate seems to be particularly sensitive to the operations involved in target detection. (See Figure 2).

The anterior cingulate gyrus is an area reported by Goldman-Rakic (1988) to have alternating bands of cells that are labeled by injections into the posterior parietal lobe and the dorsolateral prefrontal cortex. These findings suggest that the anterior cingulate should be shown to be important in tasks requiring the posterior attention system as well as in language tasks. It has often been argued from lesion data that the anterior cingulate plays an important role in aspects of attention, including neglect (Mesulam 1981, Mirsky 1987).

Does attention involve a single unified system, or should we think of its functioning as being executed by separate independent systems? One way to test this idea is to determine whether attention in one domain (e.g. language) affects the ability of mechanisms in another domain (e.g. orienting toward a visual location). If the anterior cingulate system is important in both domains, there should be a specific interaction between even remote domains such as these two. Studies of patients with parietal lesions (Posner et al 1987) showed that when patients were required to monitor a stream of auditory information for a sound, they were slowed in their ability to orient toward a visual cue. The effect of the language task was rather different from engaging attention at a visual location because its

effects were bilateral rather than being mainly on the side opposite the lesion. Thus, the language task appeared to involve some but not all of the same mechanisms that were used in visual orienting.

This result is compatible with the view that visual orienting involves systems separate but interconnected with those used for language processing. A similar result was found with normal subjects when they were given visual cues while shadowing an auditory message (Posner et al 1989). Here, the effects of the language task were most marked for cues in the right visual field, as though the common system might have involved lateralized mechanisms of the left hemisphere. These findings fit with the close anatomical links between the anterior cingulate and the posterior parietal lobe on the one hand and language areas of the lateral frontal lobe on the other. They suggest to us a possible hierarchy of attention systems in which the anterior system can pass control to the posterior system when it is not occupied with processing other material.

A spotlight analogy has often been used to describe the selection of information from the ventral pattern recognition system by the posterior attention system (Treisman & Gormican 1988). A spotlight is a very crude analogy but it does capture some of the dynamics involved in disengaging, moving, and engaging attention. This analogy can be stretched still further to consider aspects of the interaction between the anterior attention system and the associative network shown to be active during processing of semantic associates and categories by studies of cerebral blood flow (Petersen et al 1988a). The temporal dynamics of this type of interaction between attention and semantic activation have been studied in some detail (see Posner 1978, 1982, for review).

ALERTING

An important attentional function is the ability to prepare and sustain alertness to process high priority signals. The relationship between the alert state and other aspects of information processing has been worked out in some detail for letter and word matching experiments (Posner 1978). The passive activation of internal units representing the physical form of a familiar letter, its name, and even its semantic classification (e.g. vowel) appears to take place at about the same rate, whether subjects are alert and expecting a target, or whether they are at a lower level of alertness because the target occurs without warning. The alert state produces more rapid responding, but this increase is accompanied by a higher error rate. It is as though the build-up of information about the classification of the

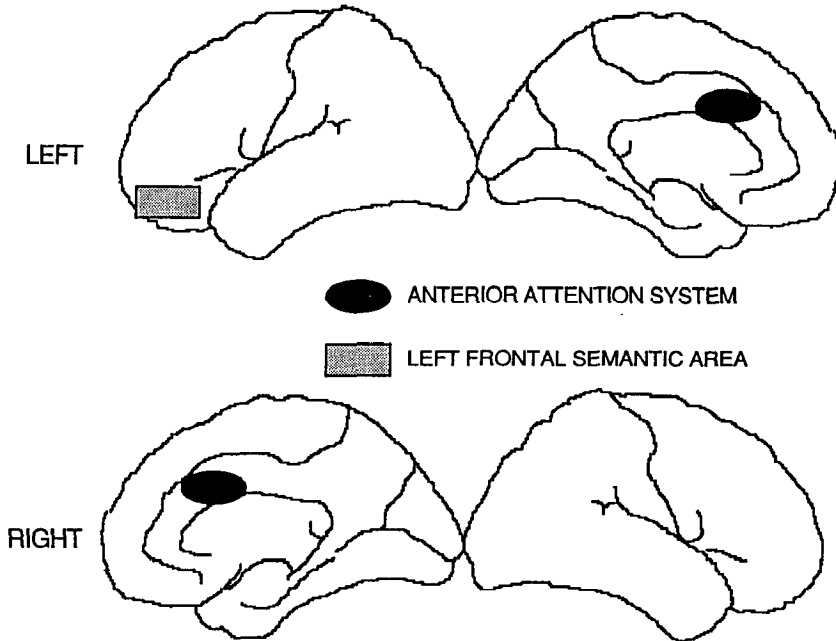


Figure 2 The anterior attention system. The *upper two drawings* are the lateral (*left*) and medial (*right*) surface of the left hemisphere. The *lower two drawings* are the medial (*left*) and lateral (*right*) surfaces of the right hemisphere. The semantic association area on the lateral aspect of the left hemisphere is determined by blood flow studies (Petersen et al 1988b). The anterior attention area is also from blood flow studies (Petersen et al 1988b, Posner et al 1988).

target occurs at the same rate regardless of alertness, but in states of high alertness, the selection of a response occurs more quickly, based upon a lower quality of information, thus resulting in an increase in errors. These results led to the conclusion that alertness does not affect the build-up of information in the sensory or memory systems but does affect the rate at which attention can respond to that stimulus (Posner 1978).

Anatomical evidence has accumulated on the nature of the systems producing a change in the alert state. One consistent finding is that the ability to develop and maintain the alert state depends heavily upon the integrity of the right cerebral hemisphere (Heilman et al 1985). This finding fits very well with the clinical observation that patients with right-hemisphere lesions more often show signs of neglect, and it has sometimes led to the notion that all of spatial attention is controlled by the right hemisphere. However, the bulk of the evidence discussed below seems to

associate right-hemisphere dominance with tasks dependent upon the alert state.

Lesions of the right cerebral hemisphere cause difficulty with alerting. This has been shown with measurement of galvanic skin responses in humans and monkeys (Heilman et al 1985) and with heart rate responses to warning signals (Yokoyama et al 1987). Performance in vigilance tasks is also more impaired with right rather than left lesions (Coslett et al 1987, Wilkins et al 1987). It has also been observed in split-brain patients that vigilance is poor when information is presented to the isolated left hemisphere, but is relatively good when presented to the isolated right hemisphere (Dimond & Beaumont 1973). In summary, the isolated right hemisphere appears to contain the mechanism needed to maintain the alert state so that when lesioned, it reduces performance of the whole organism.

Studies of cerebral blood flow and metabolism involving vigilance tasks have also uniformly shown the importance of areas of the right cerebral hemisphere (Cohen et al 1988, Deutsch et al 1988; J. Pardo, P. T. Fox, M. E. Raichle, personal communication). Other attention demanding activity, e.g. semantic tasks and even imagery tasks, do not uniformly show greater activation of the right hemisphere (Petersen et al 1988b, Roland 1985). Thus, blood flow and metabolic studies also argue for a tie between the right cerebral hemisphere and alerting. Some of these studies provide somewhat better localization. Cohen et al found an area of the midfrontal cortex that appears to be the most active during their auditory discrimination task. This is an area also found to be active in both visual and somatosensory vigilance conditions (J. Pardo et al, personal communication). Of special interest is that Cohen et al report that the higher metabolic activation they found in the right prefrontal cortex was accompanied by reduced activation in the anterior cingulate. If one views the anterior cingulate as related to target detection, this makes sense. In tasks for which one needs to suspend activity while waiting for low probability signals, it is important not to interfere with detecting the external signal. Subjectively, one feels empty headed, due to the effort to avoid any thinking that will reduce the ability to detect the next signal.

There is evidence that the maintenance of the alert state is dependent upon right-hemisphere mechanisms, and also that it is closely tied with attention. These two facts both suggest the hypothesis that the norepinephrine (NE) system arising in the locus coeruleus may play a crucial role in the alert state. In a review of animal studies, Aston-Jones et al (1984) argue that NE cells play a role in changes in arousal or vigilance. Moreover, Robinson (1985) has shown in rats that lesions of the right cerebral hemisphere but not of the left hemisphere lead to depletion of NE

on both sides, and that the effects are strongest with lesions near the frontal pole. These findings are consistent with the idea that NE pathways course through frontal areas, dividing as they go backward toward posterior areas. Thus, an anterior lesion would have a larger effect.

Morrison & Foote (1986) have studied the parts of the posterior visual system that are most strongly innervated by NE pathways. They find that in monkeys, NE innervation is most strongly present in the posterior parietal lobe, pulvinar, and superior colliculus. These are the areas related to the posterior attention system. Much weaker innervation was found in the geniculo-striate pathway and along the ventral pattern recognition pathway. These findings support the ideas that NE pathways provide the basis for maintaining alertness, and that they act most strongly on the posterior attention systems of the right cerebral hemisphere. In accord with these ideas, Posner et al (1987) found that patients with right parietal lesions were greatly affected when a warning signal was omitted before a target, while those with left parietal lesions were not. Clark et al (1989) have found that manipulation of NE levels by drugs had specific effects on attention shifting.

In summary, alertness involves a specific subsystem of attention that acts on the posterior attention system to support visual orienting and probably also influences other attentional subsystems. Physiologically, this system depends upon the NE pathways that arise in the LC and that are more strongly lateralized in the right hemisphere. Functionally, activation of NE works through the posterior attention system to increase the rate at which high priority visual information can be selected for further processing. This more rapid selection is often at the expense of lower quality information and produces a higher error rate.

CONSEQUENCES

Study of attention from a neuroscience viewpoint has been impeded because attention has been thought of as a vague, almost vitalistic capacity, rather than as the operation of a separate set of neural areas whose interaction with domain-specific systems (e.g. visual word form, or semantic association) is the proper subject for empirical investigation. Even a crude knowledge of the anatomy of the selective attention system has a number of important consequences for research. It allows closer coordination between brain imaging studies using human subjects and animal studies involving recording from individual cells. In the case of the posterior attention system, we have outlined hypotheses about the connections between neural systems that can best be tested and expanded by studies designed to work out the connections at the cellular level. At higher levels,

coordinated studies of PET and ERP imaging may tell us more details about communication between posterior visual word form systems and anterior semantics, and how attention is involved in this form of information transfer. A systems level analysis provides a framework for the more detailed studies that must follow.

A number of recent observations depend upon a better understanding of how attention relates to semantic activation. The psychological literature reflects a continuing effort to understand the limits to automatic priming of semantic systems (Posner 1982). In the study of sleep, we find challenging new hypotheses that tell us that during sleep, ongoing neural activity may be interpreted semantically by networks primed by daily activity (Hobson 1988). Similarly, research on split brain subjects (Gazzaniga 1970) has led to the idea of an interpreter system present in the left hemisphere that attempts to impose explanations for our behavior. Patients with lesions of the hippocampus, who show no memory that can be retrieved consciously, are able to demonstrate detailed storage by their performance (Squire 1986). This implies that for memory, as for performance, the distinction between automatic and conscious processing marks different neural mechanisms.

Finally, many disorders of higher level cognition are said to be due to deficits of attention. These include neglect, schizophrenia, closed head injury, and attention-deficit disorder, among others. The concept of an attentional system of the brain with specific operations allocated to distinct anatomical areas allows new approaches to these pathologies. One such example is the proposal that a core deficit in schizophrenia is a failure of the anterior attention system of the left hemisphere to impose the normal inhibitory pattern on the left lateralized semantic network (Early et al 1989). This proposal provides specific ideas on integration at the level of neurotransmission, anatomy, and cognition. Similar ideas may link attention-deficit disorder to the right hemisphere mechanisms that control sustaining of attention. A combined cognitive and anatomical approach may be useful in integrating the long separate physiological and psychosocial influences on psychopathology.

ACKNOWLEDGMENTS

This research was supported by Office of Naval Research Contract N-0014-86-0289 and by the Center for Higher Brain Function of Washington University School of Medicine. We acknowledge special appreciation to Drs. J. Pardo, P. Fox, M. Raichle, and A. Snyder for allowing citation of ongoing experiments. Dr. Pardo contributed heavily to our analysis of the alerting literature. Drs. Mary K. Rothbart, Asher Cohen, and Gordon Shulman were helpful in the presentation of this analysis.

Literature Cited

- Aston-Jones, G., Foote, S. L., Bloom, F. E. 1984. Anatomy and physiology of locus coeruleus neurons: Functional implications. In *Frontiers of Clinical Neuroscience*, Vol. 2, ed. M. G. Ziegler. Baltimore: Williams & Wilkins
- Bashinski, H. S., Bachrach, R. T. 1984. Enhancement of perceptual sensitivity as the result of selectively attending to spatial locations. *Percept. Psychophys.* 28: 241-48
- Bisiach, E., Luzzatti, C., Perani, D. 1981. Unilateral neglect, representational schema and consciousness. *Brain* 102: 757-65
- Clark, C. R., Geffen, G. M., Geffen, L. B. 1989. Catecholamines and the covert orienting of attention. *Neuropsychol.* 27: 131-40
- Cohen, A., Ivry, R. 1989. Illusory conjunctions inside and outside the focus of attention. *J. Exp. Psychol. Hum. Percept. Perf.* In press
- Cohen, R. M., Semple, W. E., Gross, M., Holcomb, H. J., Dowling, S. M., Nordahl, T. E. 1988. Functional localization of sustained attention. *Neuropsych. Neuropsychol. Behav. Neurol.* 1: 3-20
- Coslett, H. B., Bowers, D., Heilman, K. M. 1987. Reduction in cerebral activation after right hemisphere stroke. *Neurology* 37: 957-62
- Crick, F. 1984. Function of the thalamic reticular complex: The searchlight hypothesis. *Proc. Natl. Acad. Sci.* 81: 4586-90
- Deutsch, G., Papanicolaou, A. C., Bourbon, T., Eisenberg, H. M. 1988. Cerebral blood flow evidence of right cerebral activation in attention demanding tasks. *Int. J. Neurosci.* 36: 23-28
- Dimond, S. J., Beaumont, J. G. 1973. Difference in the vigilance performance of the right and left hemisphere. *Cortex* 9: 259-65
- Downing, C. J. 1988. Expectancy and visual-spatial attention effects on vision. *J. Exp. Psychol. Hum. Percept. Perf.* 14: 188-97
- Duncan, J. 1980. The locus of interference in the perception of simultaneous stimuli. *Psychol. Rev.* 87: 272-300
- Duncan, J., Humphreys, G. W. 1989. Visual search and stimulus similarity. *Psychol. Rev.* 96: 433-58
- Early, T., Posner, M. I., Reiman, E., Raichle, M. E. 1989. Left striato-pallidal hyperactivity in schizophrenia. *Psychiat. Develop.* In press
- Eriksen, C. W., Hoffman, J. E. 1972. Temporal and spatial characteristics of selective encoding from visual displays. *Percept. Psychophys.* 12: 201-4
- Eriksen, C. W., Yeh, Y. 1985. Allocation of attention in the visual field. *J. Exp. Psychol. Hum. Percept. Perf.* 11: 583-97
- Farah, M. J. 1988. Is visual imagery really visual? Overlooked evidence from neuropsychology. *Psych Rev.* 95: 307-17
- Fischer, B., Breitmeyer, B. 1987. Mechanisms of visual attention revealed by saccadic eye movements. *Neuropsychology* 25(1A): 73-84
- Friedrich, F. J., Walker, J., Posner, M. I. 1985. Effects of parietal lesions on visual matching. *Cog. Neuropsychol.* 2: 253-64
- Gazzaniga, M. S. 1970. *The Bisected Brain*. New York: Appleton. 171 pp.
- Goldman-Rakic, P. S. 1988. Topography of cognition: Parallel distributed networks in primate association cortex. *Annu. Rev. Neurosci.* 11: 137-56
- Grabowska, A., Semenza, C., Denes, G., Testa, S. 1989. Impaired grating discrimination following right hemisphere damage. *Neuropsychologia* 27(2): 259-64
- Heilman, K. M., Watson, R. T., Valenstein, E. 1985. Neglect and related disorders. In *Clinical Neuropsychology*, ed. K. M. Heilman, E. Valenstein. pp. 243-93. New York: Oxford
- Hillyard, S. A., Picton, T. W. 1987. Electrophysiology of cognition. *Handb. Physiol.* (pt. 2): 519-84
- Hobson, J. A. 1988. *The Dreaming Brain*. New York: Basic. 319 pp.
- James, W. 1890. *Principles of Psychology*, Vol. 1. New York: Holt
- Kahneman, D. 1973. *Attention and Effort*. Englewood Cliffs, NJ: Prentice Hall. 246 pp.
- Kosslyn, S. M. 1988. Aspects of a cognitive neuroscience of mental imagery. *Science* 240: 1621-26
- LaBerge, D., Brown, V. 1989. Theory of attentional operations in shape identification. *Psychol. Rev.* 96: 101-24
- LaBerge, D., Buchsbaum, M. S. 1988. Attention filtering and the puvinar: Evidence from PET scan measures. *Program 29th Annu. Meet. Psychonom. Soc.*, p. 4. (Abstr.)
- Lecours, A. R., Mehler, J., Parente, M. A. 1988. Illiteracy and brain damage. *Neuropsychologia* 26(4): 575-89
- Luria, A. R. 1973. *The Working Brain*. New York: Basic. 398 pp.
- Mangoun, G. R., Hillyard, S. A. 1987. The spatial allocation of attention as indexed by event-related brain potentials. *Hum. Factors* 29: 195-211
- Mesulam, M. M. 1981. A cortical network for directed attention and unilateral neglect. *Ann. Neurol.* 10: 309-25

- Mirsky, A. F. 1987. Behavioral and psychophysiological markers of disordered attention. *Environ. Health Persp.* 74: 191-99
- Morrison, J. H., Foote, S. L. 1986. Noradrenergic and serotonergic innervation of cortical, thalamic and tectal visual structures in old and new world monkeys. *J. Comp. Neurol.* 243: 117-28
- Mountcastle, V. B. 1978. Brain mechanisms of directed attention. *J. R. Soc. Med.* 71: 14-27
- Navon, D. 1977. Forest before trees: The precedence of global features in visual perception. *Cog. Psychol.* 9: 353-83
- Petersen, S. E., Fox, P. T., Miezin, F. M., Raichle, M. E. 1988a. Modulation of cortical visual responses by direction of spatial attention measured by PET. *Assoc. Res. Vision Ophthalm.* p. 22 (Abstr.)
- Petersen, S. E., Fox, P. T., Posner, M. I., Mintun, M., Raichle, M. E. 1988b. Positron emission tomographic studies of the cortical anatomy of single word processing. *Nature* 331: 585-89
- Petersen, S. E., Robinson, D. L., Morris, J. D. 1987. Contributions of the pulvinar to visual spatial attention. *Neuropsychology* 25: 97-105
- Posner, M. I. 1978. *Chronometric Explorations of Mind*. Englewood Heights, NJ: Erlbaum. 271 pp.
- Posner, M. I. 1982. Cumulative development of attentional theory. *Am. Psychol.* 32: 53-64
- Posner, M. I. 1988. Structures and functions of selective attention. In *Master Lectures in Clinical Neuropsychology*, ed. T. Boll, B. Bryant. 173-202 pp. Washington, DC: Am. Psych. Assoc.
- Posner, M. I., Boies, S. J. 1971. Components of attention. *Psychol Rev.* 78: 391-408
- Posner, M. I., Cohen, Y. 1984. Components of performance. In *Attention and Performance X*, ed. H. Bouma, D. Bowhuis. 531-56 pp. Hillsdale, NJ: Erlbaum
- Posner, M. I., Inhoff, A., Friedrich, F. J., Cohen, A. 1987. Isolating attentional systems: A cognitive-anatomical analysis. *Psychobiology* 15: 107-21
- Posner, M. I., Petersen, S. E., Fox, P. T., Raichle, M. E. 1988. Localization of cognitive operations in the human brain. *Science* 240: 1627-31
- Posner, M. I., Sandson, J., Dhawan, M., Shulman, G. L. 1989. Is word recognition automatic? A cognitive-anatomical approach. *J. Cog. Neurosci.* 1: 50-60
- Posner, M. I., Walker, J. A., Friedrich, F. J., Rafal, R. D. 1984. Effects of parietal lobe injury on covert orienting of visual attention. *J. Neurosci.* 4: 1863-74
- Raichle, M. E. 1983. Positron emission tomography. *Annu. Rev. Neurosci.* 6: 249-67
- Remington, R. 1980. Attention and saccadic eye movements. *J. Exp. Psychol. Hum. Percept. Perf.* 6: 726-44
- Riddoch, M. J., Humphreys, G. W. 1983. The effect of cueing on unilateral neglect. *Neuropsychology* 21: 589-99
- Riddoch, M. J., Humphreys, G. W. 1987. Perceptual and action systems in unilateral neglect. In *Neurophysiological and Neuropsychological Aspects of Spatial Neglect*, ed. M. Jeannerod, pp. 151-181. Amsterdam: North Holland
- Rizzolatti, G., Gentilucci, M., Matelli, M. 1985. Selective spatial attention: One center, one circuit or many circuits. In *Attention and Performance XI*, ed. M. Posner, O. S. M. Marin, pp. 251-65. Hillsdale, NJ: Erlbaum
- Robertson, L., Delis, D. C. 1986. Part-whole processing in unilateral brain damaged patients: Dysfunction of hierarchical organization. *Neuropsychology* 24: 363-70
- Robertson, L., Lamb, M. R., Knight, R. T. 1988. Effects of lesions of temporal-parietal junction on perceptual and attentional processing in humans. *J. Neurosci.* 8(10): 3757-69
- Robinson, R. G. 1985. Lateralized behavioral and neurochemical consequences of unilateral brain injury in rats. In *Cerebral Lateralization in Nonhuman Species*, ed. S. G. Glick, pp. 135-56. Orlando: Academic
- Roland, P. E. 1985. Cortical organization of voluntary behavior in man. *Hum. Neurobiol.* 4: 155-67
- Sergent, J. 1982. The cerebral balance of power: Confrontation or cooperation? *J. Exp. Psychol. Hum. Percept. Perf.* 8: 253-72
- Shulman, G. L., Wilson, J. 1987. Spatial frequency and selective attention to local and global structure. *Perception* 16: 89-101
- Sieroff, E., Pollatsek, A., Posner, M. I. 1988. Recognition of visual letter strings following damage to the posterior visual spatial attention system. *Cog. Neuropsychol.* 5: 427-49
- Sieroff, E., Posner, M. I. 1988. Cueing spatial attention during processing of words and letter strings in normals. *Cog. Neuropsychol.* 5: 451-72
- Snyder, A. Z., Petersen, S., Fox, P., Raichle, M. E. 1989. PET studies of visual word recognition. *J. Cerebral Blood Flow Metab.* 9: Suppl. 1-S576. (Abstr.)
- Sperry, R. L. 1988. Psychology's mentalist paradigm and the religion/science tension. *Am. Psychol.* 43: 607-13
- Squire, L. R. 1986. Mechanisms of memory. *Science* 232: 1612-19

- Treisman, A. M., Gormican, S. 1988. Feature analysis in early vision: Evidence from search asymmetries. *Psychol. Rev.* 95: 15-48
- Wilkins, A. J., Shallice, T., McCarthy, R. 1987. Frontal lesions and sustained attention. *Neuropsychology* 25: 359-66
- Wise, S. P., Desimone, R. 1988. Behavioral neurophysiology: Insights into seeing and grasping. *Science* 242: 736-41
- Wurtz, R. H., Goldberg, M. E., Robinson, D. L. 1980. Behavioral modulation of visual responses in monkeys. *Prog. Psychobiol. Physiol. Psychol.* 9: 42-83
- Yokoyama, K., Jennings, R., Ackles, P., Hood, P., Boller, F. 1987. Lack of heart rate changes during an attention-demanding task after right hemisphere lesions. *Neurology* 37: 624-30
- Zeki, S., Shipp, S. 1988. The functional logic of cortical connections. *Nature* 335: 311-17