

Review

Attention: The mechanisms of consciousness

(psychology/awareness/selection/visual search)

Michael I. Posner

Institute of Cognitive and Decision Sciences, University of Oregon, Eugene, OR 97403

ABSTRACT A number of recent papers and books discuss theoretical efforts toward a scientific understanding of consciousness. Progress in imaging networks of brain areas active when people perform simple tasks may provide a useful empirical background for distinguishing conscious and unconscious information processing. Attentional networks include those involved in orienting to sensory stimuli, activating ideas from memory, and maintaining the alert state. This paper reviews recent findings in relation to classical issues in the study of attention and anatomical and physical theories of the nature of consciousness.

What is it to be conscious? This has become a central question in many serious scientific circles (1–6). Proposals range from the anatomical, for example, locating consciousness in the thalamus (6) or in thalamic–cortical interactions (2, 6), to the physical, for example, the proposal that consciousness must rest on quantum principles (1, 4). Some proposals combine physical and anatomical reasoning. For example, Beck and Eccles (1) argue that conscious processing acts to increase the probability of quantal discharge at the synapse.

In this paper I propose to discuss the issue of consciousness in light of recent findings about attentional networks of the human brain that lead to selection of sensory information, activate ideas stored in memory, and maintain the alert state. I don't believe that any of these mechanisms are "consciousness" itself, just as DNA is not "life," but I do believe that an understanding of consciousness must rest on an appreciation of the brain networks that subserve attention, in much the same way as a scientific analysis of life without consideration of the structure of DNA would seem vacuous.

Attention

The study of attention has a long history within psychology. William James (7) wrote at the turn of the century, "Everyone knows what attention is. It is the taking possession by the mind in clear and vivid form of one out of what seem

several simultaneous objects or trains of thought."

The dominance of behavioral psychology postponed research into the internal mechanisms of selective attention in the first half of this century. The finding that the integrity of the brain stem reticular formation was a necessity to maintain the alert state provided some anatomical reality to the study of an aspect of attention (8). The quest for information-processing mechanisms to support the more selective aspect of attention began after World War II with studies of selective listening. A filter was proposed that was limited for information (in the formal sense of information theory) and located between highly parallel sensory systems and a limited-capacity perceptual system (9).

Selective listening experiments supported a view of attention that suggested early selection of relevant message, with nonselective information being lost to conscious processing. However, on some occasions it was clear that unattended information was processed to a high level because there was evidence that an important message on the unattended channel might interfere with the selected channel.

In the 1970s psychologists began to distinguish between automatic and controlled processes. It was found that words could activate other words similar in meaning (their semantic associates), even when the person had no awareness of the words' presence. These studies indicated that the parallel organization found for sensory information extended to semantic processing. Thus, selecting a word meaning for active attention appeared to suppress the availability of other word meanings. Attention was viewed less as an early sensory bottleneck and more as a system for providing priority for motor acts, consciousness, and memory (10).

Another approach to problems of selectivity arose in work on the orienting reflex (11). The use of slow autonomic systems (e.g., skin conductance as measures of orienting) made it difficult to analyze the cognitive components and neural systems underlying orienting. During the last 15 years there has been a steady advancement in our understanding of the neural systems related to visual

orienting from studies using single-cell recording in alert monkeys (12). This work showed a relatively restricted number of areas in which the firing rates of neurons were enhanced selectively when monkeys were trained to attend to a location, at the level of the superior colliculus (i.e., the midbrain), selective enhancement could only be obtained when eye movement was involved, but in the posterior parietal lobe of the cerebral cortex, selective enhancement occurred even when the animal maintained fixation. An area of the thalamus, the lateral pulvinar, was similar to the parietal lobe in containing cells with the property of selective enhancement.

Until recently, there has been a separation between human information processing and neuroscience approaches to attention using nonhuman animals. The former tended to describe attention, either in terms of a bottleneck that prevented limited-capacity central systems from overload or as a resource that could be allocated to various processing systems in a way analogous to the use of the term in economics. On the other hand, neuroscience views emphasized several separate neural mechanisms that might be involved in orienting and maintaining alertness. Currently, there is an attempt to integrate these two within a cognitive neuroscience of attention. An impressive aspect of current developments in this field is the convergence of evidence from various methods of study. These include performance studies using reaction time, dual-task performance studies, recording from scalp electrodes, and lesions in humans and animals, as well as various methods for imaging and recording from restricted brain areas, including individual cells (13).

Current progress in the anatomy of the attention system rests most heavily on two important methodological developments. (i) The use of microelectrodes with alert animals allowed evidence for the increased activity of cell populations with attention (12). (ii) Anatomical (e.g., computerized tomography or magnetic resonance imaging) and physiological [e.g., positron emission tomography

Abbreviation: PET, positron emission tomography.

(PET) and functional magnetic resonance imagery] methods of studying parts of the brain allowed more meaningful investigations of localization of cognitive function in normal people (13). The future should see the use of localizing methods together with methods of tracing the time course of brain activity in the human subject. This combination should provide a convenient way to trace the rapid time-dynamic changes that occur in the course of human information processing.

Three fundamental working hypotheses characterize the current state of efforts to develop a combined cognitive neuroscience of attention. (i) There exists an attentional system of the brain that is anatomically separate from various data-processing systems that can be activated passively by visual and auditory input. (ii) Attention is carried out by a network of anatomical areas. It is neither the property of a single brain area nor is it a collective function of the brain working as a whole. (iii) The brain areas involved in attention do not carry out the same function, but specific computations are assigned to different areas (13).

It is not possible to specify the complete attentional system of the brain, but something is known about the areas that carry on three major attentional functions: orienting to sensory stimuli, particularly locations in visual space; detecting target events, including ideas stored in memory; and maintaining the alert state. Each of these areas of research provides information that relate to the theories of consciousness discussed in my first paragraph, but as will be apparent from the discussion below, each relates only partially to common definitions of conscious processing.

Visual Orienting

How can one study attention? Crick argues for the selection of a model system that involves consciousness in a limited domain. His choice is awareness during visual search. Visual search has also been a traditional vehicle for the study of attention. For example, if you are asked to report a vertical rectangle in Fig. 1, the time to do so is linearly related to the number of distractors. This situation is thought to occur because one has to orient attention to each location. An individual may do so by making an eye movement, but it is also clear that the eyes can remain fixed and each position examined covertly. We now know quite a lot about the mechanism that performs this covert operation from studies of normal subjects, brain-lesioned patients, and monkeys (13).

When subjects switch attention from location to location, they activate processes in the parietal lobe of the opposite hemisphere (14). These cortical areas are

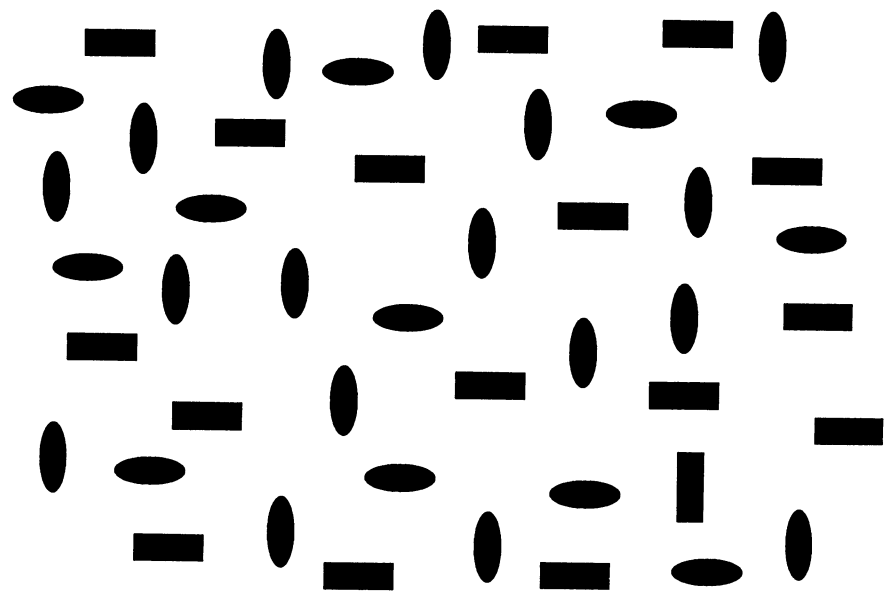


FIG. 1. Searching this display for a vertical rectangle requires attention to successive locations because the nontargets include both vertical (ellipses) and rectangles (horizontal). Reaction times in this task are linearly related to the number of distractors. [This figure was reproduced with permission from ref. 37 (copyright Elsevier, Cambridge, U.K.).]

involved in programming the switch of attention in the opposite visual field. The mechanisms of the parietal lobe are not symmetric. PET evidence shows that the right parietal lobe is involved with attention shifts in both visual fields, whereas the left parietal lobe seems restricted to rightward shifts of attention (14). There is a further hemispheric specialization as well. The left hemisphere seems to be more involved when attending to local information that might be important in recognizing objects, whereas the right hemisphere seems more involved when global features are involved, such as in general navigation in an environment (15).

These hemispheric differences are especially important in understanding how brain damage influences our awareness of the visual world. In normal people the two hemispheres operate as a unit in visual search, so that it does not matter if all of the distractors are located in one visual field or if they are distributed across the visual fields. However, if the two hemispheres are separated surgically by cutting the fiber tract that runs between them, this unity no longer applies, and each hemisphere's system operates separately, yielding a search rate that is twice as fast (16). Yet the patient is not really aware that a change has taken place due to the operation. If there is damage to the right parietal lobe, subjects will be very likely to neglect targets in search tasks like those of Fig. 1. In other words, they can be unconscious of information on the side of space opposite the lesion. These same mechanisms are used when these neglect patients recall infor-

mation from memory, and they neglect the left side of visual images (17).

We know something of the route by which the parietal mechanism influences information about the target identity. The most prominent hypothesis about this route is that it involves the pulvinar nucleus of the thalamus. There is good evidence of activity in this general region when subjects must pull out a target from surrounding clutter (18). Thus the interaction of thalamus and the cortex plays an important role in our consciousness of the target. This finding fits well with the general idea outlined by Crick.

What are the consequences of attending to a visual object? We know from cellular recording studies in monkeys (12) and from neuroimaging studies in people (13) that attention provides a relative increase of neural activity when compared with comparable unattended information. For example, an instruction to attend to the color, form, or motion of visual input increases neural activity in the regions that process this information (19). This finding is certainly consonant with the proposal that mental events work on the rate of transmission of neural impulses that has been suggested by several theories of consciousness (1, 3).

However, the principle of relative amplification by attention is a very general one (13). It is found in all areas of the brain that have been studied. Attention to sensory information amplifies brain areas used to processes that modality; similarly, attention to motor output activates brain areas used to generate the movement. This principle also appears to apply to higher-level cognitive processes (13). For example, creating a visual im-

age from a verbal instruction is now known to produce activation in visually specific areas of the cortex that would be used to process visual input of the same type.

What is still not known is exactly how this amplification is accomplished. There are theories at the neural level (20) and cellular observations that suggest a role for suppression of the unattended processes (21, 22), but the detailed cellular mechanisms remain to be clarified.

Are the thalamic-visual cortex interactions we have been describing "consciousness" as suggested by Crick? One definition of consciousness involves awareness of the outside world, and the interactions of thalamic areas with the visual cortex are certainly important for achieving focal awareness. By focal awareness I mean the type of recognition that one has of the target in Fig. 1. To locate the target one must effortfully engage different locations to be certain that they contain the constellation of features (form and orientation) required. However, it would not be appropriate to say you are unaware of other objects in the field that are not the focus of attention. One is roughly aware of the density of nonattended objects—their extent and basic format. It is possible to distinguish the type of focal awareness needed to locate the target from a more general awareness of the background (23). Damage to the attention network involving the parietal lobe and associated thalamic areas produces a kind of loss of focal awareness on one side of the world. Neglect induced by parietal lesion may leave the patient unconscious of this lack of awareness, just as the split brain person is unaware that search of the visual world has lost integration. However, patients with parietal lesions usually recover awareness of information opposite the lesion but show a permanent loss of the ability of stimuli arising there to produce orienting away from already attended events. This may lead to a failure to see objects on the left side of Fig. 1, but if cued to that location, they become conscious of them. In addition, normal subjects can attend to aspects of visual stimuli, such as their color or form, without activation of the parietal mechanisms we have been describing. These facts seem to argue that the parietal-thalamic system represents an important pathway by which conscious processing is achieved, rather than consciousness itself. Nonetheless, the clarification of neglect that has arisen from recent studies has helped us grasp some important elements of achieving focal awareness.

Attending to Ideas

Suppose you are asked to locate the vertical rectangle in Fig. 1. Must you

search all the target locations or can you confine your search to the vertical objects only? There is considerable evidence that search can be guided by information about the color or orientation or other nonlocational features of the target (24). How is this implemented in the brain? It seems that the recruitment and control of posterior brain areas, in this case, is supervised by an anatomically distinct system that involves more anterior structures that have sometimes been called an executive network (ref. 13, pp. 168–174) (Fig. 2). In the study of attentional amplification of color, form, or motion mentioned above there was evidence for activation of a frontal attentional system, but no parietal activation was found (19). It thus appears that two different attentional systems serve as sources of activation for color or form (frontal areas) and for location (parietal), although both may enter via the thalamus to amplify activity within the visual system at the same site (e.g., V4).

In guided search, selection by location and selection by color or form occur simultaneously with relatively little interference (24), unlike the situation for location when the corpus callosum is intact, in which attention cannot be shared between the two fields (16). One speculative possibility would be that time sharing is possible when two anatomically distinct attentional sources are involved.

The frontal areas that serve to guide search appear to involve a network that includes at least portions of the basal ganglia and of the anterior cingulate gyrus (ref. 13, pp. 168–174). The anterior portion of the cingulate gyrus appears to be involved in a wide range of activities that have been termed collectively "executive function" (25). In PET language studies, when subjects were required to name the use of familiar nouns (e.g., pound to hammer) activation of the anterior cingulate along with left lateral cortex language areas was most promi-

nent. When subjects were required to respond to the ink color in which a conflicting color name was presented (Stroop effect), there was strong activation of the anterior cingulate along with prefrontal color areas (13). The detection of multiple color form or motion targets in comparison with passive viewing of the same stimuli also activated the anterior cingulate (19). All of these situations involve selection of targets from competing inputs, which is considered a traditional role of attention. In the case of this executive attentional network, the nature of the target does not seem to matter very much.

The term "executive" suggests two important overall functions. (i) An executive is informed about the processes taking place within the organization. A system that would be related to our subjective experience of focal attention would clearly play this function for a subset of current (sensory) and stored (memory) information. There are reasons for relating anterior cingulate function to focal awareness of the target (13). For example, the intensity of cingulate activity tends to increase with number of targets in a set of stimuli and decreases with practice on any single stimulus set. These findings correspond to cognitive theories linking focal attention to number and difficulty of target detection.

(ii) A second function of an executive is to exercise some control over the system. The anatomy of the anterior cingulate provides pathways for connecting it to both the posterior parietal area and to anterior areas active during language tasks (26). Working memory is generally thought to involve both a representation of past events and an executive system involved in sustaining and transforming this representation (27). Recent PET (28, 29) and neurophysiological (30, 31) studies show that lateral areas of the prefrontal cortex play a key role in holding on-line a representation of past events.

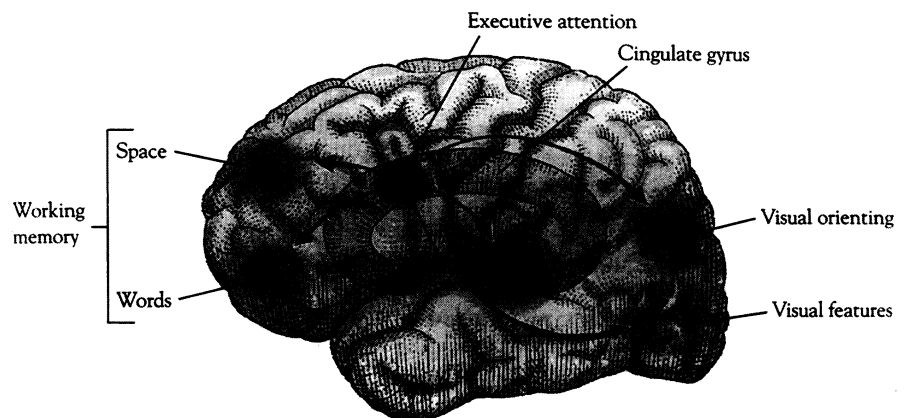


FIG. 2. The executive attentional system involves frontal structures, including the anterior cingulate, and acts upon many different brain areas [reproduced with permission from ref. 13 (copyright Freeman, New York)].

Cellular recordings in the awake monkey indicate that cells within the dorsolateral prefrontal cortex maintain a representation of the spatial environment when monkeys have to hold in mind a location to which to move their eyes after the stimulus disappears (30). Other cells within the inferior convexity hold a representation of the identity of past stimuli (31). Lateral areas of the left frontal and posterior cortex are also active in studies when people must obtain a quick association to word stimuli (13). While specialized areas of the lateral prefrontal cortex appear to hold the relevant information on-line, the anterior cingulate would be playing a role in the executive functions of awareness and control discussed in cognitive studies and often found impaired in subjects with frontal damage. Previously, the empirical results that support the important role of the anterior cingulate as a part of this network were summarized as follows (32):

The anterior attention network seems to be much more directly related to awareness than the posterior network, as has been indicated by the PET studies cited previously. The use of subjective experience as evidence for a brain process related to consciousness has been criticized by many authors. However, we note that the evidence for the activation of the anterior cingulate is entirely objective; it does not rest upon any subjective report. Nevertheless, if one defines consciousness in terms of awareness, it is necessary to show evidence that the anterior attention network is related to phenomenal reports in a systematic way. In this section, we note *five points*, each of which appears to relate *subjective experience* to activation of the anterior attention system. First, the degree of activation of this network increases with the number of targets presented in a semantic monitoring task and decreases with the amount of practice in the task. At first one might suppose that target detection is confounded with task difficulty. But in our semantic monitoring task the same semantic decision must be made irrespective of the number of actual targets. In our tasks no storage or counting of targets was needed. Thus, we effectively dissociated target detection from task difficulty. Nonetheless, anterior cingulate activation was related to number of targets present. The increase in activation with number of targets and reduction in such activation with practice corresponds to the common finding in cognitive studies that conscious attention is involved in target detection and is required to a greater degree early in practice. As practice

proceeds, feelings of effort and continuous attention diminish, and details of performance drop out of subjective experience.

Second, the anterior system appears to be active during tasks requiring the subject to detect visual stimuli, when the targets involve color form, motion, or word semantics.

Third, the anterior attention system is activated when listening passively to words, but not when watching those words. This finding appears to correspond subjectively to the intrusive nature of auditory words to consciousness when they are presented in a quiet background. They seem to capture awareness. Reading does not have this intrusive character. For a visual word to dominate awareness, an act of visual orienting is needed to boost its signal strength.

Fourth, the anterior attention system is more active during conflict blocks of the Stroop test than during nonconflict blocks. This is consistent with the commonly held idea that conflict between word name and ink color produces a strong conscious effort to inhibit saying the written word. Finally, there is a relation between the vigilance system and awareness. When one attends to a source of sensory input in order to detect an infrequent target, the subjective feeling is of emptying the head of thoughts or feelings. This subjective "clearing of consciousness" appears to be accompanied by an increase in activation of the right frontal lobe vigilance network and a reduction in the anterior cingulate. Just as feelings of effort associated with target detection or inhibiting prepotent responses are accompanied by evidence of cingulate activation, so the clearing of thought is accompanied by evidence of cingulate inhibition.

Dennett (33) provided a strong philosophical critique of those who implicitly cling to a view that there is an arena of consciousness or what he calls the Cartesian Theater of the Mind. Nonetheless, the specific points made above seemed to identify cingulate activation with aspects of awareness in so much tighter a way than previous efforts that it seems reasonable to set them down with as much clarity as possible. A somewhat similar view of the role of the cingulate in conjunction with the hippocampus has been discussed by Edelman (3). Edelman views these two brain structures as involved in the integration of interoceptive and exteroceptive information needed for conscious processing. In his work he distinguishes what he calls attention

(which is the increase in neural activity within brain areas currently of the organism's concern) from consciousness, which is the source of these activations in the cingulate-hippocampal system. There is a semantic difference in that I have called the former, the site at which attention works, and the latter, attentional networks, but the distinction appears minor.

One new development is an increased understanding of how the brain actually executes a voluntary instruction to attend to something (ref. 13, pp. 141–148). Studies employing PET have revealed important anatomical aspects of word reading. Two major areas of activation appear within the visual system. A right posterior temporal parietal area is activated passively by visual features, whether in consonant strings or words. In PET studies, areas of the left frontal area are active when subjects deal with the meaning of a word. When the process is extended by requiring association of several words to a given input or by slowing the rate of presentation, this left frontal area is joined by a posterior activation in Wernecke's area.

To study semantic and feature activation together, we used tasks that clearly involved both. We measured electrical activity from scalp electrodes. One task was looking for a visual feature; the semantic task required the subject to determine if the word referred to a natural or a manufactured item. Our reasoning was that in the visual task, subjects would be attending to the feature level, and in the semantic task attention would be directed to the meaning of the word. If, as has been described in the PET work, attention serves to amplify computations, it should be possible to see amplifications of the voltages in the waveforms in the right posterior area in feature analysis and in the left frontal area in semantics, depending upon the task used. We used exactly the same stimuli in the two tasks.

Results showed that electrical activity from the left frontal area was more positive at ≈ 200 – 300 msec when the task was semantic, whereas the right posterior area showed more positivity when the task was feature search. These effects were not confined to single electrode sites. For the posterior area, it was possible to compare the electrode sites first showing the greater right hemisphere activation at 100 msec associated with the processing of visual attributes automatically with those showing the amplification due to voluntary attribute search at ≈ 250 msec. Our comparison supported the idea that roughly the same areas that first carried out the visual-attribute computations on the letter string were reactivated 100 msec later when subjects were looking for the thick letter. This fit

with the idea that subjects can voluntarily reactivate areas of the brain that performed the task automatically when they are instructed to deal with that computation voluntarily. The semantic effect was found at several frontal sites bilaterally. This result differs from the PET data, which were strictly left lateralized, although there was some evidence that the left frontal area showed the effect more strongly than the right.

A popular idea in modern physiology is called reentrant processing. Basically, this is the idea that higher-level associations are made by fibers that reenter the brain areas which processed the initial input (3, 34). Reentrant processing may be contrasted with more traditional notions that higher functions are confined to higher-associational areas of the brain. In our studies, the visual computation occurs at 100 msec, followed by a semantic computation that begins at ≈ 200 msec. When the instruction is to search the string for a visual feature, the electrodes around the area originally performing the visual computation are reactivated. Similarly, when asked to make a semantic computation, the area thought to perform such computations was amplified in electrical activity.

If the brain operates in this way, we might then be able to instruct the subject to compute the same functions in different orders and thus reprogram the order of the underlying computations. To investigate this, we defined what we call a conjunction task by asking subjects either to respond to targets that had thick letters and were animate or were inanimate and had thick letters. Both tasks were identical except for the order of the computations.

We did not expect the subjects to actually compute the functions in a serial fashion. The reaction times for targets suggested that the subjects were able to reorder the priority of the underlying computations in the conjunction task. The electrical activity also reflected the instructed priority. The results provide us with a basis for understanding how the brain can carry out so many different tasks upon visual input. Some aspects of the underlying computations are not affected by instructions. The visual attribute area of the right posterior brain seems to carry out the computation on the input string at 100 msec, irrespective of whether the person is concerned with visual features as a part of the task or not. However, when the task is identified as looking for a thick letter, these same brain areas are reactivated and presumably carry out the additional computations necessary to make sure that one of the letters has just enough thickening to constitute a target. Attention thus can amplify computations within particular areas but often does so by reentering the

area, not by amplifying its initial activation. The order of these underlying computations can be reprogrammed by attending at different times, just as the order of attended locations in visual search can be changed at will.

The data on computing conjunctions implies two important ideas related to the attentional control of information processing. (i) The results of attentional control are widely distributed, resulting in amplification of activity in the anatomical areas that originally computed that information. (ii) The source of this attentional control need not involve a system that has access to the information being amplified but can be a system that has connections to places where the computations occur.

As the result of activity within the attention network, the relevant brain areas will be amplified and/or irrelevant ones will be inhibited, leaving the brain to be dominated by the selected computations. If this were the correct theory of attentional control, one would expect to find the source of attention to lie in systems widely connected to other brain areas, but not otherwise unique in structure. As pointed out by Goldman-Rakic (26), this appears to be the basic organization of frontal midline networks. Anterior cingulate connections to limbic, thalamic, and basal ganglia pathways would distribute its activity to the widely dispersed connections we have seen to be involved in cognitive computations.

Maintaining the Alert State

The earliest studies of the anatomy of attention involved maintenance of the alert state. Cognitive psychologists have studied changes in alerting, by warning signals to prepare for the task. There is evidence that an increase in alertness improves the speed of processing events. The trade-off between improved speed and reduced accuracy with warning signals has led to a view that alerting does not act to improve the buildup of information concerning the nature of the target but, instead, acts on the attentional system to enhance the speed of actions taken toward the target (ref. 13, pp. 174–176).

There has been some improvement in our understanding of the neural systems related to alerting over the last few years. Patients with lesions of the right frontal area have difficulty in maintaining the alert state. In addition, experimental studies of blood flow in normal people during tasks that require maintaining alertness show right frontal activation.

The neurotransmitter norepinephrine appears to be involved in maintaining the alert state. This norepinephrine pathway arises in the midbrain, but the right frontal area appears to have a special role in

its cortical distribution. Among posterior visual areas in the monkey, norepinephrine pathways are selective for areas involved in visual spatial attention. Recent studies (35) using drugs to reduce norepinephrine in alert monkeys show that this reduction blocks the increased processing speed usually found with warning signals, thus supporting the role of norepinephrine in achieving alertness.

Applications and Future Directions

We have a start on understanding the circuitry that underlies orienting of attention. However, more detailed cellular studies in monkeys are necessary to test these hypotheses and to understand more completely the time course and the control structures involved in covert orienting of attention. Even more fascinating is the possibility that the microstructure of areas involved in attention will be different somehow in organization from those areas carrying out passive data processing. Such differences could give us a clue as to the way in which brain tissue might relate to subjective experience.

Much remains unknown concerning the more anterior executive system. Studies of blood flow and metabolism in normal people should be adequate to provide candidate areas involved in aspects of attention. It will then be possible to test further the general proposal that these constitute a unified system and that constituent computations are localized.

The idea of attention as a network of anatomical areas makes relevant study of both the comparative anatomy of these areas and their development in infancy (ref. 13, pp. 181–192). In the first few months of life, infants develop nearly adult abilities to orient to external events, but the cognitive control produced by the executive attention network requires many months or years of development. Studies of orienting and motor control are beginning to lead to an understanding of this developmental process. As more about the maturational processes of brain and transmitter system is understood, it could be possible to match developing attentional abilities with changing biological mechanisms. The neural mechanisms of attention must support not only common development among infants in their regulatory abilities, but also the obvious differences among infants in their rates and success of attentional control.

There are many disorders that are often supposed to involve attention—including neglect, depression, schizophrenia, and attention-deficit disorder. The specification of attention in terms of anatomy and function has already proven useful in clarifying some of the underlying bases for these disorders (ref. 13, pp. 217–222). The development of theories of deficits might also foster the integration

of psychiatric and higher-level neurological disorders, both of which might affect the brain's attentional system.

Consciousness

The issues of selection and control central to the study of attention are also important aspects of most theories of consciousness. Sperry (36), in particular, has argued that cognitive control over earlier evolving neural systems represents an emergent property of complex networks.

The study of visual attention has implicated a cortical-thalamic network used for orienting that has many similarities to the visual awareness system favored by Crick (2) as a model for the study of consciousness. Although there may be doubts about whether it is a complete model, the importance of studies of this system as a way of integrating human and monkey research is clear. Study of higher forms of attentional selectivity has focused on frontal structures that have something in common with the analysis of consciousness proposed by Edelman (3) and others. The role of the cingulate and other frontal areas in the development of volition remains of critical importance. Neuroimaging studies have tended to confirm the role of attention in providing a relative amplification of neural activity within specific sensory or motor sites at which computations take place. This is a view favored by Beck and Eccles (1), as well as many others, as a critical aspect of consciousness. Whether the progress in studies of attention and brain mechanisms will provide a complete analysis of consciousness or whether fundamentally new mechanisms such as those that might come from quantum physics (1, 4) will be needed is, of course, a matter of opinion, but what seems clear is that there has been very considerable recent progress toward understanding brain networks relevant to the production of conscious experience,

and the tools are present for considerable future development.

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1. Beck, F. & Eccles, J. C. (1992) *Proc. Natl. Acad. Sci. USA* **89**, 11357–11361.
2. Crick, F. (1994) *The Astonishing Hypothesis* (Scribner's, New York).
3. Edelman, G. M. (1989) *The Remembered Present* (Basic, New York).
4. Penrose, R. (1989) *The Emperor's New Mind* (Oxford Univ. Press, Oxford).
5. Zeki, S. (1993) *A Vision of the Brain* (Blackwell, Oxford).
6. Baars, B. (1988) *A Cognitive Theory of Consciousness* (Cambridge Univ. Press, Cambridge, U.K.).
7. James, W. (1907) *Psychology* (Holt, Rinehart & Winston, New York).
8. Moruzzi, G. & Magoun, H. V. (1949) *Electroencephalogr. Clin. Neurophysiol.* **1**, 445–473.
9. Broadbent, D. E. (1958) *Perception and Communication* (Pergamon, London).
10. Allport, D. A. (1989) in *Foundations of Cognitive Science*, ed. Posner, M. I. (Bradford Books/MIT Press, Cambridge, MA), pp. 636–682.
11. Sokolov, Y. N. (1963) *Perception and the Conditioned Reflex* (Pergamon, London).
12. Wurtz, R. H., Goldberg, M. E. & Robinson, D. L. (1980) *Prog. Psychobiol. Physiol. Psychol.* **9**, 43–83.
13. Posner, M. I. & Raichle, M. E. (1994) *Images of Mind* (Sci. Am. Library, New York).
14. Corbetta, M., Miezin, F. M., Shulman, G. L. & Petersen, S. E. (1993) *J. Neurosci.* **13**, 1202–1226.
15. Robertson, L. C., Lamb, M. R. & Knight, R. T. (1988) *J. Neurosci.* **8**, 3757–3769.
16. Luck, S. J., Hillyard, S. A., Mangun, G. R. & Gazzaniga, M. S. (1989) *Nature (London)* **342**, 543–545.
17. Bisiach, E. (1992) in *The Neuropsychology of Conscious*, eds. Milner, A. D. & Rugg, M. (Academic, London), pp. 113–137.
18. LaBerge, D. & Buchsbaum, M. S. (1990) *J. Neurosci.* **10**, 613–619.
19. Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L. & Petersen, S. E. (1991) *J. Neurosci.* **11**, 2388–2402.
20. Van Essen, D. C., Anderson, C. H. & Olshausen, B. A. (1994) in *Large Scale Neuronal Theories of the Brain*, eds. Koch, C. & Davis, J. (MIT Press, Cambridge, MA), pp. 271–300.
21. Moran, J. & Desimone, R. (1985) *Science* **229**, 782–784.
22. Chelazzi, L., Miller, E. K., Duncan, J. & Desimone, R. (1993) *Nature (London)* **363**, 345–347.
23. Iwasaki, S. (1993) *Cognition* **49**, 211–233.
24. Wolfe, J. K. M., Cave, K. R. & Franzel, S. L. (1989) *J. Exp. Psychol. Hum. Perception Performance* **15**, 419–433.
25. Vogt, B. A., Finch, D. M. & Olson, C. R. (1992) *Cereb. Cortex* **2/6**, 435–443.
26. Goldman-Rakic, P. S. (1988) *Annu. Rev. Neurosci.* **11**, 137–156.
27. Baddeley, A. D. (1990) *Working Memory* (Oxford Univ. Press, Oxford).
28. Jonides, J., Smith, E. E., Koeppe, R. A., Awh, E., Minoshima, S. & Mintun, M. A. (1993) *Nature (London)* **363**, 623–635.
29. Paulsen, E., Frith, C. D. & Frackowiak, R. S. (1993) *Nature (London)* **363**, 342–345.
30. Funahashi, S., Chafee, M. V. & Goldman-Rakic, P. (1993) *Nature (London)* **365**, 753–756.
31. Wilson, F. A. W., Scalaidhe, S. P. O. & Goldman-Rakic, P. (1993) *Science* **260**, 1955–1958.
32. Posner, M. I. & Rothbart, M. K. (1992) in *The Neuropsychology of Conscious*, eds. Milner, A. D. & Rugg, M. (Academic, London), pp. 91–112.
33. Dennett, D. (1991) *Consciousness Explained* (Little Brown, Boston).
34. Edelman, G. & Mountcastle, V. (1978) *The Mindful Brain* (MIT Press, Cambridge, MA).
35. Witte, E. A. (1993) Doctoral dissertation (Univ. of Oregon, Eugene).
36. Sperry, R. W. (1988) *Am. Psychol.* **43**, 607–613.
37. Posner, M. I. & Dehaene, S. (1994) *Trends Neurosci.* **17**, 75–79.