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## Attentional networks

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*Recent brain-imaging and neurophysiological data indicate that attention is neither a property of a single brain area, nor of the entire brain. While attentional effects seem mediated by a relative amplification of blood flow and electrical activity in the cortical areas processing the attended computation, the details of how this is done through enhancement of attended or suppression of unattended items, or both, appear to depend on the task and brain-area studied. The origins of these amplification effects are to be found in specialized cortical areas of the frontal and parietal lobes that have been described as the anterior and posterior attention systems. These results represent substantial progress in the effort to determine how brain activity is regulated through attention. While many philosophical and practical issues remain in developing an understanding of attentional regulation, the new tools available should provide the basis for progress.*

The study of selective attention has been an important area of research since the inception of psychology in the late 1800s. However, it has remained controversial whether there are any separate brain mechanisms that subserve attention. Attention does not give rise to a unique qualitative experience like vision or touch, nor does it automatically produce motor responses. While we appear to be able to select sensory stimuli, information in memory or motor responses, this might not indicate a separate attention system, since all brain systems play a role in selection.

There has been evidence of more general mechanisms related to visual selection. One way to select information is to orient to it. Eye movements to foveate a visual stimulus is a clear case, since without foveation there is little ability to examine details of the visual scene. There are also brain mechanisms for visual orienting that do not involve any overt changes in head or eye. In the 1970s, it was found that cells in the parietal lobe increased their firing rate in response to stimulation of their receptive field when monkeys attended to peripheral stimuli even when no eye movements were allowed<sup>1</sup>. It was also shown that humans could covertly shift attention to peripheral stimuli and when they did so they responded more rapidly, at lower threshold and with enhanced electrical activity to stimuli at the attended location. Lesions of the parietal lobe specifically damaged this covert orienting ability on the side of space opposite the lesion. These findings supported the idea that portions of the parietal lobe were involved in covert orienting to visual stimuli<sup>2</sup>.

Since 1987, when we last reviewed this topic<sup>2</sup>, it has become possible to use neuroimaging methods to observe the networks of brain areas that become active when people perform complex tasks<sup>3,4</sup>. Certain brain areas appear active when subjects have to orient, select or transform information in ways that would be said, by most psychological models, to involve attention. These brain areas appear to fit quite well with the idea of selection and control as properties of attention outlined in our previous article. In this

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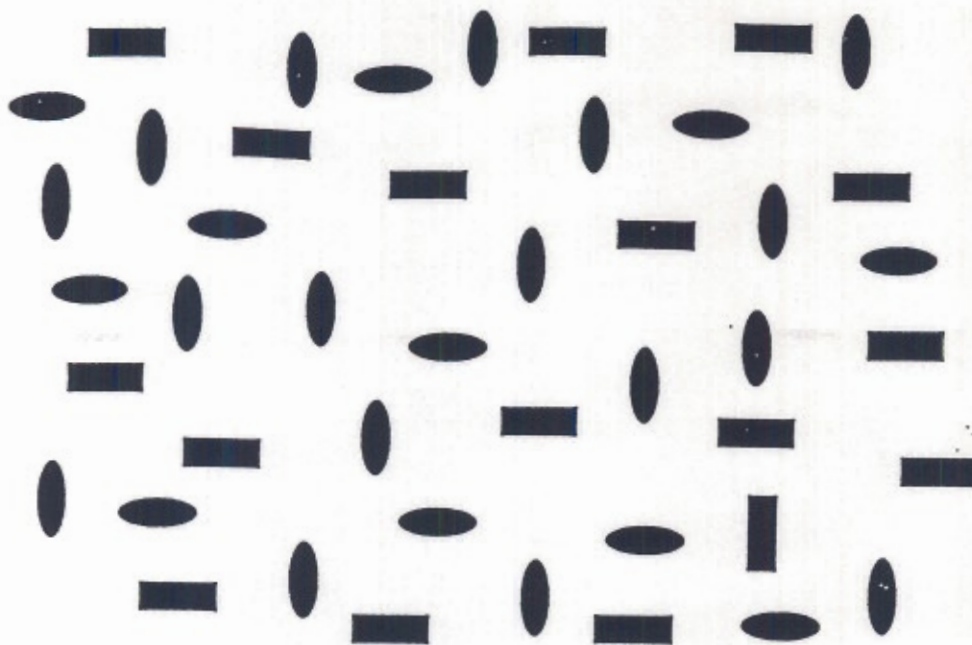


Fig. 1. Visual search for a vertical rectangle among a large number of distractors (horizontal and vertical ellipses and rectangles). The target is defined by a conjunction of form and orientation. In most cases, selective attention is used to sequentially search the display until the target is found<sup>5</sup>.

article, we use the neuroimaging data to outline what is known about networks of brain areas involved in selection during visual search and then extend the discussion to mechanisms of selection and control more generally.

#### Visual search

Throughout this article, we use the example of a simple visual-search task in order to illustrate the role of attention in finding objects<sup>5</sup>. Data indicate that the time for a subject to locate a target (for example, the vertical rectangle in Fig. 1) increases almost linearly with the number of distractors, as though the subject attended to each item in turn. The reaction time when there is no target has twice the slope found for 'yes' responses, indicating that one stops as soon as the target is found<sup>5</sup>.

A simplified view of the problem faced by the brain in this task is presented in Fig. 2. The visual array is processed through a diverging tree of cortical areas<sup>6</sup>. Cortical cells early in the stream have narrow receptive fields and respond mechanically whenever their preferred stimuli are present, whether they correspond to a target or not. As one moves up in the hierarchy, however, receptive fields widen and the cells become more sensitive to attentional and intentional influences, and react less effectively to the passive presentation of a stimulus.

The simple illustration in Fig. 2 makes it clear that selective attention serves at least two distinctive functions. First, the brain must enhance the processing of the selected stimulus relative to other stimuli present, otherwise all stimuli would be processed to a similar degree (Fig. 2, top). Second, processing of the selected stimulus must be actively oriented or guided towards the cortical areas appropriate for a given task. The diverging tree of cortical areas, each of which specializes for a distinct aspect of the stimuli, must be selectively 'pruned' to focus only on those

stimulus characteristics that are relevant to the task. This 'pruning' is depicted on the bottom of Fig. 2 in a static manner, but in complex tasks such as serial search, the appropriate processing stream might change as a function of time (for example, the subject might attend to each stimulus in turn or to all vertical items first and then to all horizontal items).

Recent advances in functional brain imagery, such as positron emission tomography (PET) scan, have provided new evidence concerning the cortical and subcortical networks responsible for these two functions of selective attention. As it turns out, the two functions seem to be carried out by two distinct systems<sup>7</sup>: the posterior attention system (superior parietal cortex, pulvinar and superior colliculus) is largely responsible for selecting one stimulus location among many and for shifting from one stimulus to the next, whereas the anterior attention system (anterior cingulate and basal ganglia) serves a more executive function (attention for action) and is involved in the attentional recruitment and control of brain areas to perform complex cognitive tasks. This network is also involved in selecting visual objects when the instructions emphasize properties of the object. Ultimately, however, the effect of both systems is relative amplification of activity within the cortical areas relevant to a given task.

#### Attentional amplification

In the visual display of Fig. 1, if you are attending to the correct location it is easy to see the target. Otherwise, the target is not seen. How does the brain implement such target detection? It appears that brain activity, in many cortical areas, can be selectively amplified or suppressed as a function of attentional set. When subjects are instructed to pay attention to one particular dimension of the stimuli, the brain areas that specialize in the processing of this stimulus dimension are selectively enhanced. These findings are striking in the prestriate areas of the visual system. In one experiment, subjects viewed passively either stationary or moving objects, presented every second for a minute<sup>8</sup>. When blood flow during the stationary control condition was subtracted from that found in the moving condition, a prestriate area of the midtemporal lobe was found to have a significant increase in blood flow. This might be the human equivalent of area V5 or MT which, in the monkey, contains cells with a strong selectivity for moving stimuli. In a different experiment<sup>9</sup>, subjects always viewed moving objects of varying color and form, but in one set of trials they were instructed to detect differences in velocity, whereas in a control set they had to detect changes in other stimulus parameters. Even though the physical stimuli were the same in the two conditions, the instruction to attend to velocity activated a brain area that was similar to that found in



the comparison of moving and stationary targets. In other words, attention to velocity activates a brain area that is similar in location to what is found when motion is physically added to the stimulus.

The same general correspondence also occurs between brain areas activated by presenting color and form stimuli and those activated when the person is instructed to selectively process color or form information<sup>9</sup>. Increases in blood flow have also been reported in motor areas<sup>10</sup> when subjects are instructed to attend to motor actions. In general, there appears to be a relative increase in blood flow in nearly any area of the brain when subjects are instructed to attend to a sensory or motor computation thought to be related to that brain area. A possible exception is the primary visual cortex, which does not seem to be affected by attentional manipulations<sup>1,9</sup>.

So far we have looked at the effects of attention when people are instructed to attend to sensory dimensions such as color, form or motion. But in the search task above, neither the orientation nor the form of the target is sufficient to find it. Only a combination of the two dimensions at the same location will work<sup>5</sup>. Under these conditions, subjects often search serially by shifting their attention from location to location. If there are no eye movements allowed, these shifts must be mediated covertly, and they should produce a sequence of amplification at each successive location. Indeed, electrical recordings of the scalp have been used to measure such location-specific amplification<sup>11,12</sup>. First, the time for subjects to find a target conjunction was found. At this time, a white square was presented as a probe stimulus, either at this attended target location or at another unrelated location that did not contain a target, and the brain event-related potential generated by this probe was recorded. The results showed that by 80 ms after the probe, the potential elicited over the posterior regions of the scalp was greater when the probe occurred at the target location. The covert shift of attention to the target location had amplified the scalp electrical activity for probes presented at this location. The scalp amplification was strongest over posterior sites contralateral to the hemifield where the probe appeared. In other studies, where attention was deliberately cued to a location, a similar amplification of target ERPs at the cued location was also found<sup>13</sup>. In these cueing studies<sup>13</sup>, current source density analysis has shown that the amplification originates from prestriate areas similar in location to those shown to be activated in the above cited PET studies<sup>9</sup>.

Cellular recordings in awake monkey have shown that the relative amplification of the attended stimulus might actually involve suppression of activity evoked by unattended events. When monkeys were required to attend to a particular location in order to respond to a change in color at that location, cells in area V4 stopped responding to a stimulus at an unattended location that would otherwise be optimal in initiating cell firing<sup>14</sup>. Similar suppression effects have been observed in the inferior temporal cortex during a visual search task: cells that initially fired strongly to a given visual object stopped responding when the monkey attended to a different object at another location, even though the preferred object was still present in the receptive field<sup>15</sup>.

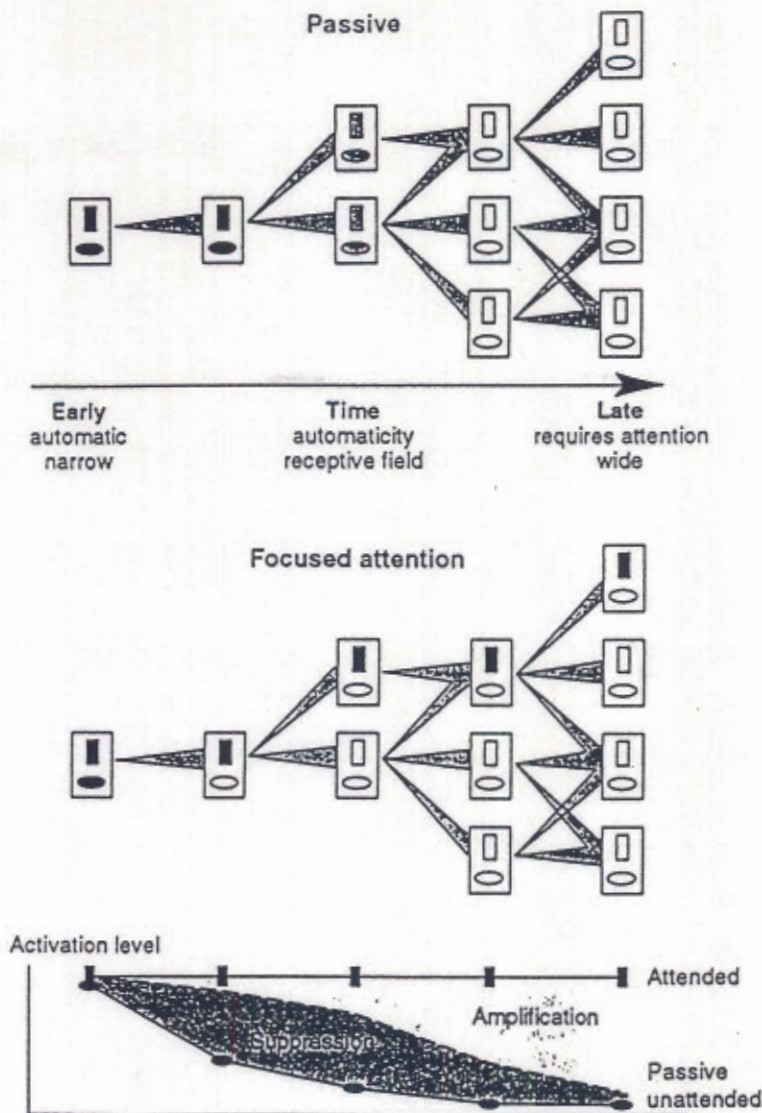


Fig. 2. Schematic diagram of the effects of attention on visual processing. Boxes depict the diverging tree of visual cortical areas, with activation flowing from left to right. Shading is used to represent the strength of activation at each stage. Passive presentation of two visual objects, a rectangle and an ellipse (top), induces a high level of responding in early visual areas, with a progressive decrease further down the processing stream as receptive fields widen and the neurons become less stimulus-driven and more sensitive to attentional influences. When attention is selectively oriented towards the vertical rectangle (middle), there is an early suppression of the irrelevant ellipse. This is followed by an amplification of the activity evoked by the target rectangle in the cortical pathways relevant to the task (for example, those extracting its location, but not those extracting its color). The bottom diagram summarizes the time course of suppression and amplification effects in successive areas as compared to the passive situation.

Based on the model in Fig. 2, we speculate that attentional effects should generally appear as a suppression of unattended information early on in the processing stream, and as an enhancement of relevant information later on. The reason is that neurons in earlier visual areas are already activated to a near optimal level by visual stimuli even in a passive situation (or in the anesthetized animal), and that therefore there is little room for firing enhancement of the target, but more room for firing suppression of the



non-targets. Neurons in the retina, lateral geniculate and area V1 fire strongly to their preferred stimuli whether they are attended or not. Extra-striate areas such as V4 seem to be the first visual areas to show the influence of attention<sup>14</sup>. Because the neurons in early visual areas already respond at a high-firing rate even in a passive condition, attention has the effect of selectively suppressing some or all of this automatic activation. Later on, as the cell responses become less automatic, attention can have the effect of boosting the activation of cells coding for the attended stimulus, as well as suppressing those coding for unattended stimuli. Finally, even further downstream, in cortical areas that activate only during specific tasks and not in a passive situation, attention appears necessary for any activation to occur.

Indeed this predicted sequence of suppression followed by enhancement has been observed recently in studies of event-related potentials during cued attention tasks<sup>12</sup>. The task involved three conditions. In the correctly cued condition, attention was brought to the correct location prior to presentation of the target. In the neutral condition, the cue provided no information on target location. In the miscued condition, attention was brought to a location other than that at which the target was presented. The P1 component of the evoked potential, an early positive electrical event which appears about 80 ms following stimulus presentation, was the same for correctly cued and neutral conditions and both were larger than when the target occurred following a miscue. For this component, activity is suppressed when attention is located at the wrong location. However, for the subsequent N1, a negative component that arises about 150–200 ms after the stimulus, there was increased electrical activity for correctly cued stimuli with respect to the neutral or miscued conditions. In the N1 component of the evoked potential, the relative amplification appears due to boosting the attended location.

According to our interpretation, this suppression-enhancement sequence should be observed most readily with stimuli that are sufficiently intense to passively activate the early visual system and therefore leave little room for an early enhancement by attention. On the contrary, with low-intensity stimuli that cause little passive activation, enhancement should be seen earlier in time and suppression should hardly be perceptible at all.

### Control of orienting

In visual search, attention moves from location to location until the target is detected. How is the internal focus of attention moved? In order to isolate the attentional network responsible for searching locations, a cue can be used to direct attention to that location. Such cueing experiments have shown that stimuli that are presented at the cued location are responded to more rapidly, have a lower perception threshold and generate brain potentials of a larger amplitude<sup>7,16</sup>. When brain-lesioned patients are tested in this form of cued attention, different forms of deficit are found depending on the site of the lesion. For example, patients with lesions of the right parietal lobe are severely impaired when cues are in the good right visual field and targets in the bad left visual field, but not much impaired in other situations, suggesting

a deficit of disengaging attention from a cued location<sup>16</sup>.

Recent PET data<sup>17</sup> from normal subjects show that when attention is shifted from location to location either voluntarily or as a result of being summoned by external events, the major focus of increased blood flow is in the left and right superior parietal lobes. This is the only activation to be specifically related to the attention shift. As mentioned earlier, cellular recordings in the parietal lobe of awake monkeys have also supported the involvement of parietal neurons in visual attention. Parietal areas appear to be implementing aspects of the act of shifting attention rather than being sites at which attention is affecting target detection<sup>1,7</sup>.

The PET data also support the clinical observation that the attentional functions of the two hemispheres are not symmetric. The right superior parietal lobe increases in blood flow for attention shifts in both fields, while the left increases only for right field shifts<sup>17</sup>. This finding might explain the clinical observation that right-hemisphere lesions produce greater attention deficits than do left-hemisphere lesions. In the normal subject however, the left and right parietal areas are integrated into a single mechanism, so that covert attention has a single focus. The corpus callosum appears crucial in unifying the attentional focus. In visual search tasks, normal subjects are not faster when the same number of distractors is distributed across the two visual fields than when all are concentrated in one field. However, patients whose corpus callosum is cut can search at twice the rate when distractors are split evenly between the two visual fields in comparison to when they are concentrated within a single field<sup>18</sup>. This suggests that attentional mechanisms in the left and right hemispheres can become decoupled after callosotomy.

Positron emission tomography studies suggest that the anatomical circuitry which enables the parietal areas to selectively modulate brain activity in other prestriate areas passes through the pulvinar nucleus of the thalamus. When one visual field contains an array with only one large target, while the other contains a target surrounded by distractors, there is evidence of increased metabolism specific to the thalamus of the side opposite the complex array. The act of filtering out the distractors or amplifying the target seems to produce a larger effect in the pulvinar of the opposite side than in other structures<sup>19</sup>.

### Guiding and controlling search

Suppose you are asked to locate the vertical rectangle. 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 non-locational features of the target<sup>20</sup>. 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 which has been called the anterior attention system<sup>7</sup>. 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<sup>9</sup>. 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 might enter and amplify activity within the visual system at the same site (for example, V4).

In guided search, selection by location and selection by color or form occur simultaneously with relatively little interference<sup>20</sup>, unlike the situation for location when the corpus callosum is intact in which attention cannot be shared between the two fields<sup>18</sup>. 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<sup>7,21</sup>. The anterior portion of the cingulate gyrus appears to be involved in a wide range of activities that have been termed collectively 'executive function'<sup>21</sup>. In PET language studies, when subjects were required to name the use of familiar nouns (for example, pound to hammer), activation of the anterior cingulate along with left lateral areas were most prominent<sup>4,22</sup>. 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 pre-striate color areas<sup>23,24</sup>. The detection of multiple color form or motion targets in comparison to passive viewing of the same stimuli also activated the anterior cingulate<sup>9</sup>. All of these situations involve selection of targets from competing inputs, which is considered a traditional role of attention. In the case of this area of the brain, the nature of the target does not seem to matter very much.

The term 'executive' suggests two important overall functions. First, 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<sup>25</sup>. The strongest reason is that the intensity of cingulate activity tends to increase with the number of targets in a set of stimuli<sup>3</sup> and decreases with practice on any single stimulus set<sup>4</sup>. These findings correspond to cognitive theories linking focal attention to number and difficulty of target detection<sup>25</sup>.

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<sup>26</sup>. Working memory is generally thought to involve both a representation of past events and an executive system involved in sustaining and transforming this representation<sup>27</sup>. Recent PET (Refs 28 and 29) and neurophysiological<sup>30,31</sup> studies show that lateral areas of the prefrontal cortex play a key role in holding on-line a representation of past events. 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<sup>24</sup>. Lateral areas of the frontal and posterior cortex are also active in studies when people must obtain a quick association to word stimuli<sup>3,4,22</sup>. While specialized areas of the prefrontal

cortex appear to hold the relevant information on-line, the anterior cingulate is playing a role in the executive functions of awareness and control discussed in cognitive studies and often found impaired in subjects with frontal damage.

### Concluding remarks

Recent brain-imaging and neurophysiological data indicate that attention is neither a property of a single brain area, nor that of the entire brain. While attentional effects seem mediated by a common principle of attentional amplification at all levels of the cortical circuitry, the origins of these amplification effects are to be found in specialized cortical areas of the frontal and parietal lobes. These results represent substantial progress in the effort to determine how brain activity is regulated through attention. While many philosophical and practical issues remain in developing such an understanding, the new tools now available should provide the basis for the efforts still ahead.

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