
Localization of Cognitive Operations in the Human Brain

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The human brain localizes mental operations of the kind posited by cognitive theories. These local computations are integrated in the performance of cognitive tasks such as reading. To support this general hypothesis, new data from neural imaging studies of word reading are related to results of studies on normal subjects and patients with lesions. Further support comes from studies in mental imagery, timing, and memory.

THE QUESTION OF LOCALIZATION OF COGNITION IN THE human brain is an old and difficult one (1). However, current analyses of the operations involved in cognition (2) and new techniques for the imaging of brain function during cognitive tasks (3) have combined to provide support for a new hypothesis. The hypothesis is that elementary operations forming the basis of cognitive analyses of human tasks are strictly localized. Many such local operations are involved in any cognitive task. A set of distributed brain areas must be orchestrated in the performance of even simple cognitive tasks. The task itself is not performed by any single area of the brain, but the operations that underlie the performance are strictly localized. This idea fits generally with many network theories in neuroscience and cognition. However, most neuroscience network theories of higher processes (4) provide little information on the specific computations performed at the nodes of the network, and most cognitive network models provide little or no information on the anatomy involved (5). Our approach relates specific mental operations as developed from cognitive models to neural anatomical areas.

The study of reading and listening has been one of the most active areas in cognitive science for the study of internal codes involved in information processing (6). In this article we review results of studies on cognitive tasks that suggest several separate codes for processing individual words. These codes can be accessed from input or from attention. We also review studies of alert monkeys and brain-lesioned patients that provide evidence on the localization of an attention system for visual spatial information. This system is apparently unnecessary for processing single, foveally centered words. Next, we introduce data from positron emission tomography (PET) concerning the neural systems underlying the coding of individual visual (printed) words. These studies support the findings

in cognition and also give new evidence for an anterior attention system involved in language processing. Finally, we survey other areas of cognition for which recent findings support the localization of component mental operations.

Internal Codes

The most advanced efforts to develop cognitive models of information processing have been in the area of the coding of individual words through reading and listening (6, 7). These efforts have distinguished between a number of internal codes related to the visual, phonological, articulatory, and semantic analysis of a word. Operations at all these levels appear to be involved in understanding a word.

This view began with efforts to develop detailed measurements of the time it takes to execute operations on codes thought to be involved in reading. Figure 1 shows the amount of time needed to determine if two simultaneously shown visual letters or words belong to the same category (8). The reaction time to match pairs of items that are physically identical (for example, AA) is faster than reaction time for matches of the same letters or words in the opposite case (Aa), which are in turn faster than matches that have only a common category (Ae). These studies have been interpreted as involving a mental operation of matching based on different codes. In the case of visual identity the code is thought to be the visual form, whereas in cross-case matching it is thought to be the letter or word name. The idea that a word consists of separable physical, phonological, and semantic codes and that operations may be performed on them separately has been basic to many theories of reading and listening (7). Thus the operation of rotating a letter to the upright position is thought to be performed on the visual code (9), whereas matching to determine if two words rhyme is said to be performed on a phonological representation of the words (10). These theories suggest that mental operations take place on the basis of codes related to separate neural systems.

It is not easy to determine if any operation is elementary or whether it is based on only a single code. Even a simple task such as matching identical items can involve parallel operations on both physical and name codes. Indeed, there has been controversy over the theoretical implications of these matching experiments (11). Some results have suggested that both within- and cross-case matches are performed on physical (visual) codes, whereas others have suggested that they are both performed on name codes (11). A basic question is to determine whether operations performed on different codes involve different brain areas. This question cannot be resolved by performance studies, since they provide only indirect evidence about localization of the operations performed on different codes.

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Table 1. Conditions for PET subtractive studies of words.

| Control state | Stimulus state | Computations |
|---------------|-------------------|---|
| Fixation | Passive words | Passive word processing |
| Repeat words | Generate word use | Semantic association, attention |
| Passive words | Monitor category | Semantic association, attention (many targets)* |

*The extent of attentional activation increases with the number of targets.

It has been widely accepted that there can be multiple routes by which codes interact. For example, a visual word may be sounded out to produce a phonological code and then the phonology is used to develop a meaning (6, 7). Alternately, the visual code may have direct access to a semantic interpretation without any need for developing a phonological code (6, 7). These routes are thought to be somewhat separate because patients with one form of reading difficulty have great trouble in sounding out nonsense material (for example, the nonword “caik”), indicating they may have a poor ability to use phonics; but they have no problems with familiar words even when the words have irregular pronunciation (for example, pint). Other patients have no trouble with reading nonwords but have difficulty with highly familiar irregular words. Although there is also reason to doubt that these routes are entirely separate, it is often thought that the visual to semantic route is dominant in skilled readers (7).

Visual Spatial Attention

Another distinction in cognitive psychology is between automatic activation of these codes and controlled processing by means of attention (6, 7). Evidence indicates that a word may activate its internal visual, phonological, and even semantic codes without the person having to pay attention to the word. The evidence for activation of the internally stored visual code of a word is particularly good. Normal subjects show evidence that the stimulus duration necessary for perceiving individual letters within words is shorter than for perceiving the same letter when it is presented in isolation (12). This idea suggests that feedback from the stored visual word assists in obtaining information about the individual letters (12).

What is known about the localization of attention? Cognitive, brain lesion, and animal studies have identified a posterior neural system involved in visual spatial attention. Patients with lesions of many areas of the brain show neglect of stimuli from the side of space opposite the lesion (13). These findings have led to network views of the neural system underlying visual spatial attention (4). However, studies performed with single-cell recording from alert monkeys have been more specific in showing three brain areas in which individual cells show selective enhancement due to the requirement that the monkey attend to a visual location (14). These areas are the posterior parietal lobe of the cerebral cortex, a portion of the thalamus (part of the pulvinar), and areas of the midbrain related to eye movements—all areas in which clinical studies of lesioned patients find neglect of the environment opposite the lesion.

Recent studies of normal (control) and patient populations have used cues to direct attention covertly to areas of the visual field without eye movements (15). Attention is measured by changes in the efficiency of processing targets at the cued location in comparison with other uncued locations in the visual field. These studies have found systematic deficits in shifting of covert visual attention in

patients with injury of the same three brain areas suggested by the monkey studies. When the efficiency of processing is measured precisely by a reaction time test, the nature of the deficits in the three areas differs. Patients with lesions in the parietal lobe show very long reaction times to targets on the side opposite the lesion only when their attention has first been drawn to a different location in the direction of the lesion (15). This increase in reaction time for uncued but not cued contralesional targets is consistent with a specific deficit in the patient’s ability to disengage attention from a cued location when the target is in the contralesional direction. In contrast, damage to the midbrain not only greatly lengthens overall reaction time but increases the time needed to establish an advantage in reaction time at the cued location in comparison to the uncued location (16). This finding is consistent with the idea that the lesion causes a slowing of attention movements. Damage to the thalamus (17) produces a pattern of slowed reaction to both cued and uncued targets on the side opposite the lesion. This pattern suggests difficulty in being able to use attention to speed processing of targets irrespective of the time allowed to do so (engage deficit). A similar deficit has been found in monkeys performing this task when chemical injections disrupt the performance of the lateral pulvinar (18). Thus the simple act of shifting attention to the cued location appears to involve a number of distinct computations (Fig. 2) that must be orchestrated to allow the cognitive performance to occur. We now have an idea of the anatomy of several of these computations.

Damage to the visual spatial attention system also produces deficits in recognition of visual stimuli. Patients with lesions of the right parietal lobe frequently neglect (fail to report) the first few letters of a nonword. However, when shown an actual word that occupied the same visual angle, they report it correctly (19). Cognitive studies have often shown a superiority of words over nonwords (12). Our results fit with the idea that words do not require scanning by a covert visual spatial attention system.

Attention for Action

In cognitive studies it is often suggested that attention to stimuli occurs only after they have been processed to a very high degree (20, 21). In this view, attention is designed mainly to limit the conflicting actions taken toward stimuli. This form of attention is often called “attention for action.” Our studies of patients with parietal lesions suggest that the posterior visual-spatial attention system is connected to a more general attention system that is also involved in the processing of language stimuli (22). When normal subjects and patients had to pay close attention to auditory, or spoken, words, the ability of a visual cue to draw their visual spatial attention was retarded. Cognitive studies have been unclear on whether access to meaning requires attention. Although semantic information may be activated without attention being drawn to the specific lexical unit (23), attention strongly interacts with semantic activation (24, 25). Considerable evidence shows that attention to semantic information limits the range of concepts activated. When a person attends to one meaning of a word, activation of alternative meanings of the same item tends to be suppressed (25).

PET Imaging of Words

How do the operations suggested by cognitive theories of lexical access relate to brain systems? Recently, in a study with normal persons, we used PET to observe brain processes that are active during single word reading (26). This method allows examination of

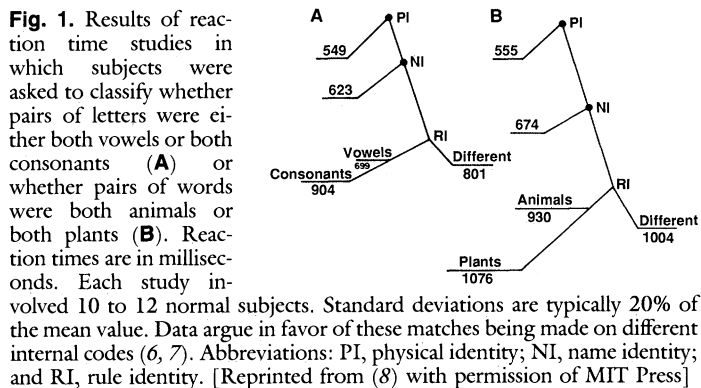
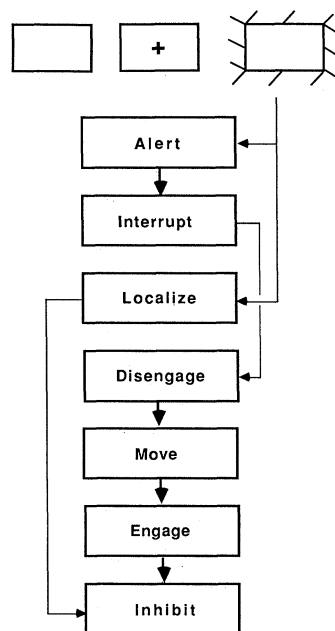


Fig. 2. Top of figure illustrates an experimental situation in which attention is summoned from fixation (center) to right-hand box by a brightening of the box. This is followed by a target at the cued location or on the opposite side. The boxes below indicate mental operations thought to begin by presentation of the cue. The last four operations involve the posterior visual spatial attention system; specific deficits have been found in patients with lesions in the parietal (disengage), midbrain (move), and thalamic (engage) areas (15-17). [Reprinted from (22) with permission of the Psychonomics Society]



averaged changes in cerebral blood flow in localized brain areas during 40 seconds of cognitive activity (27). During this period we presented words at a rate of one per second. Previous PET studies have suggested that a difference of a few millimeters in the location of activations will be sufficient to separate them (28).

To isolate component mental operations we used a set of conditions shown in Table 1. By subtracting the control state from the stimulus state, we attempted to isolate areas of activation related to those mental operations present in the stimulus state but not in the control state. For example, subtraction of looking at the fixation point, without any stimuli, from the presentation of passive visual words allowed us to examine the brain areas automatically activated by the word stimuli (29).

Visual word forms. We examined changes in cerebral blood flow during passive looking at foveally presented nouns. This task produced five areas of significantly greater activation than found in the fixation condition. They all lie within the occipital lobe: two along the calcarine fissure in left and right primary visual cortex and three in left and right lateral regions (Fig. 3). As one moves to more complex naming and semantic activation tasks, no new posterior areas are active. Thus the entire visually specific coding takes place within the occipital lobe. Activated areas are found as far anterior as the occipital temporal boundary. Are these activations specific to visual words? The presentation of auditory words does not produce

any activation in this area. Visual stimuli known to activate striate cortex (for example, checkerboards or dot patterns) do not activate the prestriate areas used in word reading (28, 30). All other cortical areas active during word reading are anterior. Thus it seems reasonable to conclude that visual word forms are developed in the occipital lobe.

It might seem that occipital areas are too early in the system to support the development of visual word forms. However, the early development of the visual word form is supported by our evidence that patients with right parietal lesions do not neglect the left side of foveally centered words even though they do neglect the initial letters of nonword strings (19). The presence of pure alexia from lesions of the occipital temporal boundary (31) also supports the development of the visual word form in the occipital area.

Precise computational models of how visual word forms are developed (5, 12) involve parallel computations from feature, letter, and word levels and precise feedback among these levels. The prestriate visual system would provide an attractive anatomy for models relying on such abundant feedback. However, presently we can only tentatively identify the general occipital areas that underlie the visual processing of words.

Semantic operations. We used two tasks to study semantic operations. One task required the subject to generate and say aloud a use for each of 40 concrete nouns (for example, a subject may say "pound" when presented with the noun "hammer"). We subtracted the activations from repeating the nouns to eliminate strictly sensory and motor activations. Only two general areas of the cortex were found to be active (Fig. 3, square symbols). A second semantic task required subjects to note the presence of dangerous animals in a list of 40 visually presented words. We subtracted passive presentation of the word list to eliminate sensory processing. No motor output was required and subjects were asked to estimate only the frequency of targets after the list was presented. The same two areas of cortex were activated (Fig. 3, circles).

One of the areas activated in both semantic tasks was in the anterior left frontal lobe. Figure 4 shows an illustration of this area from averaged scans in auditory and visual generate (minus repeat) and in visual monitoring (minus passive words). This area is strictly left lateralized and appears to be specific to semantic language tasks. Moreover, lesions of this area produce deficits in word fluency tests (32). Thus we have concluded that this general area is related to the semantic network supporting the type of word associations involved in the generate and monitoring tasks.

Phonological coding. When words are presented in auditory form, the primary auditory cortex and an area of the left temporoparietal cortex that has been related to language tasks are activated (33). This temporoparietal left-lateralized area seemed to be a good candidate for phonological processing. It was surprising from some perspectives that no visual word reading task activated this area. However, all of our visual tasks involved single common nouns read by highly skilled readers. According to cognitive theories of reading (7), these tasks should involve the visual to semantic route. One way of requiring a phonological activation would be to force subjects to tell whether two simultaneous words (for example, pint-lint or row-thought) rhymed. This method has been used in cognitive studies to activate phonological codes (10). Recent data from our laboratory (34) show that this task does produce activation near the supramarginal gyrus. We also assume that word reading that involves difficult words or requires storage in short-term memory or is performed by unskilled readers would also activate phonological operations.

Anterior attention. There is no evidence of activation of any parts of the posterior visual spatial attention system (for example, parietal lobe) in any of our PET language studies. However, it is possible to show that simple tasks that require close monitoring of visual input

or that use visual imagery (35) do activate this parietal system. We conclude, in agreement with the results of our lesion work (19), that visual word reading is automatic in that it does not require activation of the visual spatial attention system.

In recent cognitive theories the term attention for action is used to summarize the idea that attention seems to be involved in selecting those operations that will gain control of output systems (20). This kind of attention system does not appear to be related to any particular sensory or cognitive content and is distinct from the more strictly visual functions assigned to the visual spatial attention system. Although attention for action seems to imply motor acts, internal selections involved in detecting or noting an event may be sufficient to involve attention in this sense (21). Whenever subjects are active in this way, we see an increase in blood flow in areas of the medial frontal lobe (Fig. 3B, square symbols). When motor output is involved (for example, naming words), these areas tend to be more superior and posterior (supplementary motor area); but when motor activity is subtracted away or when none is required, they appear to be more anterior and inferior (anterior cingulate gyrus). The anterior cingulate has long been thought to be related to attention (4) in the sense of generating actions, since lesions of this area produce akinetic mutism (36).

We tested the identification of the anterior cingulate with attention and the left lateral frontal area with a word association network. This was done by applying a cognitive theory that attention would not be much involved in the semantic decision of whether a word belonged to a category (for example, dangerous animal) but would be involved in noting the targets even though no specific action was required. The special involvement of attention with target detection has been widely argued by cognitive studies (21). These studies have suggested that monitoring produces relatively little evidence of heavy attentional involvement, but when a target is actually detected there is evidence of strong interference so that the likelihood of detecting a simultaneous target is reduced. Thus we varied the number of dangerous animals in our list from one (few targets) to 25 (many targets). We found that blood flow in the anterior cingulate showed much greater change with many targets than with few targets. The left frontal area showed little change in blood flow between these conditions. Additional work with other low-target vigilance tasks not involving semantics also failed to activate the anterior cingulate area (37). Thus the identification of the anterior cingulate with some part of an anterior attention system that selects for action receives some support from these results.

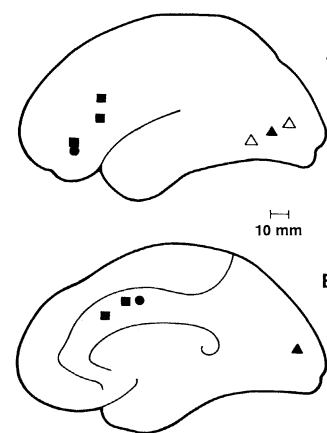
Conclusions

The PET data provide strong support for localization of operations performed on visual, phonological, and semantic codes. The ability to localize these operations in studies of average blood flow suggests considerable homogeneity in the neural systems involved, at least among the right-handed subjects with good reading skills who were used in our study.

The PET data on lexical access complement the lesion data cited here in showing that mental operations of the type that form the basis of cognitive analysis are localized in the human brain. This form of localization of function differs from the idea that cognitive tasks are performed by a particular brain area. Visual imagery, word reading, and even shifting visual attention from one location to another are not performed by any single brain area. Each of them involves a large number of component computations that must be orchestrated to perform the cognitive task.

Our data suggest that operations involved both in activation of internal codes and in selective attention obey the general rule of

Fig. 3. Areas activated in visual word reading on the lateral aspect of the cortex (A) and on the medial aspect (B). Triangles refer to the passive visual task minus fixation (\blacktriangle , left hemisphere; \triangle , right hemisphere). Only occipital areas are active. Squares refer to generate minus repeat task. Circles refer to monitor minus passive words task. Solid circles and squares in (A) denote left hemisphere activation; however, in (B), on the midline it is not possible to determine if activation is left or right. The lateral area is thought to involve a semantic network while the midline areas appear to involve attention (26).



localization of component operations. However, selective attention appears to use neural systems separate from those involved in passively collecting information about a stimulus. In the posterior part of the brain, the ventral occipital lobe appears to develop the visual word form. If active selection or visual search is required, this is done by a spatial system that is deficient in patients with lesions of the parietal lobe (38). Similarly, in the anterior brain the lateral left frontal lobe is involved in the semantic network for coding word associations. Local areas within the anterior cingulate become increasingly involved when the output of the computations within the semantic network is to be selected as a relevant target. Thus the anterior cingulate is involved in the computations in selecting language or other forms of information for action. This separation of anterior and posterior attention systems helps clarify how attention can be involved both in early visual processing and in the selection of information for output.

Several other research areas also support our general hypothesis. In the study of visual imagery, models distinguish between a set of operations involved in the generation of an image and those involved in scanning the image once it is generated (39). Mechanisms involved in image scanning share components with those in visual spatial attention. Patients with lesions of the right parietal lobe have deficits both in scanning the left side of an image (40) and in responding to visual input to their left (40). Although the right hemisphere plays an important role in visual scanning, it apparently is deficient in operations needed to generate an image. Studies of patients whose cerebral hemispheres have been split during surgery show that the isolated left hemisphere can generate complex visual images whereas the isolated right hemisphere cannot (41).

Patients with lesions of the lateral cerebellum have a deficit in timing motor output and in their threshold for recognition of small temporal differences in sensory input (42). These results indicate that this area of the cerebellum performs a critical computation for timing both motor and sensory tasks. Similarly, studies of memory have indicated that the hippocampus performs a computation needed for storage in a manner that will allow conscious retrieval of the item once it has left current attention. The same item can be used as part of a skill even though damage to the hippocampus makes it unavailable to conscious recollection (43).

The joint anatomical and cognitive approach discussed in this article should open the way to a more detailed understanding of the deficits found in the many disorders involving cognitive or attentional operations in which the anatomy is poorly understood. For example, we have attempted to apply the new knowledge of the anatomy of selective attention to study deficits in patients with schizophrenia (44).

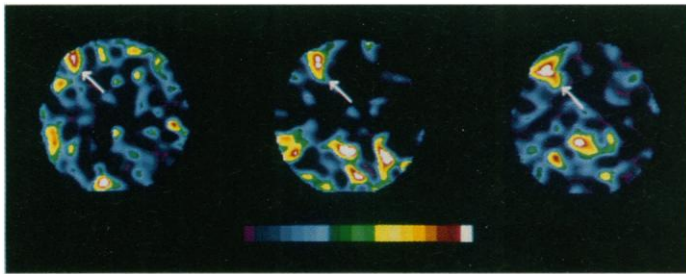


Fig. 4. Sample data from the PET activation studies. The arrows indicate areas of activation in the left inferior prefrontal cortex found active in all three semantic processing conditions. **(Left)** Monitoring visual words for dangerous animals (minus passive visual words). **(Middle)** Generating uses (minus repeat) for visual stimuli. **(Right)** Generating uses (minus repeat) for auditory stimuli. In each condition an area of cortical activation was found in the anterior cingulate gyrus on a higher slice (Fig. 3). The color scale indicates the relative strength of activation (purple indicates the minimum and white, the maximum, for that condition) (26).

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