

Brain Mechanisms of Cognitive Skills

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This article examines the anatomy and circuitry of skills that, like reading, calculating, recognizing, or remembering, are common abilities of humans. While the anatomical areas active are unique to each skill there are features common to all tasks. For example, all skills produce activation of a small number of widely separated neural areas that appear necessary to perform the task. These neural areas relate to internal codes that may not be observed by any external behavior nor be reportable by the performer. There is considerable plasticity to the performance of skills. Task components can be given priority through attention, which serves to increase activation of the relevant brain areas. Attention can also cause reactivation of sensory areas driven by input, but usually only after a delay. The threshold for activation for any area may be temporarily reduced by prior activation (priming or practice). Skill components requiring attention tend to cause interference resulting in the dual tasks effects and unified focus of attention described in many cognitive studies. Practice may change the size or number of brain areas involved and alter the pathways used by the skill. By combining cognitive and anatomical analyses, a more general picture of the nature of skill emerges. © 1997 Academic Press

COGNITIVE EXPERTISE

But actions originally prompted by conscious intelligence may grow so automatic by dint of habit as to be apparently unconsciously performed. . . . Shall the study of such machine-like yet purposive acts as these be included in Psychology? (James, 1890, pp. 6–7)

As William James' (1890) quote illustrates, the idea that practice can automate a skill has been with us since the inception of psychology. There is little question that high levels of skill require automaticity of at least some components of the task (Posner & Snyder, 1975). In this paper, we seek an understanding of the neural basis of skilled performance.

A central topic of cognition in recent years has been the study of expertise (Chi, Glaser, & Farr, 1988; Ericsson & Smith, 1991). A basic tenet of this study has been the idea that experts differ from novices in domain-specific information stored in memory. The relatively automatic access to this rich, semantic domain-specific memory provides the basis for the rapid responses, informed choice, and cognitive efficiency displayed in expert skill. A major method for studying expert performance has been the use of verbal protocols provided by the expert (Ericsson & Smith, 1991).

It is clear that expertise also involves internal operations that are hidden from the observer and even from the expert. For example, in comprehending sentences, multiple meanings of ambiguous words may become active, but be suppressed by context

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(Gernsbacher, 1993). Indeed the skill of the expert reader may depend heavily upon the ability to suppress meanings inappropriate in the present context (Gernsbacher & Faust, 1991). More generally, work on reading (Posner et al., in press) and implicit memory (Schacter, 1994) both suggest component mental operations that could not be reported by the expert.

In this paper we will examine the ability to use new methods of imaging brain activity to supplement verbal protocols as a way of understanding the acquisition and execution of high-level cognitive skills. While most of the cognitive literature on expertise involves the performance of individuals with unusual skills (e.g., chess masters), it has always been understood that in some areas (e.g., reading or object recognition) expertise is widely shared among literate adults. Because most imaging studies have not used experts with a unique skill, we confine our discussion to domains such as reading, arithmetic, object recognition, and memory in which high-level performance is widespread among educated adults. The analysis of these skills also allows us to examine skilled acquisition by adults learning new material and by children acquiring these skills during their early education.

Our goal is not so much to present new data as to organize the extant imaging and cognitive literature in terms of its relation to the acquisition and execution of skills. We seek both common principles among skills and differences between skills that might help to elucidate the acquisition of expertise.

The paper will be divided in four sections. First, we will briefly review methods that are employed to image the anatomy and circuitry of the human brain. Next we examine several common skills, including reading, listening, calculating, recognizing, and remembering. While most of these results have been published, we will concentrate primarily on findings that suggest commonalties or differences between skill domains. Our third section involves efforts to determine how brain activity changes with attention, priming, and practice. In neuroscience changes in the brain as a result of experience are often called plasticity, but recent studies of human skill suggest that the degree and types of plasticity are much more diverse than has usually been considered within the brain sciences. In the final section, we are concerned with changes during skill acquisition in both adults and children.

NEUROIMAGING METHODS

By neuroimaging we refer to a wide variety of methods designed to sense activity within large populations of neurons (Toga & Mazziotta, 1996). To understand the functional anatomy of mental processes, we discuss neuroimaging methods, such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), that involve the study of changes in blood circulation. To study the circuitry involved in task performance we examine the time course of this anatomy by use of high-density electrical recording (Posner & Raichle, 1994; Toga & Mazziotta, 1996).

Imaging Cognitive Anatomy

When neurons are active they change their own local blood supply. This change can be sensed from outside the organism either by injection of a small amount of radionuclide as in PET or by sensing the magnetic signal provided by changes

in hemoglobin content as is done in fMRI. Both of these methods have now been widely used to image discrete areas of increased neural activity during cognitive tasks (Posner & Raichle, 1994; Toga & Mazziotta, 1996; Zeki, 1993). In most cases, two experimental conditions that are thought to differ in a small number of cognitive operations are compared. These studies have almost universally found networks of cortical and subcortical areas that are altered between the two conditions and the goal then is to relate this neural anatomy to the computations required by the task.

We contrast approaches based on changing sensory input to the subject, viewing the person mainly as a passive receiver of information (bottom-up), to those that stress the design of an active task that the person performs (top-down). Of course neither method is completely pure, but the contrast does stress the difference between neural areas driven passively by input and those requiring the use of attention.

Bottom-up activation. When neuroscientists think about the operations performed by a particular brain area they usually think of it as being driven passively by input information. Thus to drive a particular brain area, they impose a stimulus that requires the operations hypothesized to involve that area. A good example of this method is in the study of the perception of motion. When subjects were asked to view a display of moving dots during an imaging session they saw motion even when no task was imposed. This condition could then be compared with viewing the same set of visual forms when they were stationary (Zeki et al., 1991). The resulting subtraction proved effective in demonstrating increased blood flow in a restricted area of the temporal lobes, which could reasonably be related to motion-sensitive areas in monkeys.

This subtractive approach can be applied quite effectively even to some higher-level processes. When subjects were shown real words, regular nonwords, consonant strings, or false font stimuli it was found that areas of the right posterior cortex were active for all strings in comparison with looking at a fixation point (Petersen, Fox, Snyder, & Raichle, 1990; Posner, et al., in press). However, left ventral occipital activation was produced only by real words or regular nonwords, not by consonant strings or false fonts. This constellation of results was viewed as support for a right hemisphere role in visual feature analysis and a left hemisphere role for the visual word form. Some authors prefer not to use a passive subtraction on the grounds that the subjects may be doing quite different things and thus less control is obtained in this condition than in other conditions. In order to avoid a passive condition, it is often possible to use two active tasks, for example, attending to the left visual field minus attending to the right visual field as a means of determining the networks related to attention to a visual stimulus (Heinze et al, 1994). Below we discuss the use of the additive factors methods, which is also a means to avoid the passive control.

Top-down activation. The essence of the bottom-up methods is to provide a change in stimulation that will reveal a difference between two conditions. The top-down approach uses exactly the same stimuli in the two conditions, but instructions to the subject differ. In this sense, it is the method most frequently used in studies of cognitive psychology. However, when using anatomical methods such as PET or fMRI, it is often necessary to block trials using a common computation in order to average tens of seconds of activity to acquire sufficient information to image the brain.

Consider the areas of the brain described above that carry out computations on motion. To study these areas, Corbetta, Miezin, Dobmeyer, Shulman, and Petersen (1991) contrasted two conditions. In both conditions the stimuli were arrays of visual objects that could differ in color, form, or velocity. The control condition required subjects to report any change between the stimulus arrays regardless of whether the disparity was in color, form, or motion. The experimental condition required the subjects to report only changes in motion and to ignore other changes. In both cases, the subjects had to be alert to the stimuli and had to make similar reports. But in the experimental condition, their attention could be directed to moving events. There was clear evidence of increased activation of the same general brain areas that have been reported to be involved in detecting moving stimuli by the bottom-up method.

In addition to being an important study of the extrastriate visual activation, this experiment illustrates the general principles of top-down studies. It is known that attention to a stimulus dimension increases the speed and accuracy of responding to that dimension. When subjects are asked to attend to a computation known to be performed by a particular brain area, one might expect them to alter the activation within that area. This is exactly what was found in the Corbetta et al. (1991) study. During the attended motion condition, the temporal motion area showed increased activity, while the areas computing color and form were about the same in experimental and control conditions. Indeed, studies using a variety of imaging methods have confirmed that attention to a computation increases blood flow in the local area that performs that computation.

Imaging Circuits

One nearly universal finding from imaging studies is that any given task activates a network of areas, including both frontal and posterior cortical areas and subcortical areas. In many cases, it has proven possible to suggest the specific operation associated with a particular activation and to test these hypotheses experimentally (Kosslyn, 1994; Posner & Raichle, 1994).

But how do these networks of brain areas become active in real time? To study this issue, methods have been used to record electrical activity from the scalp time locked to stimulus events (ERP), a technique long familiar from chronometric studies in psychology (Rugg & Coles, 1995). Efforts to determine the location of information measured from electrodes on the scalp have changed because of the use of PET and fMRI data. Since there are now hypotheses about where the generators are in a given task, that information can be used to constrain the difficult task of inferring a neural generator from electrical activity that has been distorted by tissue between it and the electrode. In order to adapt the ERP method to fit the PET data it has been useful to use a large number of scalp electrodes and to localize the generators most likely to produce the distribution of scalp electrical activity at any given moment (Abdullaev & Posner, 1997; Dehaene, 1996; Snyder, Abdullaev, Posner, & Raichle, 1995). Algorithms can then be used that seek to obtain a best fitting dipole solution to the activity recorded at the scalp (Scherg, 1989).

There have been a number of highly successful efforts to compare PET and ERP methods using similar tasks. Some of the most interesting studies involve mapping of the visual system (Clark & Hillyard, 1996; ffytche, Guy, & Zeki, 1995). For exam-

ple, the known relation between the position on the retina and the location of neuronal activity was first used to validate PET blood flow studies (Fox et al., 1986) and has now been used to show that the dipoles derived from scalp electrodes also fit this model (Clark & Hillyard, 1996). Similarly, ERP signals to moving stimuli from scalp electrodes have localized to brain areas similar to those previously found active with PET (ffytche, Guy, & Zeki, 1995). One study of brain activation in visual attention, utilizing the PET and ERP methods, used both the same subjects and the same task (Heinze et al., 1994). Subjects were asked to report targets in one visual field during a series of visual stimuli in both fields. Attending to stimuli in one visual field formed the experimental condition, while stimuli in that same field when attending to the opposite field served as the control. Both PET and ERP data suggested generators in the fusiform gyrus of the hemisphere opposite the attended visual field. However, the generators localized by the two methodologies were about 1 cm apart. Some of this difference may arise because the two methods measure different aspects of the neural activity, or it may also suggest an inherent error in the two methods. Though we will not be able to expect exact correspondence between measures, the two should localize to the same general brain area.

In our work, we have tried to approach somewhat higher-level tasks critical to human skill. To use this approach, we have generally employed the same subtractive method used with PET and, for the most part, the same task structure. For example, in our studies of word association we have been able to find good evidence of neural generators that fit the PET anatomy from the same task subtraction well (Abdullaev & Posner, 1997; McCandliss, Posner, & Givón, in press; Posner & Raichle, 1994; Snyder, Abdullaev, Posner, & Raichle, 1995). In studies of number processing, additive factor methodology has been used as a complement to the subtractive strategy (Dehaene, 1996; Dehaene, Posner, & Tucker, 1994). In the next section we turn to a survey of the results obtained in studying the circuitry of these skills.

IMAGING SKILLS

In this section we review the efforts to apply these anatomical and circuit tracing methods to the execution of common forms of human skill such as reading, number processing, object recognition, and memory.

Reading Words

One task that has been analyzed in great detail involves reading individual words. In a typical task subjects are shown a series of 40 simple nouns (e.g., hammer). In the experimental condition they indicate the use of each noun (for example, hammer → pound). In the control condition, they read the word aloud. The difference in activation between the two tasks illustrates what happens in the brain when subjects are required to develop a very simple thought, in this case how to use a hammer.

The brain activity obtained during the read-aloud condition is subtracted from the activity found in the generate condition. The results illustrate the surprising fact that the anatomy of this high-level cognitive activity is similar enough among individuals to produce focal average activations that are both statistically significant and reproducible.

There are four focal but well-separated areas that undergo increases in brain activity during the simple thought needed to find the use of the word. The first is activity in the midline of the frontal lobe in the anterior cingulate gyrus. This brain area is involved in higher-level aspects of attention regardless of whether the task involves language, spatial location, or object processing. We believe it relates to what has often been called executive attention in high-level skills (Posner & DiGirolamo, *in press*). Two additional activations are in the left lateral frontal and posterior cortex. Finally, there is activation in the right cerebellum, which is closely connected to the left frontal areas.

We have been able to find the scalp signatures of three of these activations in our high-density electrical recording studies (Abdullaev & Posner, 1997; Snyder, Abdullaev, Posner, & Raichle, 1995). When subjects obtain the use of a noun there is an area of positive electrical activity over frontal electrodes starting about 150 ms after the word appears. This early electrical activity is most likely to be generated by the large area of activation in the anterior cingulate shown by the PET studies.

Two other areas that are active during generating word meanings occur in the left frontal and left posterior cortex. The left frontal area (anterior to and overlapping classical Broca's area) begins to show activity about 220 ms after the word occurs. During this interval, both the cingulate and the left frontal semantic area are active. We assume that the left frontal activation is related to the meaning of the individual word that has been presented on that trial. The time course of the left frontal area during processing the meaning of words is further supported by results obtained from cellular recording in patients with depth electrodes implanted for neurosurgery (Abdullaev & Bechtereva, 1993). This area is active early enough to influence motor and eye movement responses, typically occurring by 300–400 ms, that can be influenced by the meaning of a word.

On the other hand, the left posterior brain area found to be more active during the processing of the meaning of visual words does not show up in the electrical maps until about 600 ms after input. This activity is near classical Wernicke's and lesions of this area are known to produce a loss of understanding of meaningful speech. We think this area is important in the storage and integration of words into larger meaningful units. Thus, damage to this area makes it difficult to understand speech or written material.

These results demonstrate how one can approach both the anatomy and the circuitry of higher mental processes. By observing the brain areas activated in PET studies and relating them to scalp electrical activity, we have a picture of the temporal dynamics in creating a simple thought.

Recent fMRI studies have confirmed the presence of the semantic areas shown by PET and have provided more information on individual differences. For example, an fMRI study (Spitzer et al., 1995) has shown that within the anterior and posterior semantic areas different portions are active when processing different semantic categories. In Spitzer's data the exact organization of the individual categories within the general anterior and posterior semantic brain areas appears to differ from one subject to another. Nevertheless, the presence of category-specific semantic areas indicates that the brain uses the same general mapping strategy to handle semantic relations as it does to handle sensory processing.

One benefit of a mapped lexicon is a speeded response to a target word if the word is preceded by a word related in meaning, known as priming (Meyer & Schvaneveldt, 1971). The advantages of coactivation of the meanings of related words are apparent: the semantic activation of related words allows faster and more accurate comprehension in reading and listening and production in speaking (Rayner & Pollatsek, 1989). Interestingly, the integration of the meaning of text across sentences seems to be related to more general mechanisms of cognition (working memory) and not specialized cognitive components of word processing (Just & Carpenter, 1992). This point will be discussed further in the section on working memory.

By bringing together methods for examining the anatomy and circuitry of brain activity it is now possible to see much of what is involved when carrying out a high-level skill. The task of reading has been studied for many years by the careful recording of eye movements in skilled readers (Rayner & Pollatsek, 1989). An important test of the brain circuitry described above is whether it is possible to account for the rapid temporal sequence of eye movements actually found during skilled reading. Eye movement studies (see Rayner, Sereno, & Raney, 1996) indicate that a skilled reader remains fixed on a given word for less than 300 ms. During this time, sufficient information must be extracted from the word to guide the next eye movement, which has been shown to depend upon the meaning of the currently fixated item.

The skill of reading a word involves separate computations sustained by distinct neural areas (see Démonet, Wise, & Frackowiak, 1993 for a review). The component computations of word reading (and its underlying neural substrates) are usually thought to consist of a visual integration of the word (Petersen, Fox, Posner, & Mintun, 1988; Posner, Peterson, Fox, & Raichle, 1988); access to the word's phonological code (Rapp & Caramazza, 1995); access to the semantic meaning of the word and its associates (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Spitzer et al., 1995); access to the structural form of the object that the word represents, if applicable (Park, Blaxton, Gabrieli, Figlozzi, & Theodore, 1994); and access to the learned output of the word (Raichle et al., 1994). Our data provide a preliminary picture of the time course of this skill as it is likely to occur during actual reading. Operations specific to reading begin by about 100 ms in the right posterior cortex with the abstraction of specific visual features that will allow identification of letters. Starting at about 150 ms areas of the left posterior visual systems are synthesizing letters into the visual word form. At about the same time executive attention becomes involved through activation of the anterior cingulate and related midline areas (e.g., supplementary motor area). Left frontal activity related to the meaning of an individual word begins by about 200 ms. All of these brain areas are active early enough to provide information to the frontal eye fields related to the start of the saccade. Our data suggest that the activation of phonological areas related to word sounds and semantic areas related to the integration of word meanings occur somewhat later in time.

Number Processing

Recently efforts have been made to apply the additive factor logic to imaging electrical scalp recordings (Dehaene, 1996). The task was one of determining if a single probe digit was greater or less than 5. The probe could be either spelled out

or in Arabic form and could be either close to 5 (e.g., 4 or 6) or far from 5 (2 or 8), and responses could be made with either the left or the right hand. Each of these manipulations made an independent (additive) contribution to the overall reaction time.

The event-related potential data suggested that each of the stages produced activation in a different brain area that corresponded closely with what would be expected based on functional anatomy. The posterior brain areas related to the encoding stage were modulated 150 ms after input by stimulus type. The spelled digits shows a strong posterior left hemisphere positivity that would fit with a generator in the visual word form area of the posterior left hemisphere. This effect contrasted sharply with the bilateral posterior positivity found for the use of Arabic numerals. The distance effect found after about 200 ms was strongest over the right parietal area. This area had been related by lesion studies to the storage of numerical quantity. Finally the use of left and right hands in response produced very clear modulations in electrodes above the motor cortex. These findings illustrate the use of additive factors as a way to examine high-level activation that might have a serial character as in the relating of an input digit to a single stored quantity.

The results obtained in this study suggest that the general finding in the study of reading also applies to this simple numerical calculation: Performance of a task activates a small number of widely separated regions corresponding to the codes involved in the task. The additive factor method has been widely used to study many simple tasks that have a structure in which the operations occur one after the other. It appears that what are identified as cognitive stages in an additive factor design may correspond to widely separated anatomical operations related to different codes. It is important to note that a numerical task can recruit a brain area related to word reading when the input items are spelled digits. This appears to be a general property of skilled performance. For example, similar semantic areas appear to be activated in reading, listening, and naming pictures. Likewise, verbal working memory areas appear to be involved when the task is storing written words, verbally encoding a location, or otherwise involves strategies incorporating verbal description.

As we have attempted to outline, separate anatomical areas provide distinct computations during skilled performance. An implication of this statement is that whenever skilled performance requires a particular cognitive task component, the neural area that calculates that computation should be active. Using a 2-back search task, Smith, Jonides, and their colleagues (Schumacher et al., 1996) have demonstrated exactly this effect. Activations of areas that calculate the verbal working memory computation (Broca's area and posterior parietal areas) are independent of the incoming modality (visual or auditory) of the material. These results strongly suggest that component operations in skilled learning rely on the same neural areas whenever those component computations are called upon.

Object Processing

Another task at which humans are exceptionally good is object recognition. Subjects are able to recognize hundreds to thousands of pictures following a single presentation (e.g., Standing, Conezio, & Haber, 1970). Biederman (1987) has suggested

that human memory is capable of storing and retrieving tens of thousands of representations. Moreover, the visual system seems to have developed specialized systems, or modules, for recognizing faces (Kanwisher, McDermott, & Chun, submitted for publication; Sergent, Ohta, & MacDonald, 1992). These specialized cognitive processes follow a developmental course in the acquisition of expertise (Carey, 1981; Ellis, 1992).

Recognition in rapid serial visual presentation suggests that subjects can accurately recognize objects even with presentation rates under 200 ms (Intraub, 1981). In continuing with our strategy of mapping the circuits of cognitive processes, we used a task in the ERP (DiGirolamo & Kanwisher, 1995) that was previously used in PET (see, Kanwisher, Woods, Iacoboni, & Mazziotta, 1997). The first differences in the electrical signal on the scalp between objects and object-like stimuli are seen in under 155 ms (DiGirolamo & Kanwisher, 1995; see also Thorpe, Fize, & Marlot, 1996). These early differences occurred over left temporal and occipital areas known to be involved in object recognition (Tanaka, 1995). The benefits of these fast processes are explicated below.

With acquisition of expertise in object recognition comes faster and more specific identification of objects. It is typical to name an object at its basic level of representation; for example, a robin is faster and more accurately identified as a bird than at the subordinate level of robin or at the superordinate level of animal (see Rosch, 1988). Experts, however, are just as fast at naming items in their area of expertise at the subordinate level of robin as at the basic level of bird (Tanaka & Taylor, 1991). Interestingly, when subjects must determine if an object (e.g., a robin) is an animal, language areas of the brain are active during this more conceptually based semantic task; however, when the same object is shown and subjects are asked to determine if it is a robin, more visual areas of the brain are active as subjects use their knowledge of the known visual features of a robin to solve the task (Kosslyn, Alpert, & Thompson, 1995).

One advantage of a large body of knowledge in object recognition is the ability to test hypotheses regarding the identity of occluded or unusual views of objects. In these cases, subjects may use their ability to create a visual image of their best guess and try to discern if the occluded object has features that match their hypothesis (see Kosslyn, 1994 for a review). When subjects are asked to identify if a name corresponds to an unusual view of an object (e.g., a fence seen from above), or if the name corresponds to a canonical view of an object (a fence seen from the side), the occipital lobe and dorsolateral prefrontal areas of the brain are more active during the unusual views than during the canonical views (Kosslyn et al., 1994). Subjects may be using their knowledge of usual objects to prime the visual areas. They are then able to test these hypotheses by comparing the features of their image to the viewed object. This same type of priming is used to explain the finding of topographic activation of primary visual cortex during some forms of visual mental imagery (Kosslyn, Thompson, Kim, & Alpert, 1995). As we have attempted to demonstrate, difficulties in object recognition are often resolved by the application of top-down conceptual information to the visual percept (Kosslyn & Sussman, 1995).

Top-down processing is important for predicting the form of the expected input items and improving performance. However, costs may also be associated with the

use of top-down conceptual information when processing incoming information (see Johnston & Hawley, 1994 for a review). A familiar example is text proofing in which authors have an extremely difficult time, because they know what the text is supposed to say and often fill in for absent or misspelled words. Top-down information also hinders performance in object recognition. In a study by DiGirolamo and Hintzman (1997), subjects saw five presentations of an object in which either the first or the final presentation was different in orientation or size than the others. When subjects saw both sizes or orientations at test, they were more likely to report seeing only the single different version if it was the initial rather than the final item. This primacy effect is interpreted as a result of a conceptual bias based on the first item's presentation. In this case, the use of conceptual information was detrimental to performance on the memory task.

Working Memory

The acquisition and organization of domain-related memory contributes to skilled performance; however, some processes, such as text comprehension (Just & Carpenter, 1992), rely on more general cognitive components such as working memory. General problem-solving ability also seems to be highly correlated with working memory, and proficiency in the two are developmentally linked (Fry & Hale, 1996; see also Newell, 1990).

Cognitive studies conducted in the 1970s suggested several different short-term memory systems and provided evidence that there could be considerable independence among them (see Baddeley, 1995, for a review). Recent imaging data support a separate anatomy for verbal, spatial, and object working memories (Smith & Jonides, in press). There is also evidence that all these forms of memory are interfaced to a common executive attentional system. These functional neuroanatomical discoveries can confirm and extend some of the findings in cognitive psychology.

For example, there was a dispute within cognitive psychology about whether acoustic or articulatory codes were more important for short-term information storage. Recent PET studies (Awh, Jonides, Smith, Schumacher, Koeppel, & Katz, 1996) suggest that in verbal memory left anterior areas are related to the rehearsal of articulatory codes, while left posterior areas are related to the passive storage of auditory code items. These findings agree with data from word reading suggesting that both posterior and anterior areas are involved in phonological processing (Posner et al., in press). The anatomical separation between anterior and posterior systems confirms the concepts of acoustic codes and articulatory codes as developed in cognitive studies and suggests that each area makes separate contributions to reading and other tasks dependent upon verbal working memory. It is interesting to note that, as yet, no separation of storage and rehearsal components has been discovered in object working memory (Smith & Jonides, in press).

Implicit and Explicit Memory

The cognitive literature (see Schacter & Tulving, 1994) has identified two quite different forms of learning simple facts. Implicit learning occurs during the course of exposure to items and changes later encoding of related stimuli. Explicit learning

occurs through active attention to the item and involves storage in a form which can be retrieved voluntarily by the subject in a variety of contexts.

PET studies have identified important brain structures related to these forms of learning (Buckner et al., 1995; Squire et al., 1992). These studies have often used a form of cued recall. Subjects are first exposed to a list of words and are later asked to generate a response to a three-letter stem (stem completion). The stem completion can take place under implicit instructions to say the first word that comes to mind starting with the stem or under explicit instructions to generate a word from the prior list. During implicit generation of the strings, these studies suggest an area of the right posterior visual system that is reduced in blood flow for words that have been presented before, in comparison with strings for which a new word has to be generated. Studies using auditory presentation of the original word list find a similar alteration in blood flow for previously presented items within the auditory system (Schacter et al., 1996a). When explicit instructions are given there is activation in both frontal and hippocampal areas at least under some conditions (Schacter et al., 1996b).

We (Badgaiyan & Posner, 1996) have been replicating the PET studies with high-density electrical recording. One intriguing result of the PET studies was that priming reduced activation in right posterior visual areas when the original words were visually presented. This brain area has often been associated with the implicit storage of visual information. If less neuronal activity was needed in this area, it could indicate that, in this paradigm, the memory trace of the previously learned word was activated with greater efficiency by the three-letter cue. Improved efficiency would be indexed by a reduction in the neuronal activity needed to reactivate the visual code of the word stored from the prior exposure. However, since PET does not provide a time course for the changed neuronal activity it is also possible that the reduced blood flow merely means that when a word has been encountered before, less attention and effort are needed to generate a response to the three-letter cue. Less attention to the visual code of the primed word would also result in less blood flow than for unprimed items. In other words, the reduced activation of the right posterior area might be either bottom-up or top-down.

Scalp electrical recording is one method for determining which of these options is true. Our results suggest that the difference between primed and unprimed targets in this paradigm begins by 100 ms after the three-letter cue was presented. We found no difference between primed and unprimed targets in the last few hundred milliseconds before the response, where we would have expected to see activation due to the subjects working actively on the input string. An important result of our study was that the right posterior reduction in blood flow was found irrespective of instructions. In this sense, the effect of the word on later string presentation was automatic.

Other results from our study suggest that the deliberate instruction to recall from the prior list differed from the priming instruction mainly in frontal areas that have been previously associated with semantic processing, as well as in the hippocampus, which has been linked with episodic recall. When subjects were given implicit instructions and the word had been presented previously in the list, there was no frontal or hippocampal activation. These brain areas appear to be associated with volitional efforts to search the prior list or determine a related word.

The study of work stem completion supports our general effort to use anatomical and circuitry data to converge with cognitive studies of priming. This theme is elaborated further in the next section.

PLASTICITY

Attentional Networks

We view attention as involving three major functions: orienting to sensory stimuli; executive control (including target detection and response selection); and maintaining the alert state (Posner & Petersen, 1990; Posner & Raichle, 1994). Although knowledge of the precise neural mechanisms responsible for these operations is not conclusive, many of the brain areas and networks have been identified. Thus, the orienting network for visual attention is believed to involve posterior structures such as the parietal lobe, pulvinar, and superior colliculus. The executive network is located more anteriorly and includes midline frontal areas and the basal ganglia. The alert state is maintained by a network involving the norepinephrine system arising in the locus coeruleus and including widespread frontal and parietal activation, most strongly of the right hemisphere (Posner & Petersen, 1990; Posner & Raichle, 1994).

What is most important is the understanding that attention as a general resource is implemented in the brain by networks of specific neural areas. For example, the executive attentional system is more active when the task involves complex discrimination and the degree of activation depends on the number of targets presented. The network is also responsible for anticipation of the target location (Murtha, Chertkow, Dixon, Beauregard, & Evans, 1996). Norman and Shallice (1986) presented a cognitive model that specifies operations involved in executive attention. Their model suggest conditions under which supervisory control is needed including planning, novelty and error detection, resolution of conflict, and increased task difficulty. Recent PET and fMRI studies have provided evidence of activation of midline frontal areas during each of these situations (see Posner & DiGirolamo, in press, for a review).

In this section we hope to clarify changes that take place in task performance that involve alterations in the underlying neural circuitry. Many of these changes are due to automaticity of component operations or to shifts of attention. Therefore, we start by describing the concepts of attention and automaticity as they are used here. Next, we describe priming and extensive practice (skill acquisition) as two possible versions of the same process of automaticity. From the cognitive models of priming (Posner, 1978), we make predictions about neuronal activity. Finally, we postulate four nonexclusive models of skill acquisition and illustrate them with recent neuroimaging studies.

Automatic processes are described as being involuntary, parallel, and usually unconscious (Kahneman & Treisman, 1984; Posner, 1978). They are processed in parallel, so that two automatic processes do not interfere nor do they require attention for their normal performance (Regan, 1981). At the subjective level, the attention-free aspect of automaticity is experienced as a lack of effort. These properties of automaticity are usually contrasted with controlled or attentional processes, which are slow, are conscious, require effort, are serially processed, and are subject to interference.

With practice, controlled processes gain automaticity, requiring less effort for their performance.

Although in most natural situations the features that characterize automatic processes co-occur, they sometimes do not coincide. These exceptions are instructive in that they reveal different meanings that researchers have attributed to the term.

(a) *Involuntary vs. attention-free.* A useful distinction must be made in identifying an automatic process either as involuntary or as attention-free. A process demanding attention can be triggered without intention. For example, the process of reading the word in the Stroop task cannot be voluntarily suppressed. Nevertheless, it draws attentional resources, as is evident in the cost of contradictory color ink and word name.

(b) *Attention is not necessary vs. attention is not useful.* Automatic sometimes means that attention is not necessary. In this sense, mental operations are automatic if they can be performed without a cost in a dual-task condition. For example, visual word form recognition is an automatic process because subjects can recognize a word while performing a secondary task that captures attention; however, visual form recognition can be modulated by attention. In contrast, automatic sometimes means that attention is useless in improving performance. This different sense of automaticity implies that the process cannot be modulated by voluntarily allocating resources.

(c) *Automatic capture of attention.* Automatic has also been used to describe the involuntary allocation of attention to an environmental stimulus even if such a process taxes the general attentional resources.

As has been discussed above, the acquisition of expert performance in word reading produces automatic activation of component cognitive processes (e.g., the integration of the orthographic form of the word, the activation of the semantic meaning). This automatic processing occurs due to the effect of practice and experience (Cohen, Dunbar, & McClelland, 1990); it is, however, not without some costs. For example, the cost in naming the color of ink that a color word is printed in (Stroop, 1935). This cost becomes larger as the semantic meaning and represented color of the written word become more difficult to discriminate from the ink color (Klopfer, 1996). This Stroop effect demonstrates one representative case in which automatic processing hinders task performance.

Another example of an automatic activation that adversely affects performance can be seen in semantic blindness (MacKay & Miller, 1994). In this phenomenon, subjects fail to detect a word in a sentence that has the same meaning as a previous word if they are presented in a rapid serial fashion. This effect applies even if the words are in different languages. In this case, the automatic activation of the similar meanings of the words prevents individuation of the token representation (see Kanwisher, 1987), even though the words are orthographically and phonologically distinct.

While the automaticity of cognitive components of a high-level skill produces great benefits, some costs are also associated with the automatic execution of these processes. Sometimes these automatic processes are begun even though the task does not require the process and, in fact, may be hindered by its execution. Below we will discuss familiar cases in which automaticity improves performance.

Defining Practice and Priming

Practice improves performance. Part of the practice effect is due to implicit memory. For example, performing a task repeatedly leads to better performance even when the subject is not aware of having performed the task. Although it is clear that practice also has an explicit, conscious component, we will limit our discussion here to the implicit component of practice.

Although extensive practice is certainly beneficial, enhancement of performance also occurs after the first experience with a task. Moreover, the benefit generalizes to other tasks that are not identical to the one practiced. Provided that the cue task and the test task share certain elemental computations, performing the cue task will enhance performance in the target task. This effect we call priming. Another defining feature of priming is its independence from conscious attention or recollection. Priming is due to implicit memory and occurs even when subjects do not intend to use the cue task to improve performance on the target task.

Researchers within the information-processing paradigm sometimes conceptualize priming as the “practice of the mental operations shared by two different tasks.” As a consequence, priming and practice are sometimes used interchangeably (e.g., Demb et al., 1995). We reserve the term priming for those cases in which cue task and target task are different. When cue and target tasks are identical, we use the term practice.

Are priming and practice the extremes of the same process of automaticity, with priming being one instance of activation of a mental computation and practice being multiple repeated instances of activation of several mental computations? Priming and practice share several features. They both lead to enhanced performance, are modality specific, and may act at the presemantic level (i.e., representing only physical information). In the following sections, we attempt to clarify the relationship between priming and practice. After analyzing priming at the computational level, we make predictions about its neural realization.

Priming

Our predictions on priming are derived from a dual cognitive model of computational enhancement, in which attention (top-down) and pathway activation (bottom-up) have similar effects on performance (see Posner, 1978); recently, the two processes have been shown to have opposite effects on neural activation.

Attention and pathway activation. After a prime is displayed, performance for a target identical to the prime is enhanced by two different mechanisms: attentional modulation and automatic pathway activation (the latter also serves a role in implicit memory). We argue that attentional modulation improves performance and increases neuronal activation, while the automatic pathway activation improves performance but decreases neural firing.

In the past decade, evidence has accumulated showing that this top-down attentional modulation leads to increased activation in sensory brain areas. For example, attending to moving objects leads to activation of an area homologous to the motion-sensitive area of monkeys (Corbetta et al., 1991). Attending to color activates ventral temporal and occipital areas, which are known to process color information. These

attentional effects cannot be accounted for by changes in the environment, since they occur even when the external stimulus remains constant. Similarly, ERP studies reveal an increased response to attended stimuli as early as 80 ms following stimulus onset (Heinze et al., 1994). Such an early activation argues that attention acts on perception, rather than simply biasing the decision criterion. This type of modulation has been named preparatory attention (LaBerge, 1995).

Studies of imagery provide convergent evidence for the top-down activation of sensory areas (Kosslyn, 1994). Brain imaging studies reveal that sensory areas are activated by imagery. Like preparatory attention, imagery also enhances performance. When subjects are instructed to imagine an object and perform a recognition task upon a target stimulus, performance is enhanced when the target stimulus is the imagined object. Presenting an unexpected (unimagined) target leads to a cost in performance. It is likely then that one of the aspects of preparatory attention is sometimes to create a mental image of the expected object.

Attention-dependent activation of neuronal activity in early sensory areas has also been revealed by single-neuron recording in alert behaving monkeys (Motter, 1993), and in monkeys performing a working memory task (Miller & Desimone, 1994). This latter study is of particular interest for our proposal, as it reveals the existence of two parallel mechanisms of short-term memory: a voluntary mechanism, dependent on attention and expressed as neuronal activation, and an automatic, involuntary mechanism, expressed as neuronal suppression. We describe here the voluntary aspect, leaving the automatic aspect for the next section.

Single neurons in the inferior temporal cortex (IT) area were recorded from monkeys performing a delayed match-to-sample task, in which a cue is displayed, followed by a sequence of items. The animal's task was to respond whenever a target, namely the repetition of the cue, appeared in the sequence. Two strategies were possible. The animal may keep the cue in mind, disregarding the distracters, and respond whenever the target is displayed. Alternatively, the animal may simply respond whenever a stimulus is repeated. This last strategy becomes useless in the condition in which the distracters are displayed repeatedly. In this variant of the task, the animal's performance depends only on the first strategy, which requires working memory (i.e., active rehearsal of the cue during the cue-target interval). In agreement with studies showing activation of attended brain areas, the working memory strategy produces neuronal activation in IT, an area important for object recognition (Tanaka, 1992). During the cue-target interval, some cells in area IT exhibit an increased tonic activation. Upon target presentation, the cells in IT show an increased phasic response, as predicted from attention studies. This phasic activation is not due to an automatic effect of stimulus repetition, because repetition of a distracter fails to produce an enhanced response.

In summary, data from imaging studies of attention and imagery, and from single-neuron recording of working memory and attention, argue for the existence of voluntary mechanisms that allocate attention into sensory brain areas, improving performance and increasing neuronal activity.

No matter how important, attention cannot fully account for the benefit of encoding a stimulus on the second occasion. A benefit exists even when encoding occurs without intention and without awareness. Moreover, a benefit is present when the first

instance of the stimulus (cue) has no predictive value for the occurrence of the second instance (target). Finally, there is a benefit even when the target follows the cue so rapidly that the voluntary allocation of attention is not possible. These findings argue for an automatic, unconscious, unintentional mechanism of facilitation.

This bottom-up facilitation reduces the neuronal response to a primed stimulus, just the opposite of the influence of attention on the same brain areas. Single-neuron recordings in monkeys have revealed the existence of this automatic pathway activation or short-term memory mechanism. Moreover this automatic mechanism is independent of working memory and is implemented by a different subset of neurons in area IT. Whenever the stimulus preferred by one of these neurons in IT is repeated, the cell's response is reduced. This reduction occurs whether or not the stimulus is a target, providing evidence that the mechanism is in some sense automatic. This automatic short-term memory, manifested by a reduction in neuronal response, is conceptually similar to habituation and it may help to explain why the second presentation of an item leads to improved reaction time but impoverished recollection (e.g., repetition blindness and massed practice effects in memory studies).

Posner (1978) proposed a cognitive model in which bottom-up priming is facilitation of the psychological pathways. The model does not specify whether the pathway facilitation is due to stronger connections between isolable subsystems that link the selected stimulus to the required response or due to improved computation within some of those subsystems. Evidence from imaging studies suggests that at least part of the facilitation occurs within the isolable subsystems. For example, in the prime condition of word stem completion, there is a modulation of the sensory-specific brain area known to be involved in input processing. Practice on a task leads to a similar reduction in brain activity (Raichle et al., 1994; Domb et al., 1995). Nevertheless, the existence of stronger connections between isolable subsystems remains an open possibility, which can be explored with ERPs by looking for a faster onset in the activation of later subsystems.

In summary, data from electrophysiological, imaging, and behavioral studies argue for the existence of an automatic pathway activation or short-term memory mechanism that improves performance and reduces neuronal activity.

Behavioral predictions. Posner and Snyder (1975) sought to separate the automatic and attentional components of priming in a RT experiment using a letter-matching task. Allocation of attention was manipulated by varying the predictability of the target. In one condition, the target was frequently identical to the prime (80% valid). Subjects were assumed to use this predictability to create an expectation by attention. In the other condition, the target was seldom identical to the prime (20% valid), and subjects were assumed to be less likely to build an expectation about the target.

The attentional mechanism was expected to be absent at very early cue-target delays, since there would not be time to create the expectation. Therefore, at short SOAs, only the faster automatic component of priming should be observed. At long SOAs the attentional mechanism should also be evident and there should be a cost in trials where the prime incorrectly predicts the target (invalid trials). The attentional mechanism, being voluntary, was assumed to have a slow decay. Therefore, at very long SOAs, the attentional mechanism should still be evident. In contrast, the automatic pathway facilitation was hypothesized to have a faster decay and to be less

evident at longer delays. However, the automatic effect might last for a longer period for unusual stimuli or for stimuli that have been processed carefully during the priming task. The automatic effect was assumed to act in parallel and thus not produce a cost on a nonprimed target.

Results over many years using a variety of behavioral paradigms have largely confirmed these patterns (e.g., Neeley, 1977). In many information processing studies, automatic priming remains present for only a very brief period. However, in some studies involving implicit memory mechanisms automatic priming may last quite a long time (Shachter, 1994). Below we use this behavioral model, together with the current literature in functional neuroimaging, to make testable predictions about the pattern of neuronal response to primed targets.

Neural predictions. An exhaustive description of the predictions would consider not only the involvement of automatic and voluntary mechanisms, but also the temporal differences in their onset and decay. Such a description would also include the relation between the neural and the behavioral patterns. In this paper we describe only a few of the major predictions.

When the subject has no expectations (low-validity condition), only the automatic short-term memory effect should be evident. The effect should be expressed as a *reduction* in the neuronal response to a repeated stimulus. This reduction should occur both for targets and for distracters, and it should be evident at shorter delay intervals. Reaction times should improve for primed target events and unprimed targets should not produce a cost in RT.

When the subject's expectations are high (high-validity condition), attentional resources should be allocated to the relevant sensory areas. We predict a tonic *increase* in neuronal activation prior to the target presentation (during cue–target delay) and a phasic increase of neuronal activation following expected targets. The effect should not be evident at very short cue–target delays, but should be evident at longer delays. Neuronal response to invalid targets (unexpected) should be reduced and this should correlate with a cost in RT. This cost should not be evident at very short delays.

Top-down preparatory attention and bottom-up pathway activation both have beneficial effects in performance (although with different onsets and decays), but opposite effects on neural activity. Tasks that do not allow a separation between automatic and attended mechanisms are likely to give ambiguous results, since the effects may cancel out.

Skill Acquisition

When we refer to skill acquisition, we are usually concerned with changes in performance as the skill is practiced, sometimes over many years. It is also obvious that the brain changes with new learning, but it is more difficult to specify exactly how these changes occur.

Attention can enhance performance through integration across modules, by changing computations within a module, or by increasing the efficiency of a module. Similarly, practice may increase the links among subsystems or increase the efficacy of a given module. In either case, practice leads to automaticity; as a consequence, less attention needs to be allocated. Efforts to outline specific ideas of how this practice

changes brain areas and to relate them to data are very new. Below we make an initial effort to do so for some recent data.

Model 1: Automaticity as an increase in the links among the isolable subsystems. Task performance requires the combination of multiple operations. When a task is performed, many isolable subsystems are integrated into a common network (Posner & Raichle, 1994). The amount of effort (i.e., attention) needed for such an integration depends on the strength of the connections among the subsystems.

This model makes explicit assumptions. By describing those assumptions in anatomical terms (e.g., integration of an isolable subsystem), explicit predictions can be formulated about the neural changes that underlie automaticity in cognitive performance. In particular, the model predicts that practice should not change the circuit used to perform a given task. Practice should, however, lead to an earlier onset of activation in subsystems without modifying the level of activation or changing the computation within those subsystems.

Model 2: Improved or altered computation within modules. Following extensive practice, brain areas involved in the task may be increased in size or number. This has been shown in electrophysiological studies of behaving animals (Nudo et al., 1996), and in brain imaging studies of humans (Karni et al., 1995). For example, expert violinists have greater representation of the fingers on their more involved hand (Ebert et al., 1995). However, it is also possible that the nature of the computation within a module could change with practice.

Model 3: A new, more efficient task. Models 1 and 2 assume that the tasks being performed by the expert and the novice are the same. However, it is possible that the task performed by the expert is different. Improved performance would be due to the replacement of the initial components by other, more efficient components. For example, patients with focal brain damage learn to achieve the desired outcome by performing the activity in a different way (Luria, 1973). In those cases, unaffected circuits make adjustments to compensate for the deficit due to damage.

Model 4: Circuit change. In the three models described so far, the circuits that perform a given task remain invariant. However, the possibility remains that practice would lead certain brain areas to start performing the mental computation formerly implemented by a different area. Some evidence from PET studies, involving the generation of uses to visually presented words, shows changes in brain circuitry that occur with a few minutes of practice of a particular set of 40 words (Raichle et al., 1994). With practice, activation of the brain areas specifically related to associating a use with a word drops away and the circuit resembles that of reading a word aloud. These findings suggest that when a skill is highly automated, such as reading words or generating highly practiced associations, a different circuitry is used than that for generating new thoughts. In addition when a new association has to be generated in the presence of a highly practiced association, the original circuitry returns and appears to recruit brain areas of the right hemisphere homologous to Wernicke's area (Abdullaev & Posner, 1997).

Although the change in brain circuitry discussed in the models above may take place very rapidly, we have extended our work using high-density electrical recording during the acquisition of reading skills in adults learning a new language and in

young children acquiring initial literacy (McCandliss, Posner, & Givón, in press). These studies approximate more closely the acquisition of skills by experts.

We found that 50 h of acquisition of a new artificial language by adults produced a word superiority for the new lexical items, very similar to that found for English words over consonant strings, learned in the study. The artificial language used in this study was similar but not identical to English. Presentation words in the new language activated posterior electrodes associated with the word form area of the left ventral occipital lobe found active in PET studies (Posner & Raichle, 1994). The new words activated the word form area about halfway between what was found for English words and what was found for consonant strings. However, this visual word form activation did not show any change over the 50 h of exposure to the newly learned lexical items. Other areas of the left hemisphere, reflecting the semantic processing of individual words, did change dramatically with practice in a manner that reflected the word superiority effect found in the new language. This study suggests that plasticity in the brain for skill learning may differ in brain regions already committed to particular modes of processing. Semantic areas were easily recruited as the subjects learned meaning for the artificial language words (as in Model 1 above). However, orthographic areas did not change their computation with practice (a change in computation would have been consistent with Model 2).

We have also been able to examine similar and more extensive changes in children as they acquire initial literacy (McCandliss, 1996). In children, these changes take place over many years of learning. It was found that 7-year-olds who could read still did not show adult development of the visual word form area. It appeared that this area was active for words that these children knew, but was not active for orthographically regular words that they did not know. It seems as though the word form area begins as an item-specific area reflecting the particular learning of the child. However, over many years of practice it comes to be strongly activated even by unfamiliar items if they obey English orthography. This corresponds to what in cognitive psychology has been discussed in terms of exemplar learning, which finally produces a system that appears to execute complex rules. In adults, unfamiliar but orthographically regular items activate the word form area, but familiar items that do not obey orthography (e.g., FBI) may not do so. This result supports the possibility of an effective change in the computation within a module (see Model 2).

Recent studies (Temple, 1997) suggest that computations underlying the appreciation of quantity may be quite different than that reported above for the visual word form. The visual word form appears to develop over many years of practice. Dehaene (1996) has found areas of the parietal lobe sensitive to the quantity of Arabic digits or spelled numbers. His additive factors studies indicate that activation of this area differs during number comparison processes according to whether the digit is close to or far from 5. He argues that this area is like a number line and is important for an appreciation of the quantity of the digit. In her studies, Temple confirmed the activation of this area in adults during number comparison using both Arabic digits and dots varying in quantity. Moreover, she found that 5-year-old children, whose experience with digits was minimal, used this same brain area during comparison of input digits or dots with the number 5. The 5-year-olds showed a very pronounced

distance effect and the electrical signal was strong over the same electrode sites previously shown by Dehaene. Despite the long reaction times for the 5-year-olds, activation of this area was only very slightly delayed over that found for adults. It is known that infants have some appreciation of numbers and thus there is evidence that number processing has an innate or nearly innate basis (Wynn, 1992). Of course quantitative skills do develop, but apparently the brain area that appreciates quantity does not change very markedly in development. Instead the efficiency of hooking up various representations to the area improves with experience as in Model 1 above. This finding contrasts strongly with the results for word reading, which showed a clear developmental progression from a word-specific module to a general rule system. It emphasizes the importance of a broad consideration of skills in dealing with issues of acquisition.

SUMMARY

This article has reviewed a variety of skills from the standpoint of neuroimaging research. There are considerable similarities in the brain systems underlying many skills. These include such findings as the presence of localized computation, the real time activation of these computations, and the role of practice or priming in short- and long-term changes in neural systems. We are just at the very start of trying to understand these brain systems, but already they have helped to clarify many of the findings and theories of cognitive psychology regarding skill learning and execution.

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