Working Memory

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Leslie Ungerleider and Susan Courtney

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Abstract

Working memory is a complex concept that underlies much of our higher cognitive abilities. It involves the selection, temporary storage, manipulation, and use of currently relevant information. Unlike long-term memory, only a very limited amount of information can be held in working memory at one time.

Leslie Ungerleider: deceased.

L. Ungerleider
Section on Neurocircuitry, Laboratory of Brain and Cognition, NIMH, Bethesda, MD, USA

S. Courtney (✉)
Department of Psychological and Brain Sciences, Johns Hopkins University, Baltimore, MD, USA
e-mail: courtney@jhu.edu

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Researchers have tried to measure this capacity of working memory, but the answer to that question depends on the type of information one is trying to remember and the way that the memory is tested. Working memory, particularly its executive component, seems to depend on the prefrontal cortex. This part of the brain has internal circuits that can sustain patterns of neural activity for a longer time than can other parts of the brain, resulting in flexible representations that can be protected from being overwritten by new sensory inputs. The prefrontal cortex also receives converging inputs from many different brain regions, enabling it to integrate and manipulate multiple pieces of information from the past and use that information to guide future behavior in new situations.

Keywords

Distributed population code · Functional magnetic resonance imaging (fMRI) · Prefrontal cortex · Recoding · Short-term memory · Working memory · Brain imaging methods · Capacity · Information storage · Executive

Brief History

Working memory is an essential cognitive ability for humans. It underlies our abilities to behave flexibly in new situations, to figure out a solution to a new problem, and to reason logically. These higher cognitive skills would not be possible without working memory, which is the ability to keep in mind and use the information that is most important for the current situation. Despite its importance, however, the concept of working memory is a relatively recent one in the history of psychology. Psychologists and neuroscientists do not all agree on a definition of what exactly working memory is. Much research is still being done to help us to understand what the capabilities and limitations of working memory are, and to understand how our brains enable this ability.

Philosophers and neuropsychologists began to make distinctions between different types of memory in the 1800s. It wasn't until the 1960s and 1970s, however, that the distinction between short-term and long-term memory, and the ideas surrounding the concept of working memory, were more fully developed. Research demonstrated that for long-term memory to be achieved, the remembered experience must cause structural changes to the brain, with the creation of new proteins. Short-term memory can be achieved through temporary changes in how effective the connections between brain cells are, or through sustained patterns of neural activity. Attention is needed to maintain these patterns of activity and protect them from possible distracting, irrelevant stimuli or thoughts. Therefore, this information is fragile, but this active state enables the information to be used and manipulated in a flexible way according to our goals in the current situation. This is why this ability is called "working memory," because it is the part of our memory that we are currently able to work with.

Starting in the 1980s, neuroscientists such as Patricia Goldman-Rakic and Joaquin Fuster identified particular populations of neurons in the prefrontal cortex that were capable of producing sustained patterns of activity during working memory tasks. In a typical experiment, the monkey is shown a sample stimulus, followed by a blank delay interval, and then a test stimulus. If the neuronal activity to the sample stimulus is sustained through the delay interval, then the monkey will likely respond correctly to the memory test stimulus. The patterns of activity in these prefrontal neurons specifically reflect the information that the animal is trying to hold in memory. Unlike activity in sensory areas, if this prefrontal activity is disrupted, then the animal will likely respond incorrectly to the memory test. Following these discoveries, much research has focused on the functional organization of the prefrontal cortex and its role in working memory. Modern research on working memory has incorporated ideas about the use and manipulation of information in working memory in addition to its simple short-term memory maintenance. Researchers now understand that the prefrontal cortex is in constant, rapid communication with many other brain areas. Working memory appears to be achieved by complex interactions among different cell populations. These interactions take place within local circuits of the prefrontal cortex, and also between the prefrontal cortex, other cortical areas, and even subcortical areas such as the striatum and the cerebellum. Researchers are beginning to understand all of the different ways that this complex, distributed circuitry can malfunction. Working memory is not optimal in both children and older adults. It can be badly impaired due to injuries to the white matter that connects these distant brain areas, as can occur during traumatic brain injury or neurological disorders such as multiple sclerosis. Working memory deficits may underlie the cognitive disturbances seen in psychiatric illnesses such as schizophrenia. With continued improvements to our understanding of the neural basis of working memory, we may be able to improve working memory abilities in these types of conditions (Figs. 1 and 2).

Storage of Information Is Different from Its Manipulation and Use

Short-term memory is a very general term that can apply to the storage of information in any form that does not become consolidated into long-term memory. Iconic memory refers to the trace of activity following a sensory stimulus that continues briefly after the stimulus is gone. It does not require any attention or effort to maintain, but it lasts less than 1 s. Information can also be stored in short-term memory due to the effects of a recent stimulus on the resting potentials of individual cells or short-term changes in synaptic strength that affect how those cells will respond if that same stimulus occurs again, either immediately or several seconds later. These kinds of short-term memory can be demonstrated through effects on behavior. You can recognize a stimulus as being the same as one you saw very recently, even if you weren't trying to maintain that information in working memory. This type of memory has sometimes been referred to as "activity-silent working memory," but it is better understood as short-term memory. In order for information in short-term memory to be stored in working memory, it needs to be in a form that can be selected, manipulated, and flexibly used in making decisions and solving problems. This requires that the information be represented in patterns of neural activity. Patterns of sustained neural activity that contain information that is relevant

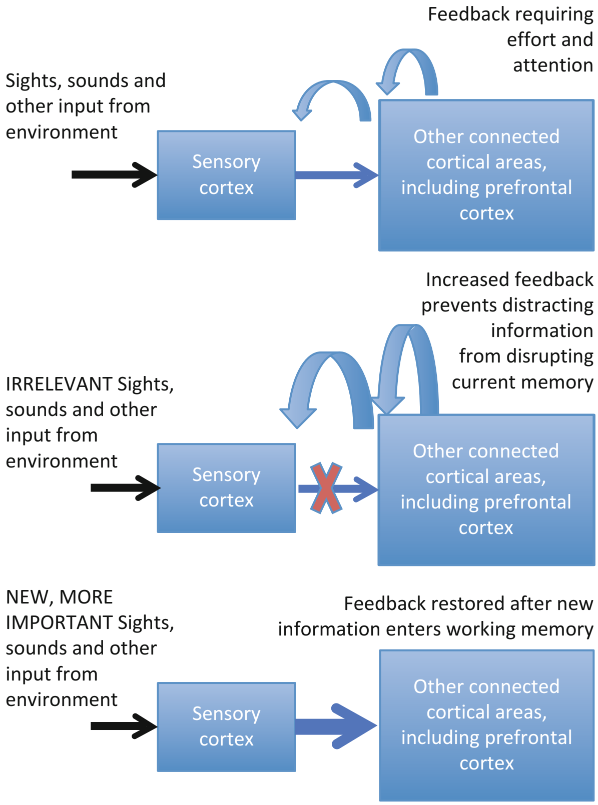

Fig. 1 Active maintenance for storage of relevant sensory information in working memory, protection of that information from distraction, and updating with new relevant information

to the person's or animal's current task have been observed in many different cortical areas, from primary sensory cortices to multimodal areas like prefrontal cortex. In order for the person or animal to do well on the task that requires that information, these patterns of activity need to be maintained throughout the memory period until the information can be used to complete the task. These patterns of activity are not necessarily constant. The activity might show a rapid series of bursts rather than being continuous. The strength of the activity might ramp up or down during the memory delay. The pattern of activity might change during the delay from representing the previous stimulus to representing the upcoming action. Nevertheless, there is always neural activity that carries information about what is in working memory. This active maintenance and flexible use of the information is what makes working memory different from other forms of short-term memory.

Many researchers believe that cognitive and neural systems for the short-term storage of information in working memory are separate from the systems that work with that information, manipulating and using it for whatever the person's current task is. One early and influential model of working memory, proposed by Baddeley and Hitch, calls the storage systems "slave systems" and the systems that manipulate and use that information the "central executive." The central executive guides decisions

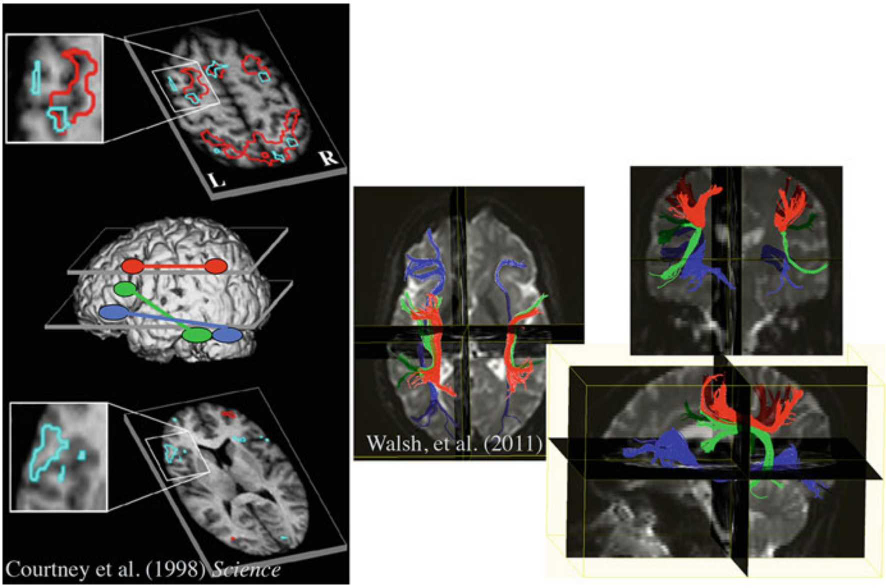

Fig. 2 **White matter tracts in humans connect prefrontal areas involved in working memory to sensory areas that process the same type of information**. In figure on *left*, areas in *red* are active when people remember the location of objects. The areas in *blue* and *green* are active when people remember the identity of faces. These same areas across prefrontal, parietal, and temporal cortex are connected to each other, enabling rapid interaction that is thought to be needed to sustain neural activity

about what information is most important be stored in working memory at the current time. It also guides attention to the most important new sensory information in the environment. When something new happens in the environment, executive processes must decide whether this new information is more important than what was already being stored in working memory. If it is more important, then the old information will be replaced by the new information. If the information that was already being stored in working memory is still more important, then the executive processes must keep out the distracting new information and protect the stored information. Sometimes, what is most important is the relationship between two pieces of information, such as how the new information is different from the old information. In this case, the central executive manipulates these multiple pieces of information, integrating them and creating a new understanding of the current situation.

Manipulation and Other Executive Processes Depend on the Prefrontal Cortex

How these executive processes actually happen in the brain is very poorly understood. The prefrontal cortex is thought to be particularly important for these processes. Neurons in prefrontal cortex are selective for combinations of different inputs that are important for whatever task the person or animal is doing at the time. Neurons in prefrontal cortex also seem to carry information that is needed to predict future outcomes. These predictions include information about the rules that govern what actions to particular stimuli, or combinations of stimuli, will result in either good or bad outcomes. To do this job, the prefrontal cortex needs access not just to all the different current sensory inputs, but it also needs access to information stored in long-term memory. So, the central executive is also thought to be involved in the controlled recall of whatever information in long-term memory may be important to making decisions about the current situation.

How can the prefrontal cortex do all these things? The answer is that it must rapidly and repeatedly interact with nearly every other part of the brain. Prefrontal cortex receives input from, and provides output to, every sensory system: vision, hearing, touch, taste and smell. It also has connections with the medial temporal lobe, which is known to be essential for long-term memory. Finally, it has connections with subcortical nuclei, such as the basal ganglia, which are involved in both habit learning (for example, acquiring skills) and switching from one action to another. Thus, the prefrontal cortex does not do executive processes on its own. Executive processes arise from all of these interactions between the prefrontal cortex and all these other brain areas. These interactions change the patterns of activity in all of the different brain areas. They strengthen patterns of activity that represent currently important information, and weaken patterns of activity that represent information that is not important right now. Those important and unimportant pieces of information may be coming from current sensory inputs, sensory inputs that happened a few seconds ago, or information recalled from long-term memory. Therefore, the stored information itself makes executive processes possible. Executive processes may be thought of as the computations resulting from interactions among different stored pieces of information. These computations result in the selection, integration, and transformation of the information, which then influence behavior. These processes do not exist within any one particular brain area, separate from the information itself. The processes are possible because there are many different parts of prefrontal cortex and many different parts of the brain outside prefrontal cortex, and all of these areas work together to create the "central executive."

Different Types of Information Are Stored (Somewhat) Separately

What the central executive is doing, therefore, is coordinating information about all the different things that are needed for the task at hand. If we are searching for a friend in a crowd of people, we need to hold in working memory what our friend looks like and maybe the color shirt that our friend might be wearing. We also may need to hold in working memory other things that we may know about our friend to succeed in finding her. What direction might she have been coming from to reach this big gathering of people? Would she be likely to be in the middle of the crowd, or does she like to stay on the edge? We would also want to hold in working memory the purpose of our search. Why are we looking for this person? What do we want to do or say once we find her? To successfully accomplish our task, we must remember all of these types of information. We also need to remember the rules of how and when to use each piece of information. We certainly do not want to start talking about what we need to tell our friend before we actually find her. All of these different kinds of information, from the color of a shirt to complex social rules, can be maintained in working memory with sustained patterns of neural activity. Different parts of the cortex are specialized to represent some of these kinds of information better than others.

Some of the earliest evidence for separate brain systems for different types of information in working memory came from comparing verbal and spatial working memory tasks. It is always more difficult to do two tasks at the same time then to do those tasks separately. Doing two verbal tasks at the same time, or two spatial tasks at the same time, however, is much harder than doing one verbal task plus one spatial task. Worse performance when doing two tasks that use the same type of information suggests that different types of information use separate neural resources. If you can use a separate part of the brain for doing the spatial task than the one you need to do the verbal task, then your performance will be better. This result has been found with many different types of spatial and verbal tasks, further indicating that verbal and spatial information are separately maintained in working memory. Other research suggests there are at least three general types of information that have separate resources for working memory: verbal, spatial, and sensory information that is neither verbal nor spatial such as colors, textures, or the identities of people (as known by a face or voice).

There are probably more types of information that have separate working memory resources, but it is hard to test exactly how many or how independent they are from each other. Like the tasks used in monkeys, the tasks we use to test people's working memory ability usually involve presenting sample images or sounds for people to remember and then asking them to respond to some sort of test image or sound to show whether they remember. During the delay between the sample and test, when they are supposed to be holding the information in working memory, people tend to use all of the parts of their brains to remember the information in many different ways. This strategy is often called "re-coding." One example of recoding is trying to remember what an image looks like by coming up with a verbal description and rehearsing the verbal description in working memory. If you are only trying to remember that image, you could use both your memory for the image and your memory for the description you created. If I also gave you some other words to remember, however, you might rely only on the visual image in memory. If I gave you another image to remember, however, you might remember the first image from its verbal description and the second image as a visual image. By switching strategies like this, you might be able to do just as well remembering two images as remembering an image plus some other words. It is difficult, therefore, for researchers to know only from behavioral performance on different types of tasks whether these different types of information use the same or different parts of the brain.

Brain Imaging Methods in Humans Have Revealed More Distinctions Between Different Types of Information in Working Memory

New methods for measuring brain activity in humans have made it possible to start to answer this question, however. As we just discussed, researchers cannot prevent people from maintaining and using multiple kinds of information to solve a working memory task. Researchers can, however, give people different tasks or different instructions that encourage them to pay attention to one type of information in working memory more than another. The brain areas responsible for holding this information in working memory will have greater levels of neural activity when the task emphasizes this information than when this same information is just in working memory as extra help. These different levels of more or less neural activity can be measured in humans by methods such as functional magnetic resonance imaging (fMRI). For example, if I give you a picture of a face to remember, you might try to create a verbal description of that picture to help you remember it. However, I might then give you a test picture that is very similar to the first picture. Your verbal description of the first picture is probably not detailed enough to enable you to know whether the second picture is identical to the first, or not. If I do this enough times, you might still keep creating verbal descriptions, but you will learn to not rely on them and will try instead to strongly maintain the image itself in working memory. When I measure the neural activity in your brain with fMRI, I will see activity related to both working memory for words and working memory for images, but the activity for the images will be stronger. Similarly, I can again give you a task of remembering images of a faces, but this time I choose the test images to be images that you would be able to know are the same or different from a simple verbal description of a couple of words, such as whether the image is of a man or a woman and whether the hair color is light or dark. Now, instead of remembering the detailed image, I am encouraging you to simply say to yourself during the memory delay “woman, light hair” repeatedly until the test image appears. When the test image of a man with dark hair appears, you know that this is not the same as the first image, just from the words you rehearsed. You did not need to remember exactly what the image looked like. Now, if I measure your brain activity using fMRI, you will likely have more activity in verbal working memory areas than in face image working memory areas. By making such small changes in working memory tasks people perform while their brain activity is measured, researchers have been able to show that different parts of the brain, including different parts of prefrontal cortex, maintain different kinds of information in working memory.

Researchers do not really understand yet what the brain considers to be a “different type of information.” As explained earlier, one distinction that is clear from both behavior and neural activity experiments is the separation of verbal information from spatial information. Other separations have also been shown, such as faces versus names, and colors versus shapes. One separation that might be expected is the difference between the senses of sight, sound, touch, smell, and taste. It is true that if you are trying to hold in working memory what something sounded like you will get more neural activity in auditory-related areas, whereas if you are trying to remember what something looked like, you will get more neural activity in vision-related areas. However, some kinds of visual and auditory information tend to get integrated and will often interfere with each other if you try to remember them at the same time. For example, if you try to remember the location of something that you heard and the location of something that you saw, the memory for one can overwrite or distort the memory for the other. Usually, in our everyday life, we try to remember the location of something that we both saw and heard. If there was only one object making both the visual image and the sound, then the locations should be the same. The brain is apparently not designed to keep track of sights and sounds completely independently of each other. Two types of effects are often seen in research. Sometimes people pay attention to one sensory input and ignore the other, such as focusing on just what is being heard and ignoring what one is seeing. You might even close your eyes to be able to understand and remember better what you are hearing. If you try to pay attention to both what you are seeing and what you are hearing, your perception and your memory will try to combine these two inputs into a unified understanding. Usually this is helpful. Watching how someone's lips move while they are talking to you helps you to understand what you are hearing them say. If the movement of their lips does not match what you are hearing, however, it will make your task much more difficult.

These interactions between the perceptual systems for processing different sensory inputs sometimes makes it difficult to understand how separate the working memory systems are. Sometimes, it is a sight or a sound itself that is important to hold in working memory. For example, we may need to remember a particular color or a bird's song. For these examples we can maintain a pattern of neural activity that keeps that visual or auditory information specifically in working memory. There are other kinds of information, however, that are not tied to sight or sound. A location in space could be first identified either by seeing where something is, or by hearing a sound coming from that location. When we then try to hold that location in working memory, it does not matter whether we know that we need to remember that location because of something we saw or something we heard. We can remember the location without attaching it to the particular sight or sound. Thus, we have visual working memory, auditory working memory, somatosensory working memory, etc., but we also have working memory for information that we can derive from any of the senses. Each of these different types of information has its own, partly independent system in the brain to hold the information in working memory.

Working Memory Has a Very Limited Capacity

One way that working memory is very different from long-term memory is that working memory has a very limited capacity. We are able to add more and more things to long-term memory every day without it necessarily causing us to forget things we already knew. In contrast, we can only hold a few items in working memory at any one time. Researchers have been very interested in this limited capacity and have performed experiments to try to answer some specific questions about it. Exactly how limited is our working memory capacity? Why do some people seem to have a bigger capacity than others and is this related to other cognitive abilities? Why do we have a limited capacity?

The question of "What is the capacity of working memory?" has been more difficult to answer than one might think. Some early researchers, such as George Miller, talked about the "magic number 7," which seemed to be the limit on the number of items most people could hold in working memory. People with smaller capacities might only be able to remember 5 items, and people with larger capacities might be able to remember 9 items. Thus, you often will hear people talk about a capacity of 7 plus or minus 2. More recently, researchers tend to talk about the capacity as being closer to only 3 items. The difference between estimating a capacity of 3 items versus a capacity of 7 seems to be mostly due to how the capacity is measured. Different types of tasks have different demands that limit performance. Researchers who advocate a capacity of 3 items usually use tasks that present the sample stimuli to be remembered very quickly. The amount of time that the information needs to be remembered is also relatively brief, often only 1 s. Researchers who advocate a capacity closer to 7 items usually use tasks in which the person being tested is given a longer time to study the items to be remembered and then must remember the items for several seconds.

How Much Information Fits into Working Memory Depends on How You Measure It

The reason that researchers studying working memory capacity often use tasks in which the items to be remembered are presented only briefly is that they are trying to limit the influence of the central executive part of working memory. By limiting the influence of the central executive, these researchers believe they are getting a more pure measure of simple storage capacity. The storage part of working memory, without the central executive, is often called "short-term memory." Therefore, you will sometimes hear researchers talk about the capacity of short-term memory rather than the capacity of working memory. When the task allows for more time in the perceptual processing of the items to be stored in working memory, then people have the opportunity to manipulate that information into a representation that can enable better memory for more items. One way to do this is called "chunking." For example, a string of 7 numbers might be separated in memory into a group of 3 numbers and a group of 4 numbers. We might decide to remember all of the even numbers together in one group, and the odd numbers together in another group. Through the central executive processes of working memory, we are able to encode such relationships among the numbers into working memory and use those relationships to better remember the numbers. The better we are at recognizing and using relationships among the items to be remembered, the bigger our working memory capacity will appear.

Experience, training, and education can enhance this executive, manipulation ability. The more kinds of relationships you have in long-term memory, such as mathematical relationships between numbers, the better you will be at reorganizing seemingly random information into some other format that you can better remember. In contrast, if I flash a group of colored squares on the screen and then test you by flashing another group of colored squares 1 s later, you will not have a chance to manipulate those colors and their locations into something you might remember better, such as groups of squares that have similar colors. Short-term memory capacity measured in this way seems to not change very much with experience or education. Some researchers consider this to be a more direct measure of storage capacity. Others argue that it is more related to the speed of perceptual processing and to attention, rather than being a measure of working memory. You might find it useful to think of capacity as being like a bucket where memories can be held. If you are trying to fill a bucket with a hose and there is only so much water that can go through the hose at a time, and you only turn on the source of water for a short period of time, then not much water will get into the bucket. This is the case with images presented very quickly for a typical short-term memory task. If you leave the hose on for a while, then more water can make it into the bucket. Given more time and tools, perhaps you can transfer some of the water in the bucket into another bucket. This other bucket might not be able to get water directly from the hose, but if you have a sponge you could take some of the water from the first bucket and put it in the second bucket. Of course you can only do this if you have a second bucket and a sponge. The second bucket, the sponge, and the ability to use them, even figuring out that you could use them, these things are like the executive functions of working memory. You end up being able to hold more water, but it requires time, effort, skill, and knowledge.

The Capacity of Working Memory Will Seem Smaller If You Remember Things You Do Not Need Right Now

Another important aspect to understanding working memory capacity is the ability to only hold in working memory the information that is most important. If you fill up your bucket with rocks, it will not be able to hold much water. For long-term memory, this remembering of unimportant things does not necessarily impair your ability to remember important things. More long-term memories can be formed by the creation of new connections among the billions of neurons in the brain and perhaps even by the creation of new neurons. For working memory, there appears to be a limit to how much information can be effectively carried by sustained patterns of neural activity. Holding irrelevant information in working memory blurs, distorts, or overwrites the important information also being held in working memory. Unlike the structural changes that result in long-term memories, patterns of neural activity can change very quickly. They are fragile. New sensory inputs, or irrelevant thoughts or information recalled from long-term memory can disrupt these patterns of activity. Effortful attention is needed to protect the contents of working memory from these potential sources of irrelevant information. The first step, however, is selecting what is important and what is not for the current situation. To solve some problems, we need a bucket full of only rocks. To solve other problems, we may need a bucket full of only water. In order to make good use of the storage capacity of working memory, the central executive part of working memory has to decide which information is most important right now.

Why don't we just have a bigger working memory capacity? With long-term memory we usually consider forgetting to be a bad thing. We often think we would like to be able to store everything we have ever tried to learn in long-term memory. The purpose of working memory, however, is to solve new problems and guide behavior for the current situation. If you are holding too many things in your hands at one time, then you are not able to use any of them very well. Your ability to make the best decision for the current situation depends on your ability to keep in working memory only those things that are most important for the current situation. If you are holding both relevant and irrelevant information in working memory, then the irrelevant information may affect your behavior or your decisions.

The Prefrontal Cortex Has the Anatomy and Physiology Necessary for Working Memory

Neurons in the prefrontal cortex demonstrate patterns of neural activity that can be sustained for several seconds. Both local and long-distance circuitry appear to make this possible. As suggested independently by Patricia Goldman-Rakic and Joaquin Fuster in the 1980s, the prefrontal cortex contains a nested hierarchy of reverberating circuits, including mini-columns, columns, and hypercolumns. These local prefrontal circuits are then incorporated into larger networks across many different brain areas, which also include reciprocal interconnections.

The neural systems that enable working memory must strike a balance between flexibility and stability. As long as the information that is being maintained in working memory remains the most important for the current situation, the neural system should continue to keep those sustained patterns of activity strong and accurate. However, the environment is constantly changing. The brain must maintain information in working memory, but at the same time monitor the environment for new information. If the new information is more important than the maintained information, then the system must disrupt these reverberating, nested circuits to enable a new pattern of sustained activity to develop. This appears to be achieved by interactions between the prefrontal cortex and the basal ganglia via its associated subcortical (pallidum and thalamus) circuits. The basal ganglia have often been referred to as a gate for motor actions. They enable us to move our bodies in ways that we want while inhibiting movements of our body that we don't want. It appears that a similar mechanism gates information into working memory circuits, so that we remember only what we want and not irrelevant, distracting information. As long as the gate is closed, the information already in working memory will be protected from being overwritten. If the gate is not completely effective, then the patterns of neural activity may decay, become distorted, or be overwritten.

Oscillations in activity across large-scale networks of brain areas appears to further support working memory. These oscillations appear to either facilitate or impede communication between brain areas. Thus, changes in the coordination of oscillatory activity between the prefrontal cortex and other brain areas may be key to the central executive functions of working memory which update information or protect it from interference. These changes in oscillatory activity appear to require precise timing. Damage to the axons or their myelin coverings from aging, disease, or injury can slow these long-distance communications. This slowing and its effect on coordination of oscillatory activity may underlie working memory impairments in these conditions.

How do the basal ganglia and the prefrontal cortex know when to maintain information or update it? Working memory has to maintain not only the particular sights and sounds that are important for the current situation, but it also has to maintain the reasons that these sights and sounds are important right now. We hold in working memory the goals we are trying to accomplish and the rules and relationships in the environment that might help or hinder us from reaching those goals. This abstract information is critical to our judgments of what is important and our predictions about what will be important in the future. Scientists are only beginning to understand how the brain represents these kinds of information. It is not clear whether the neural mechanisms for maintaining this information in working memory are the same as those for maintaining information that is more closely related to sensory information, such as the visual features of objects and their locations in space.

Functional Organization of the Prefrontal Cortex Is Related to the Different Types of Information That Can Be Held in Working Memory

Prefrontal cortex receives inputs from nearly every other part of the brain. However, different parts of the prefrontal cortex receive different inputs. It has been shown in both monkeys and humans that the dorsal visual pathways through parietal cortex project mainly to dorsal-lateral prefrontal cortex. Similarly, the ventral visual pathways through temporal cortex project mainly to ventral-lateral prefrontal cortex. These inputs result in a dorsal-ventral functional organization within the prefrontal cortex. Dorsal-lateral prefrontal cortex is more involved in working memory for the spatial location of objects, while ventral-lateral prefrontal cortex is more involved in working memory for the identity of objects. Other areas in prefrontal cortex are preferentially involved in working memory for more abstract kinds of information such as rules, relationships, or expected future consequences based on knowledge about the environment. This information appears to depend on more anterior parts of prefrontal cortex and the most ventral part of the prefrontal cortex, known as orbital frontal cortex. Therefore, even though the prefrontal cortex gets inputs from all the different parts of the brain, those inputs have a specific organization. Similarly, although many cells in prefrontal cortex respond selectively to multiple aspects of the task, demonstrating much more integration and flexibility than sensory cortex, there is also a very consistent functional map from dorsal to ventral, and from posterior to anterior, within the prefrontal cortex.

Outlook

There is still much research that needs to be done to understand the neural basis of working memory. Much progress has been made in understanding the mechanisms underlying sustained patterns of neural activity that represent sensory-related information, such as the identities and locations of objects. The area that will be the focus of most future research will be in understanding the neural mechanisms underlying the "central executive" component of working memory. This will require understanding both how abstract information is represented in working memory, and the calculations and transformations that enable the manipulation and use of that information. Scientists are still trying to understand how groups of neurons can collectively enable us to simply see and recognize an object in the environment. A single neuron only carries a small amount of information by itself. For the brain to have information about the whole object, including whether we have ever seen that object before, or eaten it, or run away from it, information must somehow be combined across multiple neurons. This type of information representation is called a distributed population code. For central executive processes to be achieved, multiple distributed population codes must be integrated and create new, distributed population codes. This requires precision in the timing of dynamic interactions across large networks of brain areas. How the brain is able to do this, in a way that is both flexible and highly controlled, in the service of solving complex problems is currently a mystery. The tools of modern neuroscience applied with theoretically sophisticated behavioral paradigms, however, are rapidly revealing new insights.

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