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Working Memory Capacity: Limits on the Bandwidth of Cognition

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Abstract: Why can your brain store a lifetime of experiences but process only a few thoughts at once? In this article we discuss “cognitive capacity” (the number of items that can be held “in mind” simultaneously) and suggest that the limit is inherent to processing based on oscillatory brain rhythms, or “brain waves,” which may regulate neural communication. Neurons that “hum” together temporarily “wire” together, allowing the brain to form and re-form networks on the fly, which may explain a hallmark of intelligence and cognition: mental flexibility. But this comes at a cost; only a small number of thoughts can fit into each wave. This explains why you should never talk on a mobile phone when driving.

Working memory holds the contents of our thoughts. It acts as a mental sketchpad, providing a surface on which we can place transitory information to hold it “in mind.” We can then “think” by manipulating this information, such as by combining it with other items or transforming it into something new. For example, working memory allows us to remember phone numbers, do mental arithmetic, and plan errands.

Given its fundamental role in thought it is surprising that working memory has such a severely limited capacity: we can only hold a few thoughts in our consciousness at once. In other words, the surface area of our mental sketchpad is quite small. This limitation is obvious whenever we try to multitask, such as when we attempt to talk on the phone while writing an email, and it is why using our mobile phones while driving increases accident risk, even if we are using a hands-free set.

This stands in contrast to other mental abilities that are not limited, such as long-term memory storage. We can store (seemingly) a lifetime of experiences, but, for some reason, we can only consciously express these thoughts a few at a time. This limited capacity may be fundamentally responsible for the

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cognitive architecture of our brains: researchers believe it to be the reason we have evolved the ability to focus on one thing at a time (to “attend” to something). Despite being well studied, no one has yet confirmed why working memory is limited. In this essay, we will review some of what is known about working memory capacity and offer our theory of why consciousness may have this limit.

Though we may feel that we are able to perceive most of the world around us, this sensation is, in fact, an illusion constructed by our brains. In reality, we sense a very small part of the world at any point in time; we “sip” at the outside world through a straw. Our brain takes these small bits of data and pieces them together to present an impression of a coherent and holistic scene. Examples of this limitation are abundant: consider the puzzles in which you must identify ten differences between two similar pictures. The brain requires a surprisingly long time to accomplish this, despite the two pictures being side by side and the changes often being obvious, such as the total disappearance of a building or tree. This effect is often referred to as *change blindness* and is a regular occurrence of natural vision. (Another example of change blindness is the large number of editing mistakes we fail to notice in movies.)

The limited bandwidth of consciousness is also apparent in studies of working memory capacity. In these experiments, subjects briefly view a screen with a variable number of objects (such as colored squares) and then, after a delay of a few seconds in which they must hold the objects in memory, they are shown another screen of objects, one of which may be different from what was previously shown.¹ Subjects are then asked whether something has changed, and if so, to identify how it has changed (whether it used to be

a different color or shape). When the number of objects on-screen increases beyond a few items, subjects begin to make errors (by missing changes), indicating that their working memory capacity has been exceeded. Experiments such as this have revealed that the average adult human can only process and retain four or five objects at a time (similar to the average monkey, as shown below).² The exact capacity of the brain varies by individual; some can remember only one or two items and others can remember up to seven.³ Interestingly, an individual’s capacity is highly correlated with measures of fluid intelligence, suggesting that individual capacity limits may be a fundamental restriction on high-level cognition.⁴ This seems intuitive: if you can hold more information in mind at the same time, then more ideas can be combined at once into sophisticated thought.

But what is the nature of the capacity limitation? Do we simply miss new items once we have filled our thoughts with four or five? Or do we always try to take in as much information as possible, eventually spreading ourselves too thin when there are more than four or five objects present? In fact, both may be true.

Models of a strict limit on the number of items you can hold in mind posit that this is because working memory has a limited number of discrete “slots,” each of which can independently hold information. And once you fill those slots, you can no longer store any new information. In contrast, other models predict that our limited capacity is due to our spreading ourselves too thin. They suggest that working memory is a flexible resource, a neural pool that can be subdivided among objects. You do not stop storing new information after you reach a fixed capacity as in the slot model; rather, as new information is received, the resource pool is continually divided until the information is spread so thin that it can no longer be ac-

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curately recalled (and therefore cannot support behavior). Much evidence has been marshaled on behalf of both models, primarily from studies of the patterns of errors humans make on tests of cognitive capacity. Recently, we examined the neurophysiological mechanisms underlying capacity limits in monkeys. We found an intriguing possibility: both the slot and flexible-resource models are correct, albeit for different reasons.

The advantages of animal work include tighter control over gaze as well as more precise measurements of neural activity than is possible with human subjects. These advantages allowed us to dig deeper into the phenomenon and led to a surprising discovery. The monkeys, like humans, had an overall capacity of four objects. But the monkeys' overall capacity was actually composed of two separate capacities of two objects each in the right and left visual hemifields (to the right and left of the center of gaze) that were *independent* of each other. The processing of objects on the right half of gaze is unaffected by objects in the left half of gaze, regardless of how many objects there were on the left (and vice versa). But adding even one object on the same side of gaze as another object resulted in a decrement in performance. It was as if the monkeys had two separate brains, each one assigned to the right or left half of vision. This right/left independence was surprising, though research focusing on a different type of task might have predicted it: humans have independent capacities to track moving objects in the right and left visual hemifields.⁵

This phenomenon is likely related to the fact that the right and left visual hemifields are respectively processed by the left and right cerebral hemispheres. This suggests that the two cerebral hemispheres can operate somewhat independently, at least for the processing required for visual infor-

mation to reach awareness. Indeed, the apparent split between the two hemispheres recalls some of the initial observations of humans who had their cerebral hemispheres split to control epilepsy. Without careful testing, these subjects usually appeared normal. Thus, there may be something of a split even in the intact brain: the two visual hemifields/cerebral hemispheres act like two independent slots for processing and holding visual information. At first blush, this seems to support the slot model, with slots for both the left and right fields of vision. But we also found evidence to support the flexible-resource model *within* each visual hemifield: on each side of visual space, information was shared and spread among objects. To show this, we looked more closely at how neurons encoded the contents of working memory.

A pure slot model predicts that encoding an object is all-or-none: if the brain successfully remembers an object, there should be an equal amount of information about it regardless of how many other objects are in the array. But we found that even when a given object was successfully encoded and retained, neural information about that specific object was reduced when another object was added to the same visual hemifield, as if a limited amount of neural information was spread between the objects. The slot model also predicts that if a subject misses an object, no information about it should be recorded in the brain; either an object fills a slot, and is remembered, or not. By contrast, the flexible-resource model suggests that even when a subject misses an object, some information about the object could have been recorded in the brain, just not enough to support conscious perception and memory. This latter prediction is exactly what we found: even when a subject did not consciously perceive the object, the brain still recorded a significant, albeit reduced, amount of information.

In sum, the two cerebral hemispheres (visual hemifields) act like discrete resource slots; within them, neural information is divided among objects in a graded fashion. A number of recent studies in humans support such a hybrid model, finding that there are multiple slots that can store graded information about objects.⁶ Thus, capacity limits may reflect interplay or blend between different types of underlying constraints on neural processing. On the one hand, neural processing on the right and left halves of visual space can be slot-like, akin to buckets that can hold a maximum volume of water (information). But, on the other hand, within each cerebral hemisphere there is no limit to the number of objects (thoughts) in each bucket. The limitation is inherent to the information, not the number of objects: if there are too many items in the bucket, only a few can get wet enough (have enough information devoted to them) to reach consciousness. The rest may get a little damp, but it is not enough to act upon.

Whether or not the two cerebral hemispheres have independent capacities for information other than vision remains to be determined. It may prove only to be a visual phenomenon, due to the fact that the right and left of gaze are primarily processed in the left and right cerebral hemispheres, respectively. But even if this independence is limited to vision, it has clear practical implications. For example, taking into account the separate capacities of the right and left of gaze can help in the design of heads-up displays, such as on automobile windshields, maximizing the amount of information that drivers can glean in each glance, or providing information without overloading their capacity to fully process important visual scenes, such as the road in front of them.

So far we have seen that despite our impression that we can store and perceive a significant amount of visual information

at once, this is not the case. We can only simultaneously think about a very limited amount of information. Our brains knit together these sips of information to give us the illusion that we have a much larger functional bandwidth. (Again, this is something to keep in mind the next time you are driving and have an urge to reach for your mobile phone.) But this still does not explain why there is a capacity limit for conscious thought. What about the brain's functioning dictates such a small bandwidth?

Why can't you hold one thousand thoughts in mind simultaneously, or even just one hundred? There is mounting evidence that the brain uses oscillatory rhythms (brain waves) for communication, especially for processes underlying high-level cognition. The theory is that the brain forms networks by synchronizing oscillations (rhythmic or repetitive neural activity) of the neurons that make up that network. Neurons that "hum" together form networks, and because only so much information can fit into each oscillatory cycle, any communication system based on an oscillating signal will naturally have a limitation on bandwidth. But before delving into the content limits of an oscillatory cycle, what is the evidence supporting a role for oscillatory activity in brain function to begin with?

It has long been known that the brain has large populations of neurons that oscillate in synchrony. These so-called brain waves occur across a wide range of frequencies from very low (less than once a second, or < 1 Hz) to very high (almost once every 15 ms, or > 60 Hz). Brain waves are not random: they vary with mental state. For example, when you are relaxed, your brain tends to show lower frequency waves; but if you suddenly focus on a task, brain regions that are needed to perform that task begin to produce higher frequency waves.

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Despite the evidence that brain waves are important for behavior, their exact role in brain function has long been a mystery. Beginning with the pioneering work of physicist and neurobiologist Christoph von der Malsburg, neurophysiologist Wolf Singer, and their colleagues, there has been increasing awareness that synchronizing the oscillations between neurons may be critical in forming functional networks.

Synchronized oscillations are useful for increasing the impact of neural impulses (“spikes,” or sharp changes in voltage that neurons use when they signal one another). Spikes from two neurons that arrive simultaneously at a third neuron downstream have a greater impact than if the impulses arrived at different times.⁷ Given this, it is easy to imagine how such a mechanism could be useful to focus mental effort on particular representations (when we pay attention). After all, if synchronizing the rhythms of neurons increases the impact of their spikes, then one way to boost the neural signals associated with an attended object would be to increase synchrony between neurons representing it.

There is growing evidence that this is exactly how attention works. Increased attentional focus increases oscillatory synchrony between the visual cortical neurons that represent the attended stimulus. For example, visual cortical neurons that process a stimulus under attentional focus show increased synchronized gamma band (30 – 90 Hz) oscillations.⁸ This higher frequency (> 30 Hz) synchrony may result from interactions within local cortical circuits,⁹ the same interactions that underlie the computations of stimulus features.¹⁰ By contrast, sensory cortical neurons representing an unattended stimulus show increased low frequency (< 17 Hz) synchronization. A variety of evidence suggests that low frequencies may help deselect or inhibit the corresponding ensembles (populations of neurons that together underlie

a particular thought, perception, memory, or neural computation), perhaps by disrupting the higher frequency.¹¹

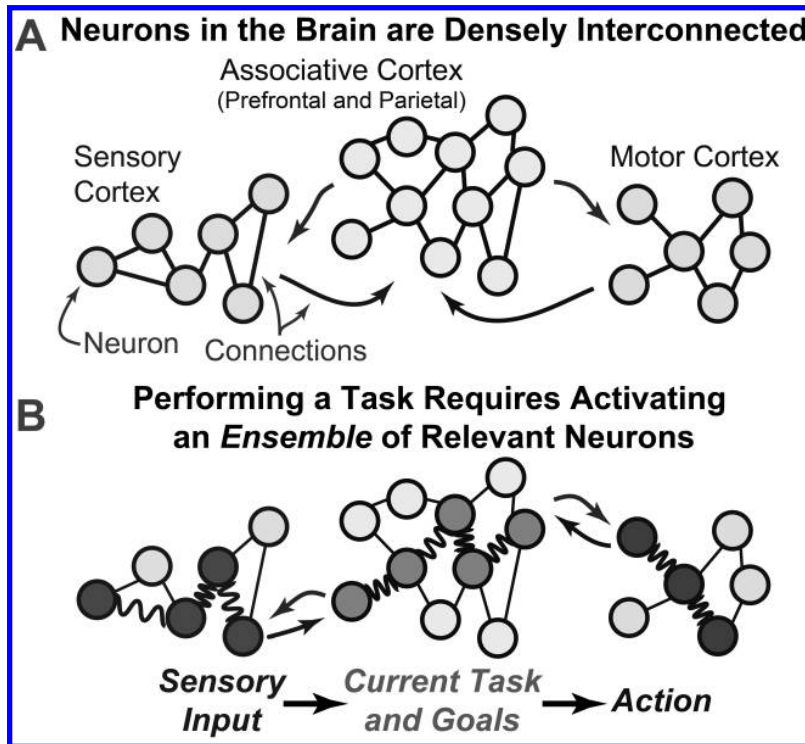
On a broader scale, synchrony between regions may also regulate communication across brain areas.¹² In short, if two different networks in different brain areas oscillate *in phase* (a particular moment with a neural oscillation, such as a specific “piece” of a brain wave) they are more likely to influence one another because both are in an excited and receptive state at the same time. Conversely, if they are *out of phase*, information will be transmitted poorly. This is supported by observations that interareal oscillatory coherence within and between “cognitive” regions and sensory areas has been found to increase with attention.¹³ In other words, if two brain areas are involved in a given cognitive function (such as visual attention), they increase their synchrony during that function.

We have discussed how synchronized rhythms can change the flow of information between neurons and between brain regions. Recent work has begun to suggest that synchrony may not only control communication between networks, it may actually form the networks themselves. The classic model suggests that if neurons are anatomically connected, then they are part of the same network; but it may be that anatomy dictates which neurons are *capable* of forming networks. The actual formation of the networks may instead come through synchrony (Figure 1). In other words, anatomy is like a system of roads; synchrony is the traffic. Importantly, dynamic formation of ensembles by oscillatory synchrony may underlie cognitive flexibility: our ability to rapidly change thoughts and behavior from one moment to the next.

Consider, for example, what is widely assumed to be the basic element of a thought: a group of neurons that are ac-

Figure 1
Synchronous Oscillations Create Neural Ensembles

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(A) The human brain consists of almost one hundred billion neurons that form a dense network of connections. This network of neurons and their trillions of connections encapsulate all possible behaviors (and their associated sensations, thoughts, and actions). (B) In order to execute a particular behavior, synchrony activates only those neurons and connections relevant to the current task. Source: Figure prepared by authors.

tive together. Such an ensemble can form a perception, memory, or idea. But how does the brain form a particular neural ensemble for a specific thought? This is not straightforward; there are billions of neurons linked to each other through trillions of connections. This is further complicated because neurons have multiple functions, particularly at “higher,” more cognitive levels of the brain.¹⁴ Thus, many neurons inhabit many different ensembles and, conversely, ensembles for different thoughts share some of the same neurons. If anatomy were all there were to forming ensembles, then attempting to activate

one ensemble would result in activity that extended to other ensembles, and subsequently a jumble of thoughts.

We propose that the role of synchrony is to dynamically “carve” an ensemble from a greater heterogeneous population of neurons¹⁵ by reinforcing mutual activation between the neurons that form the ensemble.¹⁶ Because ensemble membership would depend on which neurons are oscillating in synchrony at a given moment, ensembles could flexibly form, break-apart, and re-form *without changing their anatomical structure*. In other words, formation of ensembles by rhythmic synchrony endows

thought with flexibility, a hallmark of higher cognition. Humans can quickly adapt and change their thoughts and behaviors in order to tailor them to the constantly changing demands of our complex world. Thus, networks have to be assembled, deconstructed, and reconfigured from moment to moment as our foci, plans, and goals change. This is not meant to downplay the role of neural plasticity in changing the weights of connections between neurons and in forming new anatomical connections; it is always important to build and maintain roads.

Through a study in which we trained monkeys to switch back and forth between two tasks, we recently found evidence that synchronized oscillations can provide the substrate for dynamic formation of ensembles. As the monkeys switched tasks, different sets of neurons in the prefrontal cortex showed synchronous oscillations – one for each task – in the beta band (about 25 Hz) synchrony, as if the neurons were switching from one network to the other.¹⁷ Importantly, many of the neurons were multifunctional, synchronizing their activity to one ensemble or the other depending on the task at hand. This supports the idea that synchrony can dynamically form (and disassemble) ensembles from anatomical networks of neurons that participate in multiple ensembles.

Interestingly, one of the two tasks was much easier for the monkeys to perform; and when the monkeys prepared to engage in the harder task, the neurons that formed the network for the *easier* task showed synchrony in a low-frequency alpha range (about 10 Hz). Alpha waves have been associated with suppression or inattention to a stimulus¹⁸ and are therefore thought to inhibit irrelevant processes.¹⁹ In our experiment, alpha oscillation inhibition seemed to be acting to quiet the dominant network (the one needed for the easier task), which would have interfered with

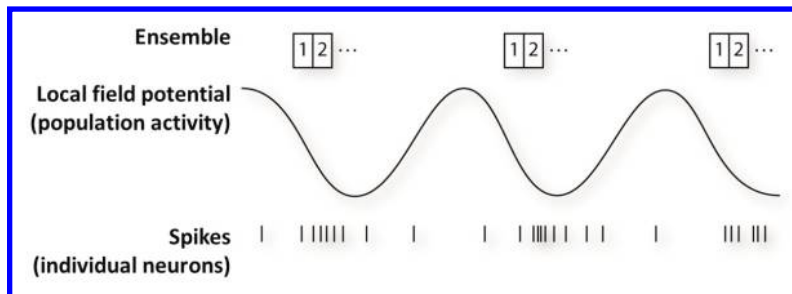
the network needed for the current, more challenging task. This suggests that synchronous oscillations helped control the formation of ensembles.²⁰ Higher (beta) frequencies defined the two task networks while lower (alpha) frequencies were used to somehow disrupt formation of the stronger network (and thus prevent an erroneous reflexive reaction) when the weaker network had to be used.

If synchronized rhythms form neural ensembles, it follows to wonder how it is that the brain can form more than one ensemble at a time. After all, would not two rhythmically defined ensembles inadvertently synchronize to each other, merging together and distorting the information they represent? In response, some researchers have proposed that the brain forms more than one ensemble at a time by oscillating different ensembles slightly out of phase with one another.

According to this theory, neurons that are part of a specific ensemble do not only synchronize their activity, but they do so by aligning their spikes to specific phases of neuronal population oscillations.²¹ By separating thoughts into different phases of population oscillations, our brain can hold multiple thoughts in mind simultaneously (Figure 2).²² In other words, the brain prevents ensembles from interfering with one another by juggling them, rhythmically activating each in turn (out of phase from each other). We recently reported evidence for this multiplexing when information is held in mind.²³ When monkeys hold multiple objects in working memory, prefrontal neurons encode information about each object at different phases of an ongoing (~ 32 Hz) oscillation. Significantly, there were bumps of information at different phases, yet in all phases the neurons still carried at least some information, supporting a hybrid slot/flexible-resource model. The bumps of information are

Figure 2
Phase Coding

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This figure illustrates oscillatory phase-coding. Neural ensembles of the two simultaneous thoughts (thoughts 1 and 2) oscillate at similar frequencies but different phases of the oscillation. In other words, the ensembles line up on different parts of the brain wave. This may explain the severely limited capacity of consciousness; in this model, only a few thoughts can fit in each wave. Source: Earl K. Miller and Timothy J. Buschman, "Brain Rhythms for Cognition and Consciousness," in *Neurosciences and the Human Person: New Perspectives on Human Activities*, ed. Antonio M. Battro, Stanislas Dehaene, and Wolf Joachim Singer (Vatican City: Pontifical Academy of Sciences, Scripta Varia 121, 2013).

somewhat slot-like in the sense that they are specific to certain phases of the oscillation; but they are not strict slots because the bump is a relative increase over information in other phases. The effect was *not* all-or-none, information-here-but-not-there, as is predicted by a strict slot model.

This finally leads us to an explanation for the severe limitation of conscious thought. Phase-based coding has an inherent capacity limitation. You have to fit all the

information needed for conscious thought within an oscillatory cycle. Consciousness may thus be a mental juggling act, and only a few balls can be juggled at once. Crucial tests of this hypothesis still need to be conducted, but these findings and theories collectively suggest that bringing thoughts to consciousness may depend on generation of oscillatory rhythms and the precise temporal relationships between them and the spiking of individual neurons.

ENDNOTES

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