Aegean Cyclades—in the Bronze Age (*15*).

How and why human cultural transmission differs from that documented in other species is a fundamental question. As the only discipline with the temporal scope to investigate patterns and processes of cultural transmission from the first hominins to the modern day, archaeology is well placed to integrate the insights of the many disparate disciplines whose work informs on the question. We must learn to tack between the large scales of cultural transmission and the small scale of social relations to gain the best possible understanding of cultural transmission past and present.

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NEUROSCIENCE

A Quiescent Working Memory

Many of our actions or decisions are guided by what we experienced in the recent past.

Stefano Fusi

When we perform a complex task like driving a car, we need to retain important information that will affect our behavior later on. For example, when we see a yield traffic sign, the image is not merely stored in our memory, but it is also "actively" held in mind so that we can react appropriately at the next crossroad. In such a case, we make use of what is known as "working memory" (*1*). It is widely believed that this type of memory is maintained by the persistent activity of a population of neurons. On page 1543 in this issue, Mongillo *et al*. (*2*) propose instead that the memory is stored in the efficacies of connections (synapses) among these neurons. This type of memory can be easily and rapidly reactivated after a period of neuronal quiescence.

Most previous models of working memory were inspired by experiments in which nonhuman primates were trained to hold in mind the identity or location of a sensory stimulus for a few seconds. During these periods of memory retention, sustained neuronal activity was observed in regions of the brain including the prefrontal cortex (*3*) and parietal cortex (*4*). The recorded activity was specific to the identity of a previously shown stimulus, suggesting that the memory of a stimulus might be stored in the pattern of persistent activity.

The mechanism for sustaining such neural activity likely involves the collective behavior of a large number of interacting cells. Circuits of cortical neurons can be forged that sustain activity reverberations for times that greatly exceed the inherent time constant of every cell in the circuit (*5*, *6*). Neurons generate strong electrical impulses (spikes) when they receive enough excitatory inputs from other connected neurons. These spikes cause a release of neurotransmitter molecules at the synaptic connections with other neurons, which triggers an electrical impulse in the postsynaptic cells. Neurons can excite each other so that each spike in one neuron causes an increasing number of other neurons to generate spikes, even in the absence of external stimulation. This growth of activity in a population of strongly interacting neurons increases until some regulatory mechanism stabilizes a constant average neuronal activity. In cortical neuronal circuits, coupling among neurons can be chosen so that there are several possible patterns of persistent activity (*7*), each corresponding to a different memory. An external stimulus simply "selects" one of the memories by activating the corresponding pattern of persistent activity.

Mongillo *et al*. propose a new neural mechanism of working memory that is based on plasticity in synaptic connections rather than persistent neural activity. Thus, a memory resides in the pattern of synaptic strengths, and can be temporarily modified by a sensory stimulus to be remembered. Synaptic strengths are continuously modulated by spikes emitted by the presynaptic neurons (*8*). At each synapse, small-molecule neurotransmitters are released by the presynaptic neuron, and stimulate receptors on the postsynaptic neuron. Each presynaptic spike not only depletes the neurotransmitter supply, but also increases the concentration of intracellular calcium. This, in turn, increases the amount of available neurotransmitters that can be released by the next presynaptic spike. Neurotransmitter depletion depresses synaptic strength until the resources are restored. However, the increased calcium concentration facilitates synaptic transmission and potentiates, temporarily, the synapse.

As with persistent activity, several possible memories are stored in the initial pattern of synaptic strengths, and a sensory stimulus selects a memory by activating one of the strongly interacting populations of neurons. The synaptic connections within this population are modulated by short-term depression and facilitation. After the stimulus is removed, total synaptic resources decrease due to depression, but the average fraction of resources used by each spike increases due to facilitation. The parameters can be chosen so that the net effect on the population activity is small, to the point that the spike activity is indistinguishable from the spontaneous activity preceding the stimulation. However, injection of a noisy current—such as when a memory recall signal is generated by another brain region—into a randomly selected subset of neurons is sufficient to reactivate the neuronal population that was previously stimulated. This indicates that memory of the sensory stimulus is still present. Indeed, any increase in neural activity facilitates all synapses. Those synapses originating from previously stimulated neurons are already

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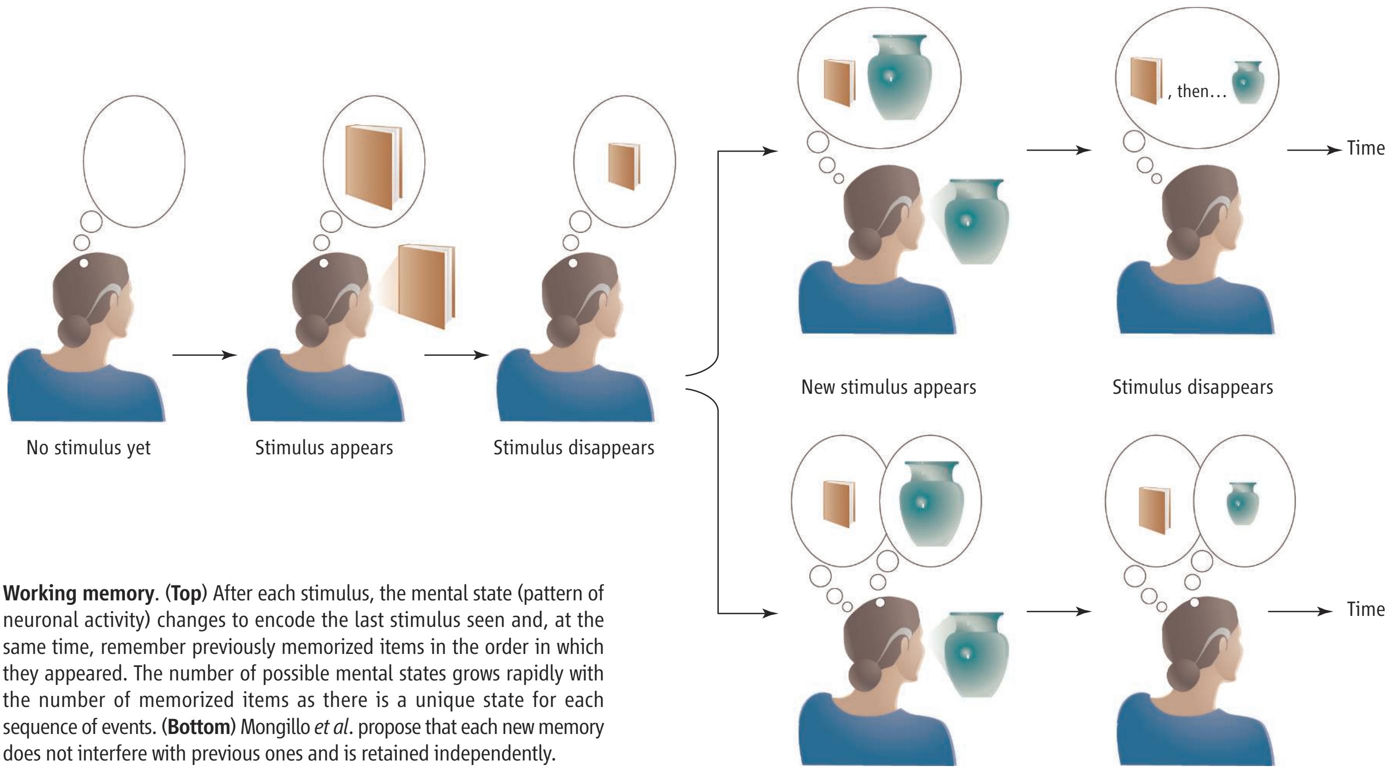

Working memory. (**Top**) After each stimulus, the mental state (pattern of neuronal activity) changes to encode the last stimulus seen and, at the same time, remember previously memorized items in the order in which they appeared. The number of possible mental states grows rapidly with the number of memorized items as there is a unique state for each sequence of events. (**Bottom**) Mongillo *et al.* propose that each new memory does not interfere with previous ones and is retained independently.

facilitated, and are strengthened even further. Eventually, each spike will activate an increasing number of neurons, leading to the activation of all cells of the previously stimulated population. After generating a spike, the neurons are quiet until the synapses recover from depression, and then a new "avalanche" will start. This oscillatory behavior will continue as long as the net synaptic efficacy remains above some critical level. Depending on the parameters of the input, the interplay between facilitation and depression can either sustain an oscillatory behavior, or a state of asynchronous enhanced activity.

This mechanism of Mongillo *et al.* has lower metabolic costs than persistent neural activity because it does not require the generation of spikes to retain memories. Moreover, it has two highly desirable features that complement those of the more traditional models of working memory. The first is that the memories are stored in the synaptic state and not in neural activity. This makes these memories quiescent until an external signal reactivates or refreshes them. During the silent period, the neural circuit responsible for holding the memory is decoupled from other brain areas because no spike is emitted, whereas any sustained activity would signal the participation of the cortical circuit in a larger network. Such a decoupling might play an important role in modular brain systems, in which different modules encode stimuli coming from different sensory modalities. For example, cortical circuits located in different modules could independently store the memory of a large number of stimuli without interfering with other mental processes. These memories would be dynamically gated (*9*). When the memories are quiescent, the gate is closed, and information about the sensory stimuli is not communicated to other brain areas. When the memories are reactivated, the gate is open, and other neural circuits can rapidly acquire information contained in the stored memories. Gate opening might happen, for example, when attention is directed to a particular sensory modality, as in the case when you are reading a text (visual modality), and somebody asks whether the phone in the next room was ringing a few seconds ago (auditory modality).

The second attractive feature of the proposed model is the ability to memorize multiple items within the same neural circuit without requiring a reverberating stable state of neuronal activity for each combination of memory items. Earlier models require a number of reverberating activity states that grow exponentially with the number of memorized items (see the figure). Although building such a system is possible when the number of items is not too large, the mechanism proposed by Mongillo *et al.* is easier to implement. Indeed, in their case, because memories are stored in the synaptic states, a strong interaction between different neurons is not required until the memories are retrieved. This allows us to hold in mind the identity of multiple stimuli that appear at different times without relying on a complex pattern of synaptic connections. Such a mechanism also permits us to retain memories in the face of distraction, as when having to remember one visual stimulus embedded in a long series of irrelevant distractors.

There may, nevertheless, be situations requiring a large number of stable states of reverberating activity—for example, complex tasks in which it is necessary to remember both the events and the temporal order in which they occur. In such a case, the interaction between different memories would play a fundamental role and a different mechanism might be required.

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