the northeast end of the lake and had risen 38.6 inches since the time it last spilled on 1 November. Checking records from previous years, we observe that when the lake spills in June, its reported rise is always equal to the annual rainfall of Lyon County. Although some winter storms that bring precipitation to the Tahoe area move on to Lyon County, there clearly must be something else at work. Indeed, in this fictitious story, we discover that there is a local law that during the summer months the dam must be lowered to keep the Truckee River flowing from Tahoe to Lyon County. On 1 November, the spillway is to be raised because the winter rains will keep the river flowing. Then on 1 June, the spillway is to be lowered to a height above its 1 November level equal to the annual rainfall recorded in Lyon County. Thus, it is not a coincidence but a law that locks the rise of Lake Tahoe to the rainfall in Lyon County.

Similarly, although the polarization created by the conduction electrons and the response of the ionic lattice contribute to determining both the Kohn anomaly and the pair binding energy, there must be something else at work that locks $2\Delta(0)$ to $\hbar\omega_{KA}$. As noted, this could mean that there is some new physics that is not captured by the Eliashberg formulation (*3*). Aynajian *et al.* raise the possibility that charge density or spin density correlations may limit the growth of the superconducting energy gap and lead to the observed convergence of $2\Delta(0)$ and $\hbar\omega_{KA}$.

Alternatively, I believe that the Eliashberg theory contains an explanation for the experimental findings, provided that one takes into account the change of the pairing interaction that occurs in the superconducting state. Suppose the Kohn anomaly is associated with the scattering process illustrated in the right panel of the figure. Then, at energies greater than $\hbar\omega_{q*}$, there will be a sudden increase in the coupling of electrons to the transverse acoustic mode because **K** is parallel to the polarization (*5*, *6*). Then in the superconducting state, if $2\Delta(0)$ is close in energy to $\hbar\omega_{q*}$ it may lock on to it. That is, for $2\Delta(0) < \hbar\omega_{q*}$, the change in the electron polarization caused by the superconducting gap will push phonon spectral weight above $\hbar\omega_{q*}$, where it can couple via an *umklapp* scattering process (from the German word for "flip over") shown in the right panel. This will lead to an increase in $2\Delta(0)$. Alternatively, if $2\Delta(0)$ increases above $\hbar\omega_{q*}$, the electron polarization will push phonon spectral weight below $\hbar\omega_{q*}$, where it will not couple, causing a decrease in $2\Delta(0)$.

Although this locking can only occur if $\hbar\omega_{KA}$ is reasonably close to the value $2\Delta(0)$ would have had in the absence of Kohn anomalies, it is not a complete accident. Furthermore, it can be understood within the traditional theory of superconductivity. It appears from the electron tunneling data that an *umklapp* Kohn anomaly in the transverse phonon is indeed present in Pb (*5*, *6*). One needs to see whether a similar feature can be observed in the Nb tunneling spectrum. A further test would be a careful measurement of the size of the superconducting gap on different parts of the Fermi surface. One only needs the "locking" on the Fermi surface regions associated with the *umklapp* Kohn anomaly.

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ARCHAEOLOGY

Standing on the Shoulders of Giants

Fiona Coward

Archaeological studies are helping to understand how humans acquired the ability for cultural transmission.

How and why did humans learn to learn? A variety of disciplines have recently provided important insights into the basic mechanisms that underpin cultural transmission. Archaeology is now beginning to place these insights in a chronological framework that will help to understand when and why these mechanisms evolved among our ancestors.

The extent to which human behaviors and knowledge are culturally transmitted within and between generations has long been considered a defining feature of our species. Parts of the behavioral repertoires of many other animals—from ants to dolphins—are neither determined by genetics nor individually acquired but learned from members of the same species. For example, the manufacture and/or use of material objects among some of our closest primate relatives are group-specific and persist between generations (*1*, *2*). However, the diversity and complexity of learned behaviors among humans by far outstrip anything known in other species; in addition, human culture is cumulative in a way that other species' socially learned repertoires are not (*3*, *4*).

A basic capacity for motor imitation—the mirror neuron system, which automatically maps the observed actions of others onto one's own motor system—is part of our primate heritage (*5*). But, although other species may learn behaviors and even act in such a way as to facilitate their offspring's learning, only humans are known to teach, which involves actively correcting learners (*4*, *6*). Furthermore, although primates are capable of complex interactions

Bead making at Makuri Village, Namibia.

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Learning traditional Micronesian navigation skills.

with one another or with objects, they do not seem to engage in relations with objects and with other individuals at the same time (*6*). The suggestion is that the human mirror neuron system may allow us to go beyond imitating the observed motor acts of others to infer their intentions and perhaps even their states of mind (*5*)—perhaps the prerequisite for true imitation and cumulative cultural transmission.

However, neither humans nor primates are born fully fledged imitators or mind readers; the necessary cognitive and motor systems take time to mature. The fossil record documents an extension of the hominin developmental period relative to that of primates: Estimates of brain size at birth, coupled with analysis of the relative development of teeth and bones of juveniles, demonstrate the birth of less-developed infants and longer, slower growth of both brains and bodies (*7*). Stone tools appear in the archaeological record from at least 2.5 million years ago (*8*), roughly at the same time as the earliest known specimens of Homo, documenting sufficient social and technical skills for the habitual targeting of higher-quality foods requiring more processing to extract, such as meat. This dietary shift in turn made it easier to provide for the longer developmental period, which required the involvement of more than one adult—an indication of more complex and longer-lasting social relationships.

This expanded period of development and maturation of the brain thus occurred in increasingly rich social and cultural environments, with longer-lived social relations facilitating the transmission of more and more complex cultural skills (*4*)—many craft skills practiced by modern humans take several years of intensive teaching to master, often in childhood (see the first photo). Neuroimaging studies of the acquisition of toolmaking skills (*9*) and modeling of early hominin social systems based on those of extant primates (*10*) are fleshing out our understanding of the basic cognitive mechanisms for motor imitation, learning, and sociality. Their social and cultural flexibility allowed hominins to colonize new and unfamiliar ecosystems and to develop the bewildering diversity of cultural traits visible today and in the archaeological record as they spread across the globe.

Archaeology can add to the debate by investigating specific patterns of cultural transmission among and between prehistoric populations. The patterns formed by the geographic and temporal distribution of material culture in the archaeological record results from the dissemination of the relevant behaviors between individuals. Thus, the process can be modeled (much as epidemiologists model the transmission of disease) to investigate the social and cultural factors that influence how learned skills spread into population-wide distributions (*3*). Application of such models to the archaeological record has provided insights into such puzzles as the loss of various technologies in Holocene Tasmania, including the manufacture of composite tools and of cold-weather clothing. Rising sea levels cut the island off from the Australian mainland in the early Holocene, resulting in a sharp drop in effective population size that reduced the pool of social learners, resulting in these cultural losses (*11*).

Furthermore, because cultural transmission occurs vertically, from parents to children (*12*), dual inheritance theory considers cultural transmission as analogous to—but distinct from—genetic transmission (*3*). The use of methodologies better known for dealing with genetic data, such as cladistics and phylogenetic analysis, is beginning to yield valuable information on the rates, timings, and directions of such processes as the colonization of the Pacific Islands, the spread of agriculture across Europe from its Near eastern origins, and the changing compositions of pottery assemblages in the later stone age (*13*).

However, cultural transmission is always first and foremost social transmission, firmly embedded in networks of social relations between individuals. Thus, large-scale models can be enhanced by considering the small-scale processes revealed by ethnography. For example, among Micronesian sailors, the traditional skills of navigation are passed down between generations, often from father to son. From a very young age, children are immersed in discussion of canoes and navigation, and from the age of perhaps five upwards, teaching becomes more explicit. Knowledge is acquired through rote learning, the rehearsal of drills, chants, and stories, and the construction of "star charts" and "stick maps" that transmit the details of voyages covering more than 1400 miles of ocean (see the second photo). But this data is only part of the package; over more than 10 years, children are educated into a practical, physical understanding of how to use stars, ocean swells, currents, and wildlife in the actual performance of navigation (*14*).

In this case, the "maps" are deliberately designed to be ephemeral and thus leave no trace in the archaeological record. Nevertheless, the social expertise and relationships that underpin the transmission of navigational skills are fundamental to the negotiation and maintenance of wider social networks. These networks connect islands through practices such as gifting, trade, and exchange, leaving material traces that could be found in the archaeological record. Thus, the entanglement of cultural transmission with social relationships creates the patterns visible in the archaeological record. The adoption of social network models to investigate their interrelations is therefore an exciting new development in archaeology that has been used to model interactions of another island group—the

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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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