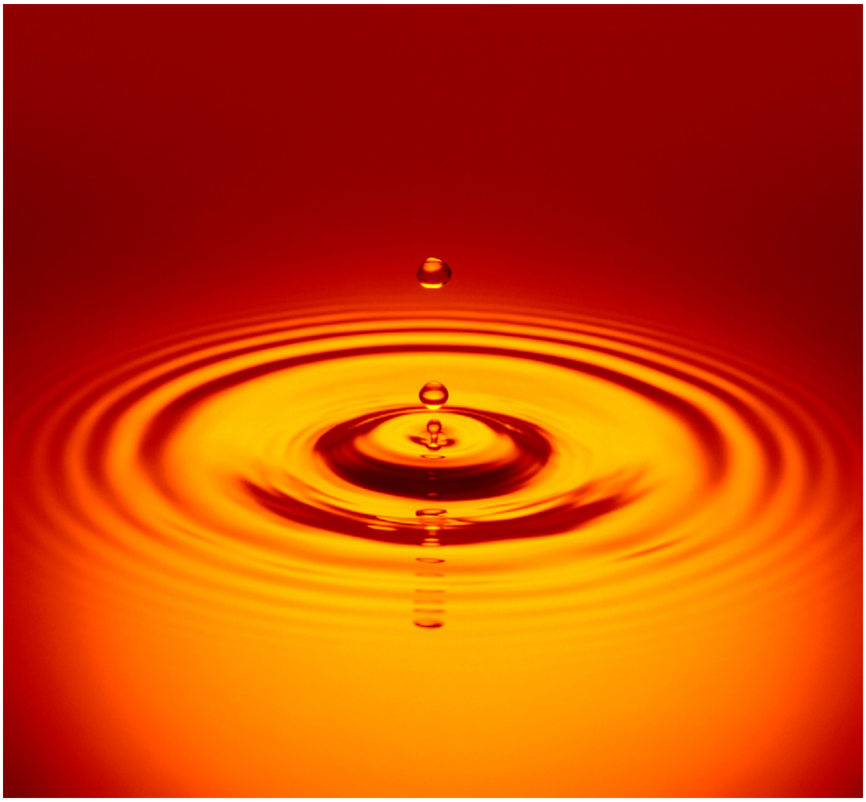

Ripple effect: Short bursts of electrical impulses known as sharp-wave ripples may, according to one hypothesis, be the key to the function of the hippocampus in consolidating memories.

a procedure to have memories associated with ex-lovers erased, but there are very real medical applications in treatment of trauma disorders that could benefit from such options. However, the misuse potential is considerable and should also be taken into account.

Another conceivable manipulation of memory is the production of false associations. In a recent paper, the group of Susumu Tonegawa at MIT used optogenetic methods based on channelrhodopsin labelling (Curr. Biol. (2011) *21*, R831–R833) to create a fear conditioning in mice that was not based on real events experienced by the animals (Science (2013) *341*, 387–389). Specifically, the researchers targeted either the dentate gyrus (DG) or the CA1 region of the hippocampus, labelled the neurons active in one situation (context A) and then optically re-activated them during a fear-conditioning experiment in a different situation (context B). When they were exposed to context A again, the animals had a fear reaction, i.e. freezing behaviour, even though this context was never associated with the feared stimulus. Remarkably, this manipulation succeeded when it was applied to the DG, but not in the CA1 region. At this stage, it is unclear why the CA1 did not produce a false association.

All this exciting research hasn't been much use for H.M., who has helped science much more than science could ever help him. Since his death in 2008, Molaison has continued to make valuable contributions to neuroscience. A unique neuroanatomical project chaired by Jacopo Annese at the Brain Observatory, University of California at San Diego, investigates slices of his brain in great detail with a view of establishing precisely which anatomical changes were producing his symptoms. Ironically, although H.M. couldn't remember a single thing that happened after 1953, his memory will stay with us for many years.

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Essay

Cultural memory

Humans have a form of externalised memory. They are able to transmit information across generations in the form of learned cultural traditions and preserve this knowledge in artefacts. How this capability evolved from the simpler traditions of other animals is an active area of research.

Kevin N. Laland* and Luke Rendell

Memory is a wonderful resource that allows individual animals to walk around with a store of relevant past experience in their brains. We not only remember those childhood games, or past events like our wedding or a sporting success, but we also file away legions of prosaic practical advice — how to drive, how to cook, how to work the TV remote — which we draw on when needed. There are other kinds of memory too. For instance, natural selection creates a genetic memory of organismal characters that proved successful in promoting survival and reproduction in ancestral environments. Likewise, human societies today benefit from extraordinary cultural memories — vast domains of information far beyond the capacity of a single human brain, banked in an array of different stores (Figure 1), from artefacts and constructed environments, through to libraries and the World Wide Web. Our very success as a species is undoubtedly in part attributable to our uniquely huge distributed memory store of cultural knowledge.

While cultural inheritance has long been recognized as important to human biology, recent research reveals that the social transmission of learned knowledge is widespread in animals, not just in vertebrates, but also in invertebrates. All sorts of creatures learn valuable life skills, such as what to eat, where to find it, how to process it, what a predator looks like, how to escape that predator, how to move safely through the environment, whom to mate with, and so forth, by observing and copying other animals. Inexperienced female fruit flies, for instance, copy the mate-choice decisions of other females. Many reef fishes learn complicated migratory pathways from more experienced individuals. Birds and whales pick up the local song dialects, which they perpetuate as vocal traditions. In some animals, this copying supports long-standing behavioural traditions. For instance, populations of chimpanzees throughout Africa each exhibit distinctive tool-using behaviour as youngsters learn the local behaviour (*e.g*. fishing for termites in one region, cracking nuts with a stone hammer in another) from their elders.

These examples beg the question of why social transmission is so widespread in nature? The answer to this question had remained elusive for many years. Copying others may be a quick way of acquiring knowledge and skills, but it provides no guarantee of success, as individuals may copy inappropriate or outdated information. Moreover, studies based on mathematical models found that copying doesn't necessarily increase the copier's fitness. A solution to this conundrum was eventually found through a computer-based competition — the social learning strategies tournament [1] (Box 1).

Copying others is smart because everyone does the best thing they know — individuals tend to perform tried-and-tested, high-payoff behaviour from their repertoire. By copying, individuals access a pool of ideas that are, on average, far more productive than what they could otherwise have picked up through trial-and-error. If this 'adaptive filtering' was switched off in the simulations, copying no longer paid. With this filtering, other individuals become a vast memory store of highly valuable information.

The social learning strategies tournament revealed that the more individuals pursued learning strategies reliant on social learning, as opposed to asocial learning, the better they performed. Moreover, the greater the reliance on social learning, the bigger the cultural memory store that accrued. In spite of the fact that social learning reduced the diversity of behaviour actually performed (Figure 2A), the diversity of knowledge about effective behaviour held in the population's collective cultural memory actually increased (Figure 2A). Increased reliance on social learning led to the persistence of adaptive knowledge for long periods of time — the equivalent of thousands of years — allowing populations to respond to environmental change highly effectively by drawing on the reservoir of past successes (Figure 2A). Cultural memory confers on populations an adaptive plasticity to cope with changing environments by allowing them to retain traces of solutions that worked in the past [2]. A real-world example of this from a pre-industrial society is the conservation of knowledge about edible wild plants by aged women in the Solomon Islands, knowledge that allowed their people to survive the destruction of gardens by infrequent but devastating cyclones [3].

Figure 1. A cultural memory store — the library of the abbey of Melk in Austria.
Languages, stories and songs, perpetuated through oral traditions, greatly boosted our species' ability to store knowledge of relevant past events and technology. External artefacts, ranging from books, articles, religious texts, and libraries, to the computers, CDs, DVDs, and other electronic stores of today, massively increased the dimensionality and accuracy of human cultural memory. Without its cultural memory store, civilization would rapidly collapse. (Image: Wikimedia Commons, Emgonzalez.)

Cultural memory requires accurate transmission

Culture depends on the passing-on of learned knowledge between individuals, through teaching and copying. The duration of cultural memories depends not just on the amount of social learning but also on the fidelity of information transmission (the accuracy with which information passes between individuals). A recent mathematical analysis revealed an exponential relationship between transmission fidelity and the longevity of cultural knowledge [4] (Figure 2B). This finding helps to explain variation in both animal social learning mechanisms and the duration of animal traditions. Most animals rely on low-fidelity mechanisms such as 'local enhancement' (learning about a location, *e.g*. a food source), and hence have very short-lived traditions. However, some animals, for instance chimpanzees, also have higher-fidelity social learning mechanisms, including imitation and emulation (i.e. copying the way others in the group remove defences to extract foods, such as fruits and nuts).

We humans possess language and teaching, which allow for very high-fidelity information transmission, and consequently lead to very long lasting traditions, and massive amounts of culture. Indeed, teaching can be defined as behaviour that functions to increase the accuracy of information transmission, whilst language allows accurate transmission of abstract concepts — imagine trying to explain Pythagoras' theorem, or how to catch trout using fake insects, without language. Further mathematical

Box 1

The social learning strategies tournament.

The 'social learning strategies tournament' was a computer-based competition in which entrants submitted a strategy specifying the best way for agents living in a simulated environment to learn [1]. There were 100 possible behaviour patterns that an agent could learn and subsequently exploit (imagine alternative foraging activities, such as hunting, fishing, gathering fruit, etc.), each with its own characteristic payoff, which could change over time (the rate of change was a model parameter). This simulated environment contained a population of 100 agents, each controlled by one of the strategies entered into the tournament.

The tournament was organized into a series of rounds, and in each round, each agent must perform one of three possible moves. The first, INNOVATE, resulted in an agent learning the identity and payoff of one new behaviour, selected at random (i.e. asocial learning). The second move, EXPLOIT, represented an agent choosing to perform a behaviour it already knew and receiving the payoff associated with that behaviour. The third move, OBSERVE, represented an agent observing one or more of those agents who chose to play EXPLOIT, and learning their behaviour and its payoff (i.e. social learning). Agents only receive payoffs by playing EXPLOIT, and the fitness of agents was determined by the total payoff received divided by the number of rounds they had lived.

When people entered the tournament their submitted strategy specified when the agents under their control would play INNOVATE, EXPLOIT and OBSERVE, such that successful strategies represented effective combinations of these moves. Evolution occurred through a simulated death–birth process, with agents dying at random and being replaced by the offspring of individuals that had accrued high fitness, and who carried the parental strategy. The most important finding was the success of strategies that relied heavily on copying (i.e. OBSERVE) to learn behaviour. Social learning in this context proved robustly successful, because the exploited behaviour patterns available to copy constituted a select subset that had already been chosen for their high payoff.

analyses [5] have established that accurate information transmission is also critical to the build-up of cumulative culture, in which technology ratchets up in complexity and diversity over time, through the continual spread of successive refinements. There is a threshold level of accuracy of information transmission necessary for cultural memories to accumulate, a threshold that most other animals apparently fail to meet.

Theoretical models have established that there are fitness advantages to individuals capable of efficient, high-fidelity copying. Natural selection for more efficient and more accurate copying may in turn have favoured specific cognitive capabilities in primates, thereby driving brain evolution. Consistent with this hypothesis, primate species that are more reliant on social learning tend to have larger brains [6,7]. This 'cultural drive' potentially favoured the evolution of a suite of cognitive adaptations, such as better visual perception to allow imitation of fine motor actions or copying over distances. Cross-modal mapping in the brain (*e.g*. the linking of the sight of another performing an action with the visual and movement sensory feedback obtained when you yourself perform it) would also have been favoured. Finally, selection also would have favoured improved social cognition to track the payoffs that others receive for their behaviour and the frequency with which behaviour is performed across the population, allowing effective social learning strategies to be deployed. It is almost certainly no coincidence that we humans are the primate species that relies the most on culture and possesses the largest brain.

Cultural memory also depends on the size and structure of the populations, which means that demographic processes can both help and hinder the build up and retention of cultural memory. Formal theory suggests that below certain population density thresholds it is hard for cumulative culture to take off [8]. It is easy to see why: if you have a good idea, but there is not enough cultural transmission for it to become distributed in shared cultural memory, then the idea dies with you; if enough people are around to take your idea on-board, it will outlive you. Larger or denser populations are capable of preserving innovations for longer (and generate more innovations), leading to bigger cultural repertoires. There are empirical examples of cultural memory being lost when the population size becomes too small, such as occurred with the separation of Tasmania from mainland Australia through rising sea levels at the beginning of the Holocene. This isolation led to a loss of numerous skills and technologies, including cold weather clothing, fishing nets, spear-throwers and boomerangs [9]. Similarly, researchers have found a positive relationship between population size and the breadth of cultural 'toolkits' in Oceania [10] — larger populations had broader toolkits.

One ramification of selection for high-fidelity copying is that mistakes and inappropriate or out-dated knowledge can also be copied precisely, leading to the transmission of maladaptive information. Here, the cultural memory persists too long. A famous example is the Norse attempt to colonize Greenland, beginning around 1000 CE (Figure 3). The Greenland colony ultimately failed because the colonists persisted in trying to raise cattle for food, a socially transmitted norm in their original society. Although cattle farming had been adaptive in the Norse's Scandinavian homeland, it failed miserably in the harsher environment of Greenland. The colony badly needed to shed reliance on their old memories, but they did not do so and the colonists starved.

Mathematical models have established that a tendency to disproportionately copy the majority behaviour — conformity — can be a highly effective strategy for individuals to use [11], but under certain conditions it is easy to see how conformity could cause problems. One strategy that guards against such maladaptive information transmission is payoff-based copying — that is, selectively copying the behaviour with the highest payoff. Another is a bias for new traits that are rapidly increasing in popularity [12], which may help explain the rise of 'viral' marketing. Understanding how different approaches to passing on cultural memory have played out in human evolution is an active area of research [11].

Humans have also, largely through cultural means, created systems of cultural memory that are external to their brains, such as books and paintings. It may yet turn out to be the case that these external systems — including material culture, mathematics, and writing — are what have been really crucial in the explosion of cumulative culture in the last 10,000 years. Non-human cultural memory relies largely on information residing in brains, and there are hard limits to both the amount and duration of information any one brain can carry. Such externalised and persistent social information appears to be a very rare thing in non-humans — some ants leave pheromone trails to food sources, for example, but these trails are highly ephemeral, hardly ever persisting longer than 24 hours [13]. Language helps, but oral tradition also has its limits in terms of fidelity and stability, even with ingenious inventions such as the Australian aboriginal use of song to maintain and transmit geographic knowledge. In contrast, modern human societies are hugely reliant on a collective externalised and persistent memory that is a characteristic of the society as much as it is of any one individual, particularly as it has far outstripped the capability of any one individual's memory to contain information.

Culture affects memory in turn

Human culture is a uniquely potent form of externalised memory, supported by a biological inheritance that makes us highly reliant on learning from others. But this is not the end of the story. Our cultural inheritance has so profoundly altered our own environments that the causal arrow has circled back on itself, and we are beginning to understand how our cultural memory bank can generate feedback that affects the development and function of our own individual neurobiological memories.

One pathway is via the evolution of differential effects on development indirectly via cultural modification of the selective environment. Through the domestication of plants and animals, agriculture has had a big impact on human diet, which has led to evolutionary interactions detectable in our genome, such as the selection of alleles that enhanced the digestion of new foods (*e.g.* [14]). For instance, populations with a cultural history of consuming dairy products typically have higher frequencies of alleles for breaking down the lactose in milk, whilst those with a high-starch diet possess elevated salivary amylase, which breaks down starch. We also know that maternal and post-natal infant nutrition can have profound effects on neural development — for example, supplements of the nutrient

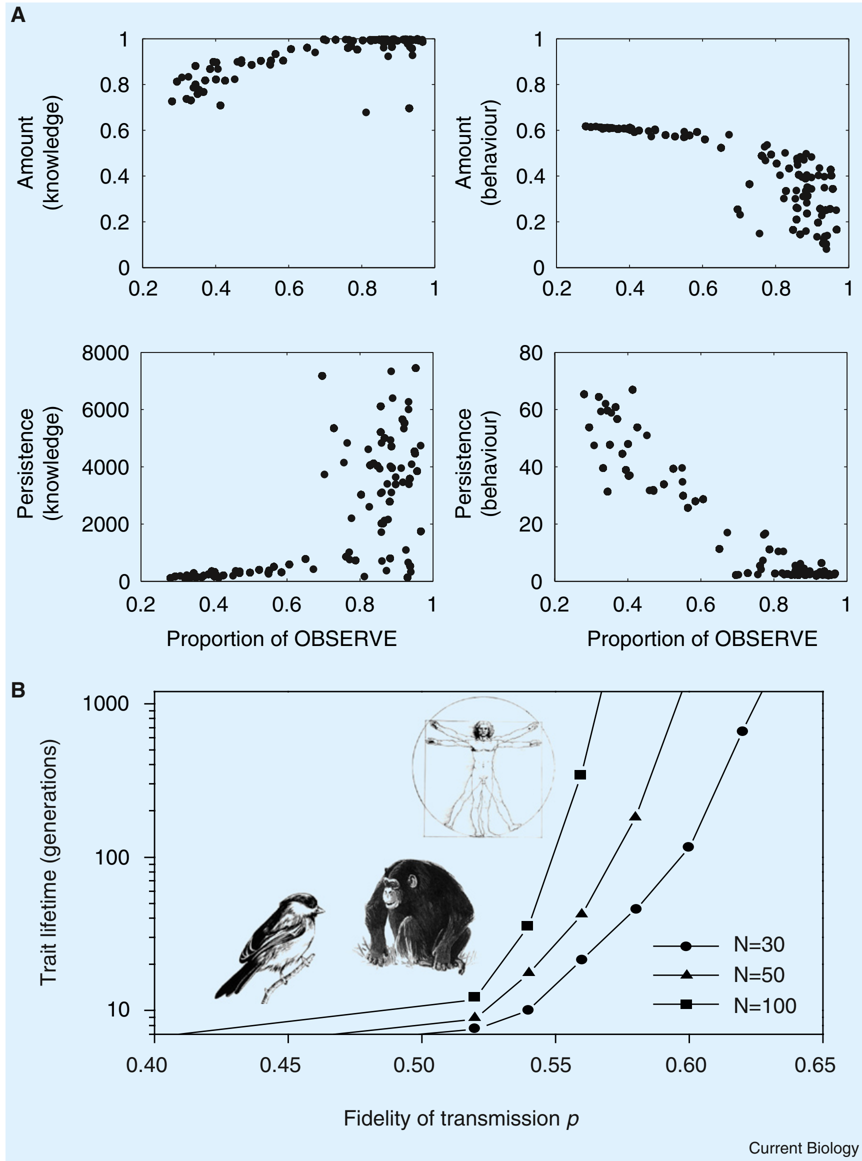

Figure 2. Effects of social learning and transmission fidelity on culture.
(A) Analysis of the social learning strategies tournament (Box 1) showed how increased reliance on social learning affects the diversity and longevity of culture. Each point is the result of a single simulation run. 'Proportion of OBSERVE' is the proportion of learning that is social as opposed to asocial, 'Amount' (top panels) is the proportion of potentially available knowledge or behaviour the population has discovered, and 'Persistence' (bottom panels) is the average number of iterations for which a single piece of knowledge or behaviour persists in the population (with the average lifespan of individuals being 50 iterations; adapted from [2]). (B) Small increases in cultural fidelity generate big increases in both the amount of culture and the longevity of cultural traits. The bigger the population size, the stronger this effect. Most animals are reliant on low fidelity social learning mechanisms, such as local enhancement, and hence have short-lived, simple traditions. Chimpanzees are capable of imitation and emulation, and as a result possess more stable and more diverse traditions. Humans have a variety of high-fidelity transmission mechanisms, including teaching, language and writing, and consequently possess extremely long-lasting and diverse cultural memories (Adapted from [4].).

Figure 3. Ruinous cultural fidelity.
The ruins of the church of Hvalsey are testimony of the Norse settlement in Greenland that vanished after several centuries, in part because the Norse adhered to cultural practices, such as cattle farming, that worked well in their homeland but proved maladaptive in the long run in Greenland. (Picture: David Trood/ilovegreenland (www.greenland.com).)

choline just before and after birth produce lifelong enhancements in learning and memory function in rodents [15] — hence cultural shifts in diet can have implications for memory development in whole populations. Similarly, the waste products of human culture pervade our environments. Environmental estrogens from the degradation of plastics or the widespread use of contraceptive pills are now at measurable concentrations in surface waters throughout the developed world, and some of these compounds have been shown to have effects on spatial memory in mice [16].

There is also a growing appreciation among psychologists of the ways in which culture can directly affect the ways memories are formed and recalled. For example, perception is the first step in memory formation, and there are several studies showing variation in the processes of perception between people with different cultural backgrounds [17], demonstrating, for example, variation in eye movements when viewing a scene [18] and varying sensitivity to contextual information in visual cues [19]. Once memories have been formed, there are also clear influences of cultural background in the way autobiographical memories are recalled [20]. In one experimental study, Asian American subjects were primed on either their Asian or American background before recalling instances of autobiographical memory, and in the former condition produced more memories of shared social experiences and fewer of personal, self-focused episodes than in the latter [21].

While other animals have their own forms of cultural memory, none of them have it like we do. It is both a consequence of, and a causal influence on, the memories we hold in our brains. Understanding how we came to have it, and the consequences of the co-evolutionary processes it has sparked, will be a focus of interdisciplinary research for decades to come.

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