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Evolution of costly explicit memory and cumulative culture

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HIGHLIGHTS

- Evolution of explicit memory is an important topic for cultural evolution.
- Explicit memory comprises encoding, storage, and retrieval. To use learned information, we have to store and retrieve it.
- How does evolution of costly explicit memory influence or modify cumulative culture?
- When low-cost social learning evolves, the repetition of forgetting and re-learning is favored without cumulative culture.
- Cumulative culture favors the coevolution of costly retrieval–storage and learning.

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ABSTRACT

Humans can acquire new information and modify it (cumulative culture) based on their learning and memory abilities, especially explicit memory, through the processes of encoding, consolidation, storage, and retrieval. Explicit memory is categorized into semantic and episodic memories. Animals have semantic memory, while episodic memory is unique to humans and essential for innovation and the evolution of culture. As both episodic and semantic memory are needed for innovation, the evolution of explicit memory influences the evolution of culture. However, previous theoretical studies have shown that environmental fluctuations influence the evolution of imitation (social learning) and innovation (individual learning) and assume that memory is not an evolutionary trait. If individuals can store and retrieve acquired information properly, they can modify it and innovate new information. Therefore, being able to store and retrieve information is essential from the perspective of cultural evolution. However, if both storage and retrieval were too costly, forgetting and relearning would have an advantage over storing and retrieving acquired information. In this study, using mathematical analysis and individual-based simulations, we investigate whether cumulative culture can promote the coevolution of costly memory and social and individual learning, assuming that cumulative culture improves the fitness of each individual. The conclusions are: (1) without cumulative culture, a social learning cost is essential for the evolution of storage–retrieval. Costly storage–retrieval can evolve with individual learning but costly social learning does not evolve. When low-cost social learning evolves, the repetition of forgetting and learning is favored more than the evolution of costly storage–retrieval, even though a cultural trait improves the fitness. (2) When cumulative culture exists and improves fitness, storage–retrieval can evolve with social and/or individual learning, which is not influenced by the degree of the social learning cost. Whether individuals socially learn a low level of culture from observing a high or the low level of culture influences the evolution of memory and learning, especially individual learning.

1. Introduction

Learning and memory are essential for the evolution of culture, and are themselves also products of evolution (Klein et al., 2002; Dukas, 2009; Schwartz et al., 2013). Neuroscientists have partially discussed the evolution of memory, especially long-term memory, which consists of implicit and explicit memories (Gazzaniga et al., 2009; Kandel et al., 2013). Squire and Kandel (2009) argued that implicit memory, which is connected with reproduction, survival, escape, and defense, evolved in the earlier stages of evolutionary history. Additional types of implicit memory evolved, followed by the evolution of explicit memory.

Explicit memory is categorized into episodic memory (memory of personally experienced events) and semantic memory (memory of general facts) (Tulving, 1972). Tulving (2002a) argued that

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humans are probably the only species with episodic memory, which makes "mental time travel" possible. Episodic memory allows individuals not only to think about the past, but also to anticipate, plan for, and think about the future, which then influences the evolution of human culture (Tulving, 2002a). Tulving (2002a) also pointed out that episodic memory evolved from semantic memory; humans share semantic memory ability with other mammals and birds. Tulving's argument (Tulving, 2002b, 2002a) is very similar to the discussions of cognitive archeologists; modern humans have better working memory abilities than Neanderthals, assuming that the multicomponent working memory model proposed by Baddeley (2000) can be applied to modern human working memory. In Baddeley's (2000) multicomponent working memory model, working memory consists of the central executive and three subsystems controlled by the central executive: the visuospatial sketchpad, episodic buffer, and phonological loop. The episodic buffer can retrieve information from storage consciously and temporarily and then manipulate and modify it if necessary. As a result, modern humans have a good ability to innovate (Coolidge and Wynn, 2004; Wynn and Coolidge, 2004, 2008). Coolidge and Wynn (2004) found that Neanderthals retrieved information from long-term working memory, which corresponds to implicit memory and some declarative knowledge (semantic memory) related to implicit memory, and that long-term working memory is not intrinsically innovative. Therefore, Neanderthals were skilled experts. It is modern humans' high enhanced working memory ability, which results from a mutation of working memory in Neanderthals, that makes modern humans innovative, even though both Neanderthals and modern humans possess long-term working memory (Wynn and Coolidge, 2004). The archaeological artifacts of Neanderthals indicate that they did not have the same cognitive functions as modern humans, such as advanced executive functions and working memory capacity that make possible long-range planning (e.g., delayed gratification and remote planning in space and time) (Wynn and Coolidge, 2008). These arguments in psychology and cognitive archaeology indicate that explicit memory is essential for the evolution of culture. Not only general facts and knowledge (semantic memory), but also long-range planning and mental time travel (episodic memory) are needed for innovations.

However, this research only provides conceptual ideas about the evolution of memory (Squire and Kandel, 2009) and human-specific memory (Tulving, 2002b; Geary, 2004; Wynn and Coolidge, 2008); there are no in-depth studies or evidence, such as experimental data, that address the evolution of memory from the viewpoint of behavioral ecology, comparative cognitive sciences, and neurosciences. Non-human memory has been studied to determine whether other species have the same or similar types of memories as humans (Zentall and Wasserman, 2012). For example, animal experiments have revealed that rats have episodic-like memory (Eichenbaum et al., 2012). The anatomical and functional study, comparing the brain regions responsible for episodic memory in humans with the brain regions in other species, suggests that amniotes have proto-episodic memory (Allen and Fortin, 2013). However, there is still no major theory that explains the evolution of memory. Recently, researchers in evolutionary psychology, developmental psychology, and neuroscience have begun to study the adaptation of human memory in research areas such as foraging, cheater detection, facial recognition, planning for the future, spatial memory, and survival processing (Schwartz et al., 2013).

From the viewpoint of cognitive science and neuroscience, learning is defined as behavioral changes resulting from information acquisition, and explicit memory is defined as the operation by which that information is encoded, consolidated, stored, and retrieved (Gazzaniga et al., 2009; Kandel et al., 2013). Encoding refers to the process by which incoming information is attended to and connected with information already existing in the brain; storage is the neural mechanism by which memory is retained; consolidation is the process that makes stored information stable; and retrieval is the process by which stored information is consciously recollected. If people fail to store information, the information is lost and will have to be relearned. If a person fails to retrieve information when they need to use it, they can neither apply it nor benefit from it. Although they may retrieve it later, this becomes a futile exercise. Hence, storage and conscious retrieval are the essential processes that make learning effective.

Learning, as well as memory, is essential for the evolution of culture. The evolution of learning is one of the most important topics in theoretical work on human evolution. However, previous studies on the evolution of learning have not addressed the evolution of (explicit) memory, but have mainly focused on the evolutionary advantage of two learning strategies: individual and social learning (Boyd and Richerson, 1985; Rogers, 1988; Feldman et al., 1996). Individual learners use trial and error and then invent information appropriate to the current environment, such as culture, innovation, and knowledge. Social learners copy and acquire information from exemplars. It is assumed that the cost of individual learning is higher than that of social learning because individual learners make the effort to use trial and error, expending much time and energy, whereas copying others' behavior does not have so many costs. Social learners can learn from the exemplars' information if the exemplars have information appropriate to the current environment. However, if they imitate the wrong information or the environment suddenly changes, social learners cannot obtain any benefit from the information. In contrast, even though individual learners pay a higher cost, they invent information appropriate to the current environment and thus gain more benefit from what they invent. This research topic has expanded in various directions (Aoki and Feldman, 2014): the analysis of mixed strategies of social and individual learning (Feldman et al., 1996); the effect of innate determination of behavior on the evolution of learning (Wakano et al., 2004; Wakano and Aoki, 2006); the effect of the population or spatial structure (Boyd and Richerson, 1985; Nakamaru and Levin, 2004; Aoki and Nakahashi, 2008; Rendell et al., 2010); the comparison of theoretical predictions with experimental outcomes (Kameda and Nakanishi, 2002); the learning schedule in an age-structured model (Aoki et al., 2012; Lehmann et al., 2013); the introduction of conditional strategies that adopt both social and individual learning (Enquist et al., 2007; Borenstein et al., 2008; Aoki, 2010; Rendell et al., 2010) or biased social learning (Boyd and Richerson, 1985; Henrich and McElreath, 2003; Laland, 2004; Nakahashi et al., 2012); the evolution of teaching (Fogarty et al., 2011); and the effect of learning on cumulative culture, which is the modification of culture over generations (Tomasello, 1999; Henrich, 2004; Tennie et al., 2009; Mesoudi, 2011; Aoki et al., 2012; Kobayashi and Aoki, 2012; Fogarty et al., 2015).

These previous studies on the evolution of learning implicitly assume that, if learning is successful, individuals can perfectly memorize and retrieve what they have learned socially or individually. Some theoretical studies assume a capacity to learn and a decay rate, which corresponds to a rate of forgetting (Henrich, 2004; Powell et al., 2009; Nakahashi, 2010; Lehmann et al., 2013).

How does explicit memory and learning coevolve with culture? It seems obvious that memory evolved with learning. However, memory is costly (Anderson, 1991; Dukas, 2009). If the cost of memory is higher than the cost of learning, the repetition of forgetting and learning may pay off more than does memorization. Consequently, memory would not evolve. Here, we will consider the hypothesis that explicit memory, especially two processes of explicit memory—storage and retrieval—promotes cumulative