The natural selection of fidelity in social learning

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Abstract

Social learning mechanisms are usually assumed to explain both the spread and the persistence of cultural behaviour. In a recent article, we showed that the fidelity of social learning commonly found in transmission chain experiments is not high enough to explain cultural stability. Here we want to both enrich and qualify this conclusion by looking at the case of song transmission in song birds, which can be faithful to the point of being true replication. We argue that this high fidelity results from natural selection pressure on cognitive mechanisms. This observation strengthens our main argument. Social learning mechanisms are unlikely to be faithful enough to explain cultural stability because they are generally selected not for high fidelity but for generalisation and adjustment to the individual's needs, capacities and situation.

TEXT

For acquired behaviour to clearly count as cultural, two conditions must be met: it must propagate in a social group, and it must remain self-similar or stable across generations in the process of propagation. In animals, a variety of behavioural patterns have been shown both to spread and to persist across generations [1-3], and it has been assumed that the same transmission mechanisms explain both the spread and the stability of animal culture [4, 5]. Imitation in particular has been claimed to exhibit a higher degree of fidelity and therefore play a major role in the evolution of culture [6]. In a recent article we have challenged this assumption by asking whether imitation can really explain both the propagation and the stability of cultural behaviours [7].

Fidelity of social learning has usually been investigated by means of transmission chain experiments. To our knowledge the first report of a transmission chain in non-human animals

is by Curio et al. who investigated the transmission of fear response in the blackbird (*Turdus merula L.*) [8]. Curio et al. taught one individual to express a fear response to an inoffensive stuffed Australian honeyeater (*Philemon corniculatus*). This individual was then shown the honeyeater in the presence of another naive blackbird staying in an adjacent aviary. Curio et al. showed that the naive bird learned to fear the innocuous honeyeater by observing the teacher's behaviour. To see whether the strength of the fear response changed through multiple transfers, they performed a transmission chain study of six steps, with the naive individual at step n serving as the teacher at step n + 1. The results suggested that the fear response could propagate without loss of intensity. Using similar transmission chain paradigms, recent studies of animal behaviour have also found substantial transmission fidelity. But to what extent does the degree of fidelity found in these experiments help explain cultural stability? In biology for instance, the relative stability of genes is to a very large extent explained by the extraordinarily high fidelity of gene replication, with fidelity ranging typically from $1\text{-}10^{-3}$ to $1\text{-}10^{-11}$ [9].

We reviewed the literature on transmission chains, including studies in chimpanzees, fish, rats and humans, studies using several tasks, including food preference, foraging decision, visual illusion and using several protocols, including group and single individual chains. In all the studies reviewed the difference introduced at the beginning progressively disappeared through time. The longest chain in these studies involved fourteen transmission steps over fourteen days. Using a simple model of social learning we found that, in the studies we reviewed, the fidelity of social learning was between 0.86 and 0.95, orders of magnitude below that of gene replication. We argued that these results undermine the common assumption that imitation and other form of social learning are faithful enough to explain the stability of animal culture

over several generations. Other mechanisms—ecological or psychological—of must be invoked to explain the very existence of culture.

Here, we want to both enrich and qualify this conclusion. Rather than just assess an average level of fidelity in social learning on the basis of the experimental literature addressing the issue, we might also look for the highest level of fidelity reported in animal transmission and see whether it might explain cultural stability (and if so, why).

Song learning in birds provides examples of the kind of high fidelity we are looking for. For example, Grant and Grant studied the transmission of songs in Darwin's medium ground finches (*Geospiza fortis*) on the Galapagos Islands. They showed that males sing a single unvarying song during their whole life and most of the time, learn that song from their father with very high fidelity (songs can sometime be faithfully transmitted over more than five generations) [10]. One factor that helps explain why male's songs are so faithfully transmitted is that females also learn to recognise their father's song and tend to mate with individuals who sing a song slightly different to their father's, thereby preventing both inbreeding and cross-species reproduction. The fidelity of social learning in this case may therefore be an evolved property of the breeding system of these birds. On the small Galapagos Islands, a male who does not faithfully reproduce the song of his father would specifically attract female relatives (because he would be singing a song slightly different from the female's father), which might reduce its fitness. On the female side, if a female is less choosy, she might also be less fit since she might end up reproducing either with males from another closely related species or with male relatives. Hence, the fidelity of social learning in this case is probably a consequence of a particular sexual selection regime linked to the specific ecology of the

Islands. If this is correct, song learning in this case has evolved to be much more faithful than most forms of social learning.

What this example suggests is that social learning can be highly faithful if it is naturally selected to be so, that is, if there is a natural selection pressure on cognitive mechanisms for them to precisely achieve a faithful reproduction of the input they receive. The analogy with DNA replication should be obvious: the fidelity of DNA replication is under the control of several biochemical mechanisms that have evolved to reproduce and repair the genetic material in order to limit the frequency of mutations. Replication has evolved to be faithful. Actually, the analogy is unsurprising since, in both cases, high fidelity is produced by—what else?—natural selection.

This observation strengthens our main argument. Social learning is unlikely to be faithful enough to explain cultural stability unless it is selected for high copying fidelity and this is not generally the case. Imitation for instance is a mechanism allowing individuals to learn a new action by watching it performed by others. In order to learn to perform a new action properly, individuals have however to adapt it to their own particular situation, to their history, their knowledge, their physiology, their character, etc. Precise copying of an observed action, without generalisation and adjustment to one's needs and capacities, would require the evolution of costly psychological mechanisms to produce sub-optimal outcome. It would therefore be counter-selected. If anything, imitation should be selected for flexibility rather than fidelity. Only when high fidelity is itself an adaptive feature, as in the case of Darwin's finches, should we expect evolved mechanisms such as the dedicated song-learning mechanisms of songbirds, known as the 'song system' [11], to produce by themselves cultural stability.

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