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OUTLOOK

Raising the bar on studying cultural evolution

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Abstract Sasaki and Biro (2017, *Nature Communications, 8*, 15049) show that pairs of pigeons can increase the efficiency of their homing routes over several 'generations' in which pair members are gradually replaced by naïve birds. Their findings show that socially transmitted cumulative alterations of behavior are not unique to humans and suggest a way to examine potential mechanisms of cultural evolution.

Keywords Cumulative cultural evolution · Collective behavior

In the early days of competitive high-jumping, athletes generally used a scissors technique, raising each leg over the bar in turn and landing on their feet. More sophisticated techniques were developed around the turn of the 20th century, such as the Eastern cut-off, a modification of the scissors technique that included flattening out over the bar. Using this method, a world record of 1.97 m was set in 1895. In the 1960s, Dick Fosbury modified the Eastern cut-off to cross over the bar backwards, head-first, and land on his back in what became known as the Fosbury Flop, the method currently used by almost all professional high-jumpers. The world record today is 2.45 m. This story is an example of cumulative cultural evolution (CCE), a process by which a series of changes to a socially transmitted behavioral technique, each building on earlier innovations, leads to a measurable 'ratcheting' up of behavioral efficiency (Tomasello, Kruger, & Ratner, 1993).

Attempts to observe or manufacture CCE in nonhuman primates, both in the lab and the field, have mostly failed (Dean, Vale, Laland, Flynn, & Kendall, 2014), lending support to the notion that CCE is a uniquely human phenomenon, largely accounting for our advanced material and intellectual cultures (Caldwell, Atkinson, & Renner, 2016). Several possible reasons for this uniqueness have been proposed (Dean et al., 2014), such as that the 'ratchet effect' requires a degree of fidelity in the transmission of information that nonverbal species struggle to achieve (Tomasello et al., 1993), or that nonhuman primates watching a demonstration, unlike humans, tend to focus on the end product—the object being manufactured or manipulated—rather than on the process, which precludes social transmission of techniques and therefore CCE; according to this view, nonhumans emulate rather than imitate (Tennie, Call, & Tomasello, 2009).

Sasaki and Biro (2017) have shown what appears to be CCE in pigeons, using a behavior that the birds perform naturally: homing. Over repeated homing flights from the same location, solitary pigeons will gradually increase the directness of their path and eventually settle on a mostly fixed route. Pigeons homing in pairs (or larger groups) tend to stay together wherever their routes are sufficiently similar. Sasaki and Biro borrowed a paradigm from experimental demonstrations of CCE in humans, in which naïve subjects observe experienced demonstrators making or modifying an object and then themselves become the demonstrators for the next "generation" of subjects (Caldwell et al., 2016). The authors allowed pigeons to repeatedly fly home from a novel location under one of three conditions: one group of birds flew alone; a second group flew in fixed-membership pairs; a third group of birds also flew in pairs but, every 12 flights, the more experienced subject was replaced by a naïve bird. After 60 flights, birds in the last generation of this third group were taking significantly more direct paths to the roost than birds in either control group. The authors further showed that the birds' routes were more similar within a lineage than between

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lineages, strongly suggesting that path-specific information was being transmitted across generations.

These results fulfil some of the criteria for CCE: information is transmitted socially from more to less experienced subjects, leading to a measurable improvement in the efficiency of the behavior. However, the behavior did not increase in complexity, nor is it probable that the final efficiency was beyond the ability of any single bird, both of which have sometimes been proposed as criteria for CCE in humans (Tomasello et al., 1993).

More importantly, in my view, Sasaki and Biro's results may allow the study of CCE to progress beyond description and begin to examine the mechanisms by which cumulative improvements are (or are not) achieved. Despite much theorizing on which specific skills that are required for CCE nonhumans lack (Dean et al., 2014), there have been few empirical attempts to test potential mechanisms. Whether or not pigeons' improvements in homing efficiency should be labelled CCE is less important than understanding how they evaluate and balance personal and social information.

For example, at each generational shift—when a naïve pigeon replaced one member of a pair—the efficiency of that pair's route initially decreased for several flights, before recovering to or surpassing the efficiency of the previous generation. Whether or not this precludes the pigeon data from demonstrating the 'ratchet effect', which has been suggested to allow little or no backsliding (Tennie et al., 2009), it does suggest some features of the mechanism by which pairs of pigeons settle on a route.

Consider a simple explanation of Sasaki and Biro's results: The preferred paths of naïve pigeons and their more experienced partners will differ at many points, with the naïve birds' variant usually the less efficient. The resulting route taken by the pair will reflect some weighted compromise between the two paths. In a few cases, purely by chance, the alteration introduced by the naïve bird will shorten the route. Such beneficial changes will be retained and those that do not increase route efficiency discarded, gradually improving the route over multiple generations. By this account, naïve birds inject noise into otherwise set homing routes, allowing them to improve. This requires only that birds mostly remain together and are able to compare past flights to determine which was more direct, so that only (or mostly) improvements to the route are retained. Additionally, improvements in efficiency, by this mechanism, depend on the number of generations (or subjects): If each bird adds independent noise, then groups that span more generations will end up with more efficient routes. Alternatively, the efficiency of a group could simply depend on the (possibly innate) ability of its most skilled member; larger groups would be more efficient as they are more likely to contain the most skilled individual. These mechanisms are similar to the 'many wrongs' principle which may underlie group-size effects on the accuracy of collective navigation. In every CCE experiment I am aware of, including Sasaki and Biro's, there are more individuals (in total) in the experimental than the control group, making it difficult to reject such simple explanations, which may have little to do with cultural transmission.

Mechanistic considerations will also help to better define CCE and perhaps demonstrate that it is not a unitary phenomenon. For example, it has been suggested that imitation of a demonstrator is required for CCE. However, human subjects that do not get to see previous generations making a paper aeroplane, but only have access to the planes and data on how far they each flew, nonetheless show gradual improvements across generations, perhaps due to the perceptual transparency (to humans) of paper aeroplane design (Caldwell et al., 2016). This suggests that different mechanisms of CCE may be involved in the 'evolution' of different behaviors or objects.

Sasaki and Biro also note that their experiment links CCE to 'collective intelligence', another term often thrown around with little consideration of the (possibly quite simple) mechanisms that drive it. It is not clear what the distinction between collective behavior and CCE should be. Must there be an experience or skill gap between demonstrator and observer for the social transmission of a behavior to count as (a step in) CCE? Is it necessary for generations to be staggered, or should gradual improvements in task efficiency emerging from a group of contemporaries also count? Are there, in other words, mechanisms specific to cultural evolution that are not found in other forms of collective information transfer?

Human cultural achievements, from iPhones to Latin, are clearly on a different scale from those observed in any other species, but an understanding of why and how these differences emerged awaits detailed studies of the mechanisms by which cultural information is transmitted. Sasaki and Biro's demonstration of CCE-like effects in a relatively simple system provides an excellent starting point. It seems likely that, as with other behavioral skills that were once considered uniquely human, we will find that CCE is the product of a set of cognitive mechanisms that we share to varying degrees with many other species.

References

Caldwell, C. A., Atkinson, M., & Renner, E. (2016). Experimental approaches to studying cumulative cultural evolution. *Current Directions in Psychological Science, 25*, 191–195.

Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E., & Kendall, R. L. (2014). Human cumulative culture: A comparative perspective. *Biological Reviews, 89*, 284–301.

Sasaki, T., & Biro, D. (2017). Cumulative culture can emerge from collective intelligence in animal groups. *Nature Communications, 8*, 15049.

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: On the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B, 364,*2405–2415.

Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993). Cultural learning. *Behavioral and Brain Sciences, 16*, 495–552.