The animal variations: When mechanisms matter in accounting for function

DOI: 10.1017/S0140525X07002555

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Abstract: We contend that Ramsey et al.'s definition of animal innovation *sensu* process may be partially misleading when investigating mechanisms underlying animal innovation. By excluding social learning from the "process" of innovation, they may be reproducing a dichotomous schema that does not accurately correspond to our knowledge of the acquisition of novel behavioral variants. This gives us some reason to doubt the functional specification of the defined process of innovation.

In their article, Ramsey et al. operationalize animal behavioral innovation in a way that is both an improvement and an extension of current methods for studying innovations. As an attempt to explicitly define the process of innovation at an individual level, as opposed to the population level, their definition could also foster progress in the study of the actual mechanisms of innovation. However, the authors remain agnostic concerning the mechanisms of behavioral innovation. We believe that in the end, this agnosticism may have some undesired side effects.

Indeed, when advancing their descriptive definition of innovation, Ramsey et al. distinguish between the learning of a new behavior by an individual (what they call the "process" of innovation) and the transmission of the new behavior between conspecifics (the spread of the innovation "as a product"). This dichotomous vision of innovation and transmission reflects the distinction between, on the one hand, mechanisms generating new variants and, on the other hand, mechanisms of faithful transmission of these different variants. We fear that this view may be unhelpful when trying to individuate processes of innovation (a purported goal of their definition) from other processes such as social learning.

Let us take, for example, the behavior of British tits (*Parus* spp.) opening milk bottles. As classical studies have shown, the spread of this behavior was not a matter of general imitation nor a process of exactly copying the behavior of other conspecifics (Hinde & Fisher 1972; Sherry & Galef 1984). Rather, those birds that were initially thought to be imitative, partially stimulated by conspecifics, had to re-learn the steps leading up to drinking milk from a previously closed bottle. However broadly construed, social learning, in this case, did not automatically lead bluetits to open milk bottles. Instead, each bluetit had to re-discover on its own how to reach the goal. By characterizing the classic example this way, we wish to convey the idea that the mechanisms that preserve the innovative behavior (*sensu* product) in the population may sometimes be as innovative (*sensu* process) as the process by which the first individual produced the first instance of the behavior in that population. We think that this is an important point that could be extended to other paradigmatic cases of diffusion of animal innovations (such as sweet potato washing or termite fishing (Galef 1992). The more general claim is that in the absence of a strong functional justification of the unity of the process of innovation we may expect it to be realized by very different mechanisms across taxa. These mechanisms may not fit with Ramsey et al.'s definition. Similarly, some innovations (*sensu* product) may often be the result of an accumulation of small modifications produced during relatively faithful transmission between individuals. Consider the case of song learning in certain species of birds: Young birds use the template of a given song sung by their surrounding conspecifics to produce what is, strictly speaking, a new song but one that nevertheless resembles those already existing in the population. This does not count as an innovation according to the definition proposed by Ramsey et al. because that slightly novel variant is functionally determined by its conspecifics and therefore would be classified as a case of general "social learning." Over time, however, the successive transformations accomplished by several individuals may change this given song in the population and therefore produce a completely new and innovative song relative to the first population template (see Slater & Lachlan [2003] for a review). Indeed, if one bird were to suddenly produce that highly different song, it would, indeed, be classified as a full innovation or "invention" from the perspective of Ramsey et al. But in our example, the process of innovation is distributed so as to make it almost undetectable from the perspective of their definition. If we are right, the understanding of the mechanisms that *preserve* innovations may be crucial to explaining the creation as much as the diffusion of those same innovations (see Podos et al. 2004). Innovations may thus arise as the outcome of an interindividual process that could not be explained without paying explicit attention to the different mechanisms of social learning. This may well be the default case in humans, a paradigmatic case of an innovative species. In our species, even when the goal of a given behavior is precisely to perfectly reproduce the model, this process is characterized by the systematic introduction of novel idiosyncratic variants that could eventually be the basis of well-known Chinese-whispers-like phenomena (Barbrook et al. 1998; Gergely et al. 2002; Sperber 2001).

Thus, we think that keeping with a dichotomous view of "innovative processes" and "preservative" or "social learning" processes may be misleading and hinder the characterization of mechanisms at the basis of much of animal innovation. Ramsey et al., on the contrary, insist on the fact that innovation – or "invention," which they define as a paradigmatic case of innovation – does not require either environmental induction or social learning. Thus their claim is that "*the individual, process-based definition of innovation excludes social learning as a source of innovation*" (target article, sect. 3.3, para. 3; emphasis added). We believe that defining innovations in opposition to social learning in a broad sense, excludes innovations that occur as the result of individuals' interactions in processes other than mysterious "*Eureka!*" events. Our view is that innovations are not the simple result of a well-defined excluding class of processes. Rather they are the complex outcome of different mechanisms some of which undergo different functional pressures and sometimes concern several individuals. Since the phenomenon of animal innovation cuts across different ecological domains (as varied as song learning or foraging), as well as different animal taxa, expectations of a unified process under the auspices of a general evolutionary function may not be justified (Burghardt 2006). On the whole, we expect Ramsey et al.'s contribution to have enormously positive outcomes. The operationalization that they propose may foster more accurate estimations of the repertoire of innovations of different species. This in turn may facilitate functional investigations into innovation rates – something tremendously useful in itself, but which will also attract further interest in underlying mechanisms.

ACKNOWLEDGMENTS

We thank Coralie Chevalier, John Hulsey, Olivier Morin, and Sabita Claidiere for useful remarks on earlier versions of this commentary.