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Review

Conformity without majority? The case for demarcating social from majority influences

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In this review, we explore the extent to which the recent evidence for conformity in nonhuman animals may alternatively be explained by the animals' preference for social information regardless of the number of individuals demonstrating the respective behaviour. Conformity as a research topic originated in human psychology and has been described as the phenomenon in which individuals change their behaviour to match the behaviour displayed by the majority of group members. Recent studies have aimed to investigate the same process in nonhuman animals; however, most of the adopted designs have not been able to control for social influences independent of any majority influence and some studies have not even incorporated a majority in their designs. This begs the question to what extent the 'conformity interpretation' is preliminary and should be revisited in light of animals' general susceptibility to social influences. Similarly, demarcating social from majority influences sheds new light on the original findings in human psychology and motivates reinterpretation of the reported behavioural patterns in terms of social instead of majority influences. Conformity can have profound ramifications for individual fitness and group dynamics; identifying the exact source responsible for animals' behavioural adjustments is essential for understanding animals' learning biases and interpreting cross-species data in terms of evolutionary processes.

Dating back to 1932, when Arthur Jenness observed that individuals' estimates of the number of beans in a jar were considerably influenced by the estimate of the majority of group members (Jenness, 1932), conformity has received extensive attention in human psychology. Defined by altering opinions or behaviour in order to match the majority, subsequent research robustly showed that a surprising number of the adult participants are conformists, even when the majority stance is conspicuously erroneous (Asch, 1956; Bond & Smith, 1996; Sherif, 1936). In later years, it was shown that opting for the majority stance does not represent a biological conundrum, but may instead bestow substantial fitness benefits (Henrich & Boyd, 1998; King & Cowlishaw, 2007; Richerson & Boyd, 2005; Wolf, Kurvers, Ward, Krause, & Krause, 2013).

The tendency to adopt the behaviour of the majority of group members is considered to be one of the driving forces behind cultural diversification (Boyd & Richerson, 1985; Henrich & Boyd, 1998). By converging on the most prevalent conventions, groups move towards behavioural homogeneity while at the same time increasing the likelihood of emergent between-group heterogeneity: the hallmark of culture (Richerson & Boyd, 2005). In recent years, majority influence has become a favourable research topic for behavioural biologists. One line of research has focused on our closest living relatives, the nonhuman primates (chimpanzees, *Pan troglodytes*: Bonnie, Horner, Whiten, & de Waal, 2007; Haun, Rekers, & Tomasello, 2012; Hopper, Schapiro, Lambeth, & Brosnan, 2011; Whiten, Horner, & de Waal, 2005; capuchin monkeys, *Cebus apella*: Dindo, Thierry, & Whiten, 2008; Dindo, Whiten, & de Waal, 2009; Perry, 2009), which could enable intriguing analysis of the evolutionary roots of this human phenomenon (MacLean et al., 2012). Another line of research has aimed to investigate the possibility of convergent evolution of conformity by focusing on phylogenetically more distant species, such as fish (Day, MacDonald, Brown, Laland, & Reader, 2001; Kendal, Coolen, & Laland, 2004; Pike & Laland, 2010), rats (Galef & Whiskin, 2008; Jolles, de Visser, & van den Bos, 2011; Konopasky & Telegdy, 1977) and fruit flies (Battesti, Moreno, Joly, & Mery, 2012).

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However, as we aim to show in this review, most studies in both lines of investigation seemed to have overlooked the distinction between social and majority influences.

Specifically, in this review, we evaluate relevant conformity studies across animal taxa (including humans) to show that most designs have been insufficiently accurate to pinpoint whether subjects' behavioural adjustment was caused by social or majority influences. Important to note here is the logical distinction between social and majority influences: although majority influence is inevitably social influence, behavioural adjustment caused by social influences need not be caused by majority influence. For instance, individuals could discard their personal preference by copying alternative behaviour from just one other individual, as opposed to the majority of individuals. This distinction would need to be taken seriously if conformity, defined by not just social but majority influence, is to be studied validly. For this reason, first, we review recent conformity findings across nonhuman animals (henceforth 'animals') in light of the distinction between social and majority influences. Second, we revisit the essential details of the human psychology studies that gave rise to the conformity definition and explore whether their findings could be explained in terms other than majority influence. Lastly, we conclude with suggestions to translate the definitional distinction between social and majority influences into empirical study designs. To be able to interpret the intriguing social phenomenon of 'conformity' in evolutionary terms, or identify the exact learning mechanisms present in species' behavioural repertoires, we need to calibrate the conformity designs across research disciplines.

To avoid confusion, it is important to explicitly distinguish between the conformity definitions that emerged from the study of human psychology and cultural evolution (see Morgan & Laland, 2012). The human psychology definition emphasizes the fact that individuals have to forgo their behavioural inclination, thereby adopting the behaviour of the majority (e.g. Asch, 1956; Jenness, 1932; Sherif, 1936). Thus, in this case, individuals possess a certain behaviour or conviction before being exposed to the conflicting stance of the majority. The cultural evolutionary approach, by contrast, investigates cost/benefit scenarios in which it would be beneficial (in terms of fitness consequences) for individuals to learn socially instead of individually, and has shown that in many cases where individuals are predicted to learn socially, they would favour not just any social information, but the information specifically transmitted by the majority of interactants (Boyd & Richerson, 1985; Henrich & Boyd, 1998; also see Aoki & Feldman, 2013). In other words, the cultural evolutionary approach analyses individuals on the verge of obtaining their first behavioural strategy, not individuals discarding their familiar behaviour. Thus, where the psychological approach to conformity focuses on the determinants of knowledgeable individuals' tendency to adjust their behaviour to the majority, the cultural evolutionary approach typically models the likelihood of naïve individuals obtaining the most common cultural variant. This subtle distinction could have important ramifications for understanding behavioural patterns indicative of conformity: where individuals in possession of a functional and/or preferred behavioural strategy might be more inclined to persevere in using their strategy than adopting random social information, individuals that are already predicted to learn socially could end up with the majority behaviour through exactly this process of random copying (e.g. see Mesoudi, 2009). We elaborate on this distinction in the section on human conformity findings. Furthermore, while the human psychology approach has traditionally been more concerned with immediately influential variables such as group size and task ambiguity (e.g. see Bond, 2005), the cultural evolutionary approach has mainly been concerned with the broader ramifications of behavioural decisions for the evolution of culture, expressed as relative within-group homogeneity and between-group heterogeneity (e.g. see Richerson & Boyd, 2005). For the reason that we are interested in the extent to which conformity can be identified through specific experimental features (i.e. the manipulation of group size) and dissected in social and majority influences, in this review we focus entirely on the human psychology operationalization of conformity.

DO PRIMATES SHOW CONFORMITY?

Most studies on conformity in animals have been conducted in nonhuman primates (henceforth 'primates'). On the one hand, the label 'conformity' has been used to describe the process by which primates obtain the strategy that gradually becomes the majority strategy. Starting with one skilled individual (natural invention or trained skill), the rest of the group acquires the same particular way of behaving by means of social learning (Hopper et al., 2011; Perry, 2009; Whiten et al., 2005). On the other hand, the label 'conformity' has been used to describe the process by which primates would revert back to the majority strategy after discovering an alternative strategy (chimpanzees: Bonnie et al., 2007; Hopper et al., 2011; Whiten et al., 2005; capuchin monkeys: Dindo et al., 2008, 2009). Here, after socially acquiring a particular way of behaving, some individuals would occasionally explore an alternative strategy, but then change back to preferring the majority strategy.

The interpretation of this latter behavioural pattern in terms of conformity has been criticized based on the fact that the same behavioural pattern could be explained by conservatism (i.e. the reluctance to switch techniques once one technique has been proficiently mastered; Hrubesch, Preuschoft, & van Schaik, 2009; van Leeuwen, Cronin, Schütte, Call, & Haun, 2013; van Leeuwen & Haun, 2013; Pesendorfer et al., 2009). In that case, the reconvergence to the majority behaviour might not even be socially mediated (see van Leeuwen & Haun, 2013). More relevant to the current focus, however, are the following issues.

First, in the case where conformity was claimed based on gradual behavioural convergence (e.g. Hopper et al., 2011, p. 6), for at least half of the group members there could not have been a majority present to conform to. In other words, for the first half of the group members, this gradual diffusion of information over individuals cannot possibly be attributed to conformity as it is typically defined. The second half of naïve learners could technically have been influenced by the majority (if all individuals of the first half adopted the behaviour demonstrated by the initiator); however, the social-learning process that was sufficient for the first half of the group to learn the target behaviour cannot be filtered out as an explanatory variable. More importantly, in this stage, none of the subjects have adjusted their behaviour to the majority; they have 'merely' acquired the behaviour that gradually becomes the majority strategy. This means that in this diffusion process, the two main features of the conformity phenomenon are compromised: copying the majority and forgoing individually acquired behaviour. In this light, the pattern in which subjects revert back to the majority strategy after discovering an alternative may have more grounds to claim conformity (i.e. in this case it could be argued that an established behaviour needs to be discarded). However, in these reversion studies, where subjects reconverged on the majority strategy after exploring an alternative strategy, it remained unexplored whether the reverting individuals had had the chance to actually observe the majority and questionable to what extent reverting back to the first-learned strategy entails forgoing individually acquired behaviour (see van Leeuwen & Haun, 2013). Moreover, a recent study found that chimpanzees who perceived a majority of group members engaging in a different (yet equally effortful and rewarding) strategy from themselves did not adjust