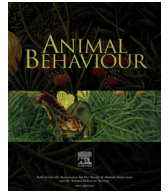




Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Forum

Conformity and its look-a-likes

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ARTICLE INFO

Article history:

Received 9 April 2015

Initial acceptance 11 May 2015

Final acceptance 11 July 2015

Available online xxx

MS. number: 15-00292

Keywords:

comparative psychology

conformist transmission

conformity

learning biases

majority influences

social learning

Following the crowd is usually dismissed as mindless acquiescence, devoid of original thought and authenticity. Despite this seemingly undesirable predicate, in human interactions majority influences seem pervasive, even beyond conscious control (Sweeny & Whitney, 2014). The influence of majorities on individuals' learning and decision making has therefore received ample attention in the scientific community. In particular, social psychologists and cultural evolutionists have been intrigued; the former group of scholars aiming at understanding the workings of specific social influences (e.g. Asch, 1956; Sherif, 1936), the latter interested in exploring evolutionarily stable strategies explaining the emergence and persistence of cultural diversity (e.g. Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981). These focused investigations have led to some seminal findings, for instance the robust fact that, in certain contexts, roughly a third of human adults adopt an erroneous majority stance against their better knowledge (Asch, 1956; Bond & Smith, 1996) and the mathematical fact that preferentially adopting the majority strategy yields culture-like phenomena (i.e. high level of within-group behavioural homogeneity induced by social-learning processes) under a wide range of

conditions (e.g. Boyd & Richerson, 1985; Henrich & Boyd, 1998; Richerson & Boyd, 2005).

Despite subtle differences in approach and interpretation (van Leeuwen & Haun, 2014; Morgan & Laland, 2012), most psychologists and cultural evolutionists have adhered to conformity's definitional aspect of adopting the preferred strategy of the majority of group members rather than simply the strategy observed most frequently (see van Leeuwen & Haun, 2014), thereby following the original definitions that emerged in the field of psychology (Asch, 1956; Sherif, 1936) and the field of the study of cultural evolution (Boyd & Richerson, 1985; Henrich & Boyd, 1998), respectively. Besides the benefits of definitional consistency, there is another reason for this particular adherence, which can be succinctly summarized by appealing to 'the wisdom of the crowd'. Mathematical and empirical analysis shows that large groups of individuals are better equipped to find correct answers to challenges than relatively small groups, a phenomenon that is also referred to as 'collective cognition' (Hastie & Kameda, 2005; King & Cowlshaw, 2007; Wolf, Kurvers, Ward, Krause, & Krause, 2013; note that 'the majority' by definition constitutes the largest portion of the population). Intuitively, this finding can be understood by acknowledging that the majority strategy is the strategy that most group members, with their unique sets of learning skills, have converged upon. As such, the majority strategy, usually, represents a robust synergy of individual capacities for discovering useful contingencies, which speaks to the adaptive potential of majority

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<http://dx.doi.org/10.1016/j.anbehav.2015.07.030>

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Please cite this article in press as: van Leeuwen, E. J. C., et al., Conformity and its look-a-likes, *Animal Behaviour* (2015), <http://dx.doi.org/10.1016/j.anbehav.2015.07.030>

influences. In contrast, the strategy observed most frequently will in many cases be biased towards the behaviour displayed by a small group of close association partners, which, given the postulated adaptiveness of the majority strategy, increases the probability of representing a suboptimal solution.

Within this definition of copying the majority of group members, the study of cultural evolution focuses on the disproportionate tendency of naïve individuals to adopt the majority strategy (originally coined 'conformist transmission', see [Boyd & Richerson, 1985](#)). In contrast, the study of social psychology typically focuses on individuals' tendencies to forgo their personal strategy and adopt the conflicting majority variant (originally coined 'conformity', see [Asch, 1956](#)). By now, a plethora of studies have evidenced conformity in both human children ([Corriveau & Harris, 2010](#); [Haun & Tomasello, 2011](#)) and adults ([Asch, 1956](#); [Bond, 2005](#)) and some evidence for conformist transmission in human adults exists as well ([Coultras, 2004](#); [Jacobs & Campbell, 1961](#); [Morgan, Rendell, Ehn, Hoppitt, & Laland, 2011](#)). Recently, scholars have similarly started to explore majority influences in nonhuman animals, either for reasons of understanding species-specific learning patterns ([Aplin et al., 2014](#)), or aiming at reconstructing the evolutionary path that led to the conformity observed in humans ([Whiten, Horner, & de Waal, 2005](#)). While this endeavour is to be applauded, crucial mismatches between the original majority influence constructs and the recent nonhuman animal studies significantly hamper our insights. By focusing on the most recent nonhuman animal study in this area ([Aplin et al., 2014](#)), we wish to clarify the study of majority-biased learning so that both species-specific behaviour and the evolutionary trajectory of (human) tendencies can be more validly assessed.

[Aplin et al. \(2014\)](#) claim an emergence and persistence of behavioural traditions via conformist transmission and conformity in wild great tits, *Parus major*. After training one individual in each of several populations to obtain a reward from an automated food dispenser by sliding a small door either to the left or to the right, the researchers were able to observe how entire populations converged on the same door-sliding technique, with some populations primarily sliding the door to the left and other populations primarily sliding the door to the right ([Aplin et al., 2014](#)). Yet, while [Aplin et al.'s](#) evidence regarding the emergence and persistence of great tit traditions (i.e. group-specific behavioural variants) seems robust, representing an admirable contribution to the limited literature on traditions in wild animals, their pivotal claims of demonstrating culture via conformist transmission and conformity seem misguided, as we argue below.

First and foremost, where [Aplin et al. \(2014\)](#) report that great tits consider the majority when learning socially, they operationalized the majority strategy as the strategy that is 'performed most frequently'. As explained above, however, in terms of both cultural evolution and the study of psychology, the meaningful operationalization is the strategy that is 'performed by most individuals'. Sometimes these two definitions will capture the same thing, but, crucially, sometimes they will not. If, for instance, individual A performs Strategy 1 six times and individuals B, C, D and E perform Strategy 2 once each, under [Aplin et al.'s \(2014\)](#) account Strategy 1 is the majority strategy, while, to the best of our knowledge, in terms of all studies on cultural evolution, Strategy 2 would be considered the majority strategy. Note that the aforementioned synergy of individuals' learning capacities (collective cognition: represented by the majority strategy) does not apply to behavioural repetitions by one individual (in this example: individual A). Hence, this critique is not just a plea for definitional consistency: (mathematical) logic and empirical work on the adaptiveness of majority influences use 'individuals' as their locus of analysis, not mere 'frequencies' of behaviour patterns (e.g. [Boyd & Richerson, 1985](#); [Day, MacDonald, Brown, Laland & Reader, 2001](#); [Hastie &](#)

[Kameda, 2005](#); [King & Cowlshaw, 2007](#); [Wolf et al. 2013](#)). Confusion over individuals versus frequencies may arise because modelling studies often use a conformist transmission function expressed in terms of frequencies, but derived from the number of individuals in a population ([Walters & Kendal, 2013](#)). Yet, a recent empirical study even shows that the effects of individuals and frequencies can be teased apart experimentally, with the evidenced differences in behavioural outcomes corroboratively indicating the necessity to refrain from confounding individuals and frequencies ([Haun, Rekers, & Tomasello, 2012](#)).

One way in which [Aplin et al. \(2014\)](#) claim that the majority influenced the birds' behaviour is through conformist transmission. Recapitulating, conformist transmission can be adaptive because it represents collective cognition: it allows a learner to integrate the output of multiple individuals' social and individual learning experiences ([Boyd & Richerson, 1985](#); [Richerson & Boyd, 2005](#)). Under [Aplin et al.'s \(2014\)](#) operationalization of the majority, however, this advantage may not have been present. Minimally, we must know how many other birds were actually observed by the learners (including their relative strategy preferences), yet these details are not provided ([Aplin et al., 2014](#)). If [Aplin et al.](#) were able to reanalyse their data such that each individual could be scrutinized in light of its unique individual-based observation records (e.g. individual A observes three conspecifics using Strategy 1 and nine conspecifics using Strategy 2), a valid investigation of conformist transmission would be possible by comparing the majority sizes they observed (in this example: 75%) to their likelihood of adopting the majority strategy (in this example: Strategy 2). Note that apart from the mathematical logic and empirical findings postulating the adaptiveness of copying the majority of individuals, which does not necessarily apply to copying the majority of occurrences (see above), conformist transmission has been coined as majority copying with the majority being operationalized in terms of individuals, not frequencies (see [Boyd & Richerson, 1985](#); [Henrich & Boyd, 1998](#)). Note further that while conformist transmission can result in tradition formation ([Boyd & Richerson, 1995](#); [Henrich & Boyd, 1998](#)), the fact that [Aplin et al. \(2014\)](#) found that birds formed traditions (i.e. behavioural homogeneity caused by social-learning processes) does not in itself evidence conformist transmission (NB this is not claimed by the respective authors, yet seems to be a common misconception in the study of majority influences in general). Traditions can arise and stabilize due to many different transmission biases, not just conformist transmission (e.g. see [Boyd & Richerson, 1985](#); [Haun, van Leeuwen, & Edelson, 2013](#); [Kendal, Coolen, & Laland, 2009](#)). Then, in order to distinguish between such transmission biases, detailed knowledge on individuals' observation records is required (e.g. [Kendal et al., 2015](#)).

[Aplin et al. \(2014\)](#) furthermore claim that the majority continued to influence the birds, even after they had acquired a working strategy. Two lines of evidence are provided for their majority influence interpretation: (1) of the birds that used both foraging solutions ($N = 78$), eight gradually switched from using the nonseeded variant to the seeded variant (while none made the reciprocal switch) and (2) 10 of 14 birds switched their strategy preference when immigrating into groups in which the alternative solution had been seeded 'to match the common variant in the new location' ([Aplin et al., 2014](#)). [Aplin et al.](#) interpret these cases as evidence for 'social conformity', a term that refers to forgoing preferred behaviour in order to match the majority of individuals (see above: [Asch, 1956](#)). [Aplin et al.'s](#) study, however, does not provide sufficient evidence for conformity because, as previously outlined, (1) frequencies do not necessarily equal individuals and (2) it is unknown what the birds observed before switching their preferences. In other words, in the cases where information was

available on how many times the two foraging solutions were observed by the respective birds (i.e. residents switching from the nonseeded to the seeded strategy), no information is presented on across how many individuals these occurrences were distributed, and in the cases where only the relative strategy preferences are reported (i.e. immigrants switching their strategy 'to match the common variant in the new location'), the observation records of the respective birds remain opaque. Hence, interpretation in terms of majority influence (here: conformity) seems premature. Indeed, a likely alternative explanation for the outlined behavioural patterns is that the great tits employed a learning strategy in which social information was always preferred over individual information, perhaps especially when this social information was the most recently acquired piece of information. For instance, the first 'conformity' case reported by Aplin et al. (preference switch within populations; see above) could be explained by the respective birds individually learning the nonseeded foraging solution followed by subsequent social learning of the seeded solution. In a similar vein, the second 'conformity' case reported by Aplin et al. (preference switch after immigrating into a new population; see above) could be explained by immigrant birds updating their foraging strategies by copying the behaviour of locally attuned conspecifics, for instance based on a 'copy when uncertain' bias, since the respective birds had entered a new group/environment. Crucially, such cases of (biased) social learning do not automatically allow for interpretation of the respective behavioural patterns in terms of majority influences: while social influences comprise many different mechanisms and biases, majority influence can only be demonstrated by providing evidence of the behavioural influence being caused by the majority of group members, e.g. by excluding alternative explanations (van Leeuwen & Haun, 2014).

In general, within-group behavioural convergence can come about in many different ways and should not be taken as evidence for majority influences without closer scrutiny, not even when individuals explore alternatives and reconverge on their first learned solution (see van Leeuwen & Haun, 2013; van Leeuwen, Cronin, Schütte, Call, & Haun, 2013 in response to e.g. Dindo, Whiten, & de Waal, 2009; Hopper, Schapiro, Lambeth, & Brosnan, 2011; Whiten et al., 2005). Not only individual-learning proclivities (e.g. 'habit formation', see Pesendorfer et al., 2009), but also social-learning tendencies other than majority influences must be ruled out before (re)convergence patterns can be interpreted in terms of majority influences (van Leeuwen & Haun, 2014). Another illustrative case of, in our view, premature majority influence conclusions is presented in a recent wild vervet monkey, *Chlorocebus aethiops*, study by van de Waal, Borgeaud, and Whiten (2013). In this study, immigrating male vervet monkeys adjusted their food colour preference (e.g. pink) to the food colour preference of the new group (e.g. blue). This preference switch was interpreted in terms of conformity, yet it was unknown what and whom the immigrating males had observed prior to their preference switching (van de Waal et al., 2013). Instead, in both the great tit and vervet monkey cases, it has been assumed (rather than empirically shown) that the target individuals had observed the distribution of strategies over the respective individuals. Apart from the lack of scientific accuracy, this assumption seems very unlikely. For example, the great tits foraged in flocks of close to 100 birds (on average), while the apparatus employed arguably only provided room for a few birds at a time, making it very improbable that all nonactors observed the actions of the actor (see Aplin et al., 2014). Similarly, the vervet monkeys most likely foraged in subgroups induced by dominance dynamics, making it plausible that not majority influences, but other social influences were at play in affecting the immigrants' food colour preferences (see van de Waal et al., 2013).

Overall, we wish to emphasize that the identification of transmission biases (e.g. copy dominant individuals, copy when uncertain, copy the majority) requires robust measurement of individuals' observation records and that it seems unnecessarily inaccurate to make assumptions about these records when such information can be approximated by more detailed analysis (Kendal et al., 2015): potentially premature conclusions, in the absence of supporting evidence regarding who observed whom perform which strategy, will only hamper the empirical study of transmission biases.

Acknowledgments

This work was supported by the University of Jena, Durham University, the University of Birmingham and a grant from the Economic and Social Research Council (ESRC) to C.T. (ES/K008625/1).

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