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Forum

Counting conformity: evaluating the units of information in frequency-dependent social learning

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In a recent study (Aplin et al., 2015), we conducted a large-scale cultural diffusion experiment in which we used trained 'demonstrator' individuals to introduce one of two alternative foraging techniques into five replicate subpopulations of wild great tits, *Parus major*. Three further subpopulations served as controls. By tracking the spread of these two techniques, we showed that information was acquired through social learning, transmitted through social network ties, and novel behaviours became established in each subpopulation, forming stable arbitrary traditions (for technique A or B). These traditions persisted over generations and were stable despite immigrating and innovating individuals, resulting in a within-group behavioural homogeneity and between-group variation. Most pertinent for this discussion, our experimental design allowed an examination of the interaction between individual decision making and population level outcomes. We found that the population level bias for each introduced technique increased by an average of 14% per day towards the common variant. This was explained both by a tendency for naïve individuals to disproportionately adopt the most common behaviour ('conformist transmission') and by a tendency for individuals with experience of both techniques to change their behaviour to match the common variant ('conformity').

While accepting our evidence for the population level patterns, van Leeuwen, Kendal, Tennie, and Haun (2015) have challenged the validity of our individual level results. This is largely because of the way conformist transmission was defined and measured within the context of the paper: as copying the majority of observed behaviours, rather than as copying the behaviour of the majority of observed individuals. They make three main arguments to this effect. First, there is a need for definitions to be consistent with previous theoretical and empirical work. Second, only copying the 'behaviour of the majority of individuals' represents adaptive collective cognition, while copying the 'majority of behaviours' is more likely to result in suboptimal information. Their third argument is that the within-group convergence in traditions observed in our study was more likely to have arisen through alternative mechanisms. We address each of these points in turn and present an alternative viewpoint: that conformity should be considered as an umbrella term with a functional focus. We then present additional analyses of our original results to demonstrate the artificiality of the

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argument that there is only one 'valid' form of positive frequency-dependent social learning.

In their article, van Leeuwen et al. (2015) argue that there is one acceptable definition of conformity: copying the behaviour of the majority of individuals. First, it is important to acknowledge that there have been a variety of definitions used in the literature (reviewed in Claidiere & Whiten, 2012). In many discussions of social-learning strategies, a conformist bias has been defined as a 'non-linear learning rule, where the probability of adopting a behaviour depends non-linearly on the frequency of that behaviour in the population' (Whalen & Laland, 2015, p.543; also Morgan & Laland, 2012) or simply as 'a propensity to preferentially adopt the cultural traits that are most frequent in the population' (Henrich & Boyd, 1998, p.219) without specifying whether the unit of frequency is behaviour or individuals (Kendal, Giraldeau, & Laland, 2009; Mesoudi, 2011, 2015; Mesoudi & Lycett, 2009; Mesoudi & Whiten, 2008; Nakahashi, 2007; Rendell, Boyd, et al., 2011; Rendell, Fogarty, et al., 2011). This second approach reflects empirical work, where the underlying unit of frequency is usually not measured or reported, and both decision-making processes are together called conformist transmission (e.g. Aplin et al., 2015; Galef & Whiskin, 2008; Hopper, Schapiro, Lambert, & Brosnan, 2011; van de Waal, Borgeaud, & Whiten, 2013; Whiten, Horner, & de waal, 2005). The exceptions to this have been in studies of shoaling fish, where individuals are necessarily making a choice between groups of demonstrators (Brown & Laland, 2002; Day, Macdonald, Brown, Laland, & Reader, 2001; Pike & Laland, 2010).

Is van Leeuwen et al.'s (2015) insistence on defining conformity as copying the behaviour of the majority of individuals therefore reasonable? It is likely that in most natural and experimental situations (as we discuss below), there will be a close correlation and functional equivalence between the 'behaviour of the majority of individuals' and the 'majority behaviour'. If so, the two can only be separable with targeted, often artificial, experiments (Haun, Rekers, & Tomasello, 2012). This raises an immediate question as to whether differentiating these definitions has any functional relevance. There is currently no evidence from natural human or nonhuman animal populations, as far as we are aware, that individuals distinguish between the behaviour of the majority of individuals and the majority of behaviours, or are more likely to use one or the other (Aplin et al., 2015; Claidiere, Bowler, Brookes, Brown, & Whiten, 2014; van de Waal et al., 2013). Therefore it seems most appropriate to take an inclusive approach, referring to all majority influences as conformity and conformist transmission, then disentangling decision-making processes under this umbrella term when it is of interest to do so. Note that, while van Leeuwen et al. (2015) state that "the majority' by definition constitutes the largest portion of the population', this is only correct if 'population' means a sample of countable entities. This might as well be behaviour as individuals: the use of the term majority implies nothing about the type of entity that is quantified.

Second, we question the assumption that copying the behaviour of the majority of individuals is the most adaptive strategy choice in all circumstances. van Leeuwen et al. (2015) argue that a strategy of copying the majority behaviour may bias observers towards those individuals seen most frequently, resulting in suboptimal information. However, in spatially heterogeneous environments such as those thought to favour the evolution of conformity (Henrich & Boyd, 1998; Kandler & Laland, 2013; Nakahashi, 2007), this bias may actually result in the acquisition of the most relevant information, and facilitate greater group level cohesion (Aplin, Farine, Mann, & Sheldon, 2014). Furthermore, useful additional information may be contained within the observed frequency of behaviours: frequently observed individuals are likely to be more resident and may also be more successful, thus possessing better local information than transient individuals observed more rarely. While the interaction between population structure and selection on social-learning mechanisms has been relatively unexplored, social network approaches give the opportunity to examine these trade-offs by quantifying each individual's social environment (Aplin et al., 2015; Whalen & Laland, 2015).

Yet even if it were true that copying the behaviour of the majority of individuals always provides better information, the most adaptive strategy does not solely depend on the quality of information. A strategy based on copying the majority of individuals imposes an additional cognitive load for individual recognition and book-keeping memory that might outweigh any selective advantage (i.e. observers need to track both the number of behaviours and the number of individuals). In addition, if individuals are not entirely consistent in the information they provide, then observers will need, in effect, to do a multistep calculation to weigh the value of observed behaviours. To illustrate this, consider a focal individual that has observed three demonstrators (i_x) performing a behaviour 10 times each, using either technique X or Y: i_A does $X = 10$, i_B does $X = 6$ and i_C does $X = 3$. If the focal individual uses a 'majority behaviour' strategy, then $(10 + 6 + 3)/30 = 63\%$ and therefore the focal individual does X. By contrast, if the focal individual uses a 'behaviour of the majority of individuals' strategy, then the calculation is, for i_A, $10/10 = 100\%$ (X is most common), for i_B, $6/10 = 60\%$ (X is most common) and for i_C: $3/10 = 30\%$ (Y is most common); thus $(i_A + i_B) / (i_A + i_B + i_C) = 67\%$ and therefore the focal individual does X. Note that this does not consider whether individuals also consider demonstrator uncertainty; for example, is i_A at 100% consistency treated as equal to i_B at 60% consistency?

Returning to Aplin et al. (2015): our results showed a sigmoidal relationship between the frequency of the variant in the social group that had preceded a naïve bird's first successful solution and the probability that the naïve observer adopted that variant. This was taken as consistent with the interpretation that naïve individuals were disproportionately copying the majority behaviour (Morgan & Laland, 2012), as illustrated in Fig. 1a. To note, the mean social group size was not 100 birds, as incorrectly reported in van Leeuwen et al. (2015) ($N = 100$ is approximately the mean subpopulation size), but rather mean ± SD = 4.2 ± 2.4. Given previous knowledge of the life history of this population and species, it is a reasonable inference that the focal individuals had observed the actions of their social group that immediately preceded their own behaviour (Aplin et al., 2014; Aplin, Farine, Morand-Ferron, & Sheldon, 2012; Aplin, Sheldon, & Morand-Ferron, 2013; Farine et al., 2015; Psorakis, Roberts, Rezek, & Sheldon, 2012; Slagsvold & Wiebe, 2011). Here, we redo this analysis, but now measuring the proportion of individuals that were observed performing each behavioural variant in the social group that preceded a naïve bird's first successful solution (Haun et al., 2012). Within these social groups, individuals could give repeated demonstrations and were not always consistent, and so were assigned to the variant they performed most often in the given time period. Doing this, we again find a sigmoidal relationship, with evidence that individuals are disproportionately likely to copy the behaviour of the majority of individuals (Fig. 1b). The estimated function is very similar to that obtained from a 'copy the majority behaviour' learning rule (Fig. 1a).

Yet on further exploration of our data, it becomes clear that it is impossible to distinguish between these two potential learning strategies. In our study, there were never any instances when the information provided to naïve observers from copying the majority of observed behaviours or the behaviour of the majority of individuals conflicted (Fig. 2). This is despite variation in the number of behaviours performed by each demonstrator and in the consistency of demonstrators. There is no evidence that the individuals