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https://doi.org/10.1016/j.anbehav.2015.07.030

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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, psychologists and cultural evolutionists have been intrigued: the former group of scholars aiming at understanding the workings of specific social influences (Asch 1956; Sherif 1936), the latter interested in exploring evolutionarily stable strategies explaining the emergence and persistence of cultural diversity (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 fact that preferentially adopting the majority strategy can yield culture-like phenomena (i.e., relatively high level of
within-group behavioural homogeneity) under a wide range of conditions (Boyd & Richerson 1985; Henrich & Boyd 1998; Richerson & Boyd 2005).

Despite subtle differences of approach or interpretation (Morgan & Laland 2012; van Leeuwen & Haun 2014), psychologists and cultural evolutionists have in principle all 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. Besides the benefits of trans-disciplinary 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 show 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 & Cowlishaw 2007; Wolf et al. 2013) (note that “the majority” by definition constitutes the largest sub-group in a 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 represents a robust synergy of individual capacities for discovering useful contingencies, which speaks to the adaptive potential of majority influences.

Within this definition of copying the majority of group members, cultural evolutionists study the disproportionate tendency of naïve individuals to adopt the majority strategy (originally coined “conformist transmission”, see Boyd & Richerson 1985). In contrast, psychologists focus 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 (Coults 2004; Jacobs & Campbell 1961; Morgan et al. 2011).
Recently, scholars have similarly started to explore majority influences in non-human
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 non-human animal studies significantly hamper our insights. By focusing on
the most recent non-human 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 and colleagues claim an emergence and persistence of behavioural
traditions via conformist transmission and conformity in wild great tits (Aplin et al.
2014). After training one individual in each of several sub-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 sub-populations converged on
the same door-sliding technique. Yet, while their evidence regarding the emergence and
persistence of great tit traditions (i.e., group-specific behavioural variants) seems robust,
and represents an admirable contribution to the limited literature on traditions in wild
animals, their pivotal claim of demonstrating culture via conformist transmission and
conformity is seemingly misguided, as we will argue below.

First and foremost, where Aplin et al. report that great tits consider the majority
when learning socially, they operationalized the majority strategy as the strategy that is
“performed most frequently” (Aplin et al. 2014). 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 one time each, under Aplin et al.’s account (Aplin et al. 2014), 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 actually indicates the central role of individuals in majority influences, not mere frequencies of behaviour patterns (Boyd & Richerson 1985; Hastie & Kameda 2005; King & Cowlishaw 2007; Wolf et al. 2013). Confusion over individuals versus frequencies may, in part, 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). 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 et al. 2013).

One way in which Aplin et al. claim the majority influenced the birds’ behaviour is through conformist transmission (Aplin et al. 2014). Recapitulating, conformist transmission is adaptive because it represents collective cognition: it allows a learner to integrate the output of multiple individuals’ social and individual learning experiences
Under Aplin et al.’s operationalization of the majority, however, this advantage may not have been present (Aplin et al. 2014). 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 re-analyse their data such that each individual could be scrutinized in light of their 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 further that while conformist transmission can result in tradition formation (Boyd & Richerson 1995; Henrich & Boyd 1998), the fact that Aplin et al. (Aplin et al. 2014) found that birds formed traditions does not in itself evidence conformist transmission. Traditions may arise and stabilize due to many different transmission biases, not just conformist transmission (Boyd & Richerson 1985; Haun, van Leeuwen & Edelson 2013; Kendal, Coolen & Laland 2009).

Aplin et al. furthermore claim that the majority continued to influence the birds, even after they had acquired a working strategy. Two cases are reported as evidence for their majority influence interpretation, i) of the birds that used both foraging solutions \( (n=78) \), 8 birds gradually switched from using the non-seeded variant to the seeded variant, and ii) 10 out of 14 birds switched their strategy preference when immigrating into groups where the alternative solution had been seeded to match the new groups’ preference (Aplin et al. 2014). Aplin et al. interpret these cases as evidence for ‘social conformity’ (or 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 (Aplin
et al. 2014), however, does not provide sufficient evidence for conformity because, as previously outlined, i) frequencies do not necessarily equal individuals, and ii) 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, there is no information presented on across how many individuals these occurrences were distributed, and in the cases where only the relative strategy preferences are reported, the observation records of the respective birds remain entirely 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 non-seeded 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 (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 re-converge on their first learned solution (see van Leeuwen & Haun, 2013 & van Leeuwen et al. 2013 in response to e.g., Dindo et al. 2009; Hopper et al. 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 premature majority-influence conclusions is present in a recent wild vervet monkey study by van de Waal and colleagues (van de Waal, Borgeaud & 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). In both the great tit and vervet monkey cases, therefore, we wish to stress that the identification of transmission biases (e.g., copy dominant individuals, copy when uncertain, copy the majority) requires robust measurement of individual’s observation records (e.g., see van Leeuwen et al. 2013; Kendal et al. 2015). Thus, 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.

Recapitulating, we believe that, due to an invalid operationalization of “the majority”, and the absence of data on birds’ observation records, Aplin et al. (Aplin et al. 2014) cannot substantiate their conclusions that the great tit traditions emerged and stabilized due to the claimed majority-influenced learning – neither conformist
transmission nor conformity has been sufficiently evidenced yet. More generally, with
the aim to streamline the study of species-typical social learning behaviour (e.g. Laland
2004) and the evolutionary trajectory of (human) cultural transmission tendencies, we
wish to emphasize that the identification of conformist transmission and conformity
necessitates scrutiny on the level of the majority of individuals.
REFERENCES


