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CHAPTER

Conformist Transmission

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Abstract

Conformist transmission is a transmission bias, or social learning strategy, that disproportionately favours popular cultural variants. Over the past 40 years it has received a great deal of attention, both theoretical and empirical. Here the authors provide an overview of the current state of this literature, including what conformist transmission is; how it relates to other similar terms; how it can be operationalized mathematically; its adaptive value; the impact it has upon cultural evolutionary dynamics; and the evidence for and against it in humans and other species. The authors conclude by identifying gaps in current theory and limitations of experimental work. In particular, the authors emphasize the need for theory that accounts for demonstrators with inconsistent preferences and the need for empirical work to carefully distinguish between conformist tendencies and conformist evolutionary dynamics.

Keywords: [conformist transmission](#), [conformity](#), [majority-biased transmission](#), [anti-conformist transmission](#), [social learning](#)

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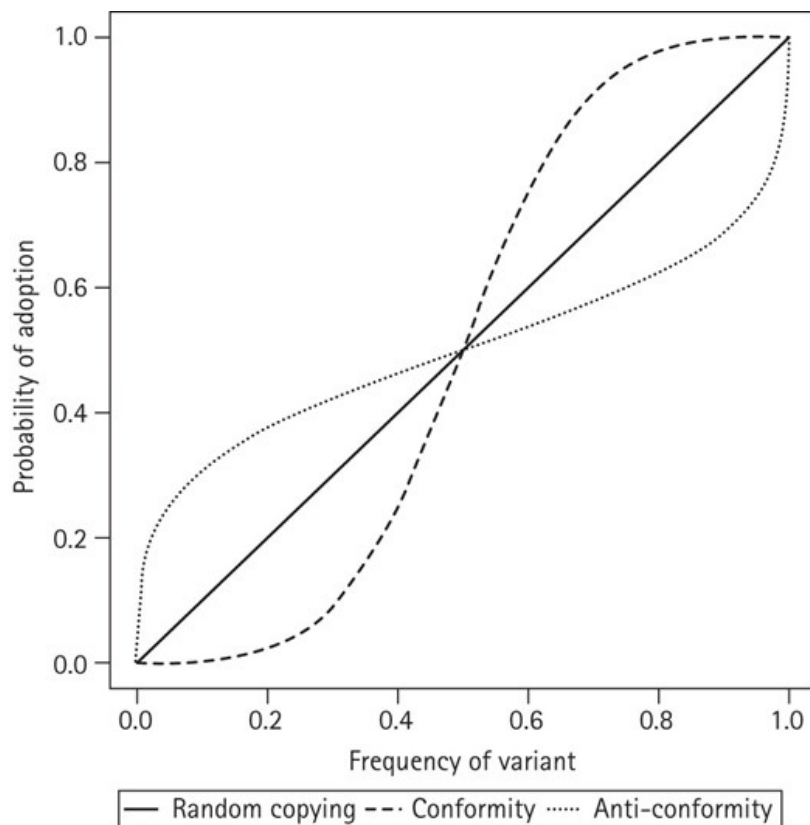
Central to cultural evolution is cultural inheritance: the processes by which information, beliefs, attitudes, and practices are transmitted between individuals. Cultural inheritance is readily observable, being a function of behaviour and psychology, and a large literature has grown around the study of social learning (Hoppitt & Laland, 2013; see Wild & Hoppitt, this volume), documenting when and how individuals learn from or are influenced by each other and how this varies across cultures and species (Clegg & Legare, 2016; Mesoudi et al., 2014; van Leeuwen et al., 2018). In particular, attention has been given to how social learning is non-random, in other words directed towards certain kinds of models, certain kinds of information, or occurring under certain conditions—collectively referred to as transmission biases (Boyd & Richerson, 1985) or social learning strategies (Laland, 2004; see Kendal & Watson, this volume). Many possibilities

have been considered, including transmission biases based on payoffs, prestige, age, kin, certainty, and survival (Kendal et al., 2018; Rendell et al., 2011). Perhaps chief among these, at least in terms of the extent of its study, is *conformist transmission*, the disproportionately likely adoption of behaviours exhibited by the majority of group members (Boyd & Richerson, 1985; Henrich & Boyd, 1998).

What Is Conformist Transmission?

As noted, conformist transmission is the disproportionate adoption of majority variants (Boyd & Richerson, 1985; Morgan & Laland, 2012). The word ‘disproportionate’ is critical and means that the probability an individual adopts the majority variant must be greater than the proportional size of the majority (see Figure 1). To illustrate, suppose a nomadic individual was choosing between relocating their camp today or waiting another week to see if more favourable conditions arise. Further suppose that some other nearby camps have already made their decision, and 73 per cent of them are relocating today, while the other 27 per cent are waiting a week. For conformist transmission to occur, the individual in question (as well as any other undecided observers) must have a probability of choosing to relocate today of more than 0.73.

Note that this definition is behavioural as opposed to psychological. That is, the definition places requirements on the probability of adoption, but not on the goals or intentions of the observer that produce this probability. For instance, it does not matter whether the learner is seeking accurate information about the best course of action or simply to fit in with their group. All that matters is whether their probability of adopting the majority variant exceeds its current prevalence. As such, conformist transmission can be said to occur provided the adoption probability exceeds the proportional size of the majority *for any reason*. More importantly, even if the observer intends to conform, if the probability of adoption falls under the size of the majority then conformist transmission will not occur. As such, while psychological processes that are not sensitive to proportion may only sporadically lead to conformist transmission, even those that *are* oriented towards the majority may not do so consistently.

Figure 1

A graphical representation of conformist transmission, random copying, and anti-conformist transmission. The definition of conformist transmission requires that the probability of adoption exceeds the variant's frequency while the latter is over 0.5 (otherwise, due to symmetry, the probability falls below the variant's frequency). The result is an 'S-shaped' relationship. Anti-conformist transmission has the opposite requirement—the probability of adopting the popular variant must fall below its frequency, and so produces a different curve.

Figure reproduced, with permission, from Morgan & Laland (2012).

What Isn't Conformist Transmission?

There exist several terms related to conformist transmission in the cultural evolutionary and social psychological literatures. Here, we will briefly introduce these terms and clarify how they differ from conformist transmission (see Table 1 for a summary).

By far the most well-known cousin of conformist transmission is 'conformity', originating with the now famous result that individuals will sometimes conform to a unanimous majority exhibiting clearly incorrect decisions (Asch, 1955). As such it is often studied in contexts where the focal behaviour is highly unusual. However, conformity has also been used to refer to the adjustment of behaviour in response to observing others, regardless of majority influences (Galef & Whiskin, 2008; Jolles et al., 2011; see Haun et al., 2013), and at times it is used interchangeably with social learning and even conformist transmission. As such, 'conformity' is a highly general term, and unlike conformist transmission it does not place any requirements on the proportional size of the majority (Bond, 2005; Cialdini & Goldstein, 2004; Morgan & Laland, 2012; van Leeuwen et al., 2015).

Another term in the literature is 'majority-biased transmission' (Evans et al., 2018; Haun et al., 2012; Van Schaik, 2012). Just like conformity, majority-biased transmission refers to any instance where the probability of adopting the majority option is greater than 0.5 and does not require that it is greater than the

proportional size of the majority. However, in contrast to ‘conformity’ (yet like conformist transmission), the focus of majority-biased transmission is on naïve subjects learning a new behaviour rather than on subjects forgoing a pre-existing behaviour in the face of majority influence (van Leeuwen & Haun, 2013). Moreover, majority-biased transmission can only be at play in the presence of majority/minority ratios (thus not with unanimous majorities) and works with individuals rather than behaviours as the unit of analysis. That is, should a demonstrator be observed to perform the same behaviour multiple times, this should carry no more weight than a single performance because majority-biased transmission is defined in terms of the number of individuals performing a behaviour, not how many times they each perform it. On this basis, chimpanzees were described to exhibit majority-biased transmission when they selectively copied the majority of individuals, not the majority of demonstrations (Haun et al., 2012). Only if their copying probability would have been significantly higher than the proportional majority size would they be said to have engaged in conformist transmission (see also Battesti et al., 2014; Chou & Richerson, 1992; Lefebvre & Giraldeau, 1994; Haun et al., 2013).

A final related term is ‘anti-conformist’ transmission, proposed as the counterpart to conformist transmission (Boyd & Richerson, 1985) and defined as a case where the probability of adopting the majority option is less than the proportional size of the majority, but nonetheless may exceed 0.5 (see Figure 1). As such, in our camp relocation example, if the observer has a 0.6 chance of relocating today this would be considered anti-conformist transmission because it falls below the current frequency of the behaviour in the population: 0.73. This definition may seem surprising as even though the observer is somewhat biased towards the majority option they are still deemed to be anti-conformist. However, the reasoning behind it becomes clear once we consider the population-level consequences of these learning rules (see below).

Table 1 The definitions and population-level consequences of conformist transmission and related terms.

Term	Meaning	Difference from conformist transmission	Population-level consequences	Example references
Conformist transmission	The disproportionate adoption of majority variants	N/A	Variation decreases within groups, but increases between groups	(Boyd & Richerson, 1985; Morgan & Laland, 2012)
Conformity	Various: The adoption of (often clearly incorrect) majority variants; the adjustment of personal behaviour towards that of others; occasionally used interchangeably with conformist transmission and/or social learning	Adoption does not need to be disproportionate	Various	(Asch, 1955; Galef & Whiskin, 2008; Jolles et al., 2011)
Majority-biased transmission	The adoption of majority variants by naïve observers	Adoption does not need to be disproportionate	Various	(Evans et al., 2018; Haun et al., 2012; Van Schaik, 2012)
Anti-conformist transmission	The sub-proportionate adoption of majority variants	Adoption probability is below variant prevalence, not above it	Variation increases within groups, but decreases between groups	(Boyd & Richerson, 1985; Morgan, 2014)

Defining Conformist Transmission Mathematically

Many possible formulas can be used to model conformist transmission. The only requirement is that the formula must take the variant’s popularity as its input and return a probability that exceeds the popularity if the popularity is over 0.5, but falls below the popularity if it is below 0.5. If we label the popularity as q and the probability as p then we can express these conditions as follows:

$$p = \begin{cases} 0, & q = 0 \\ < q, & q < 0.5 \\ 0.5, & q = 0.5 \\ > q, & q > 0.5 \\ 1, & q = 1 \end{cases} \quad (1)$$

Beyond this, there are multiple specific instantiations of conformist transmission. In their seminal definition, Boyd and Richerson (1985) used the following:

$$p = q + dq(1 - q)(2q - 1) \quad (2)$$

where d is a parameter that controls the strength of conformist transmission. This function has been used to analyse experimental data (van Leeuwen et al., 2021), and although it is relatively straightforward to work with, it nonetheless produces values of p that fall outside 0 to 1 with extreme values of d , and so this must be accounted for.

Boyd and Richerson's function was expanded by Eriksson and Coultas (2009) to relax the assumptions that (i) when $q = 0.5$, $p = 0.5$, (ii) when $q = 0$, $p = 0$, and (iii) when $q = 1$, $p = 1$. Instead, three new parameters were added such that (i) when $q = 0.5$, $p = p_{neutral}$, (ii) when $q = 0$, $p = p_0$, and (iii) when $q = 1$, $p = p_1$. This was done to maximize flexibility for fitting experimental data, producing the following equation:

$$p = p_0 + (p_1 - p_0)q - 2(p_0 + p_1 - 2p_{neutral})q(1 - q) + dq(1 - q)(2q - 1) \quad (3)$$

An alternative formulation, introduced by McElreath et al. (2008), is as follows:

$$p = \frac{q^d}{q^d + (1 - q)^d} \quad (4)$$

Here the parameters have the same interpretation, however p will always fall between 0 and 1 and so be a valid probability. The downside is that, given this function's liberal use of exponents, it is much less convenient to work with analytically. Nonetheless, it has been used both in data analysis and theoretical models (Morgan et al., 2014, 2019; Morgan & Thompson, 2020).

Conditional on d , all these functions can describe both conformist and anti-conformist transmission, and so the precise formulation to use is up to the researcher. Nonetheless there remain subtle yet potentially important differences. For instance, while equation (4) can describe anti-conformist transmission, unlike equation (2) it cannot do so to the extent that the minority option is preferred. That is, equation (4) assumes that even anti-conformist individuals will always favour the majority variant over the minority variant, if only to a miniscule extent, whereas equation (2) extends to cases where anti-conformist individuals actively favour minority variants. This seemingly modest difference can produce markedly different cultural evolutionary dynamics (Denton et al., 2020; Morgan, 2014). As such, while researchers are free to use whichever formulation best suits their needs, it is important to bear in mind the hypotheses each formulation can entertain and, therefore, test.

Conformist Transmission and Cultural Evolutionary Dynamics

The cardinal motivation for studying cultural inheritance is its relationship with cultural change. Conformist transmission increases the popularity of already popular variants, driving them to fixation (Boyd & Richerson, 1985; Morgan & Laland, 2012). It has thus been argued that conformist transmission may be integral to the emergence and maintenance of (arbitrary) group norms (Henrich & Boyd, 1998). Indeed, the fact that conformist transmission is entirely content-neutral sets it apart from other biases (such as payoff-biased transmission that inherently favours fitness-enhancing traits) because conformist transmission can lead *any* behaviour to stabilization (see Kendal & Watson, this volume, for further explanation).

The stipulation that the probability of a trait's adoption exceeds the proportional size of the majority displaying it makes sense once the population-level consequences are considered; only when this requirement is met do popular variants increase in frequency, otherwise (i.e. under anti-conformist transmission) the majority will steadily decrease in size, even if the probability of adoption is over 0.5. Anti-conformist transmission also highlights the differences between the above formulations. While anti-conformist transmission as per equation (4) always drives the population towards maximal diversity (i.e. $p=q=0.5$), anti-conformist transmission as per equation (2) is more varied, being capable of producing periodic oscillations and chaotic dynamics (Denton et al., 2020; Morgan, 2014).

Nonetheless, the above theory glosses over some of the complexities of conformist transmission in practice. For instance, individuals cannot immediately know the current frequency of a variant and instead must estimate it by making observations of other individuals. Theory including such an inferential process, and allowing for biased estimations, found that a conformist psychological tendency may not result in conformist transmission. Importantly, this means that traditions may not be stable, or may never reach fixation at all (Morgan & Thompson, 2020).

The Adaptive Value of Conformist Transmission

The evolutionary rationale for social learning is that it provides individuals with useful information more quickly or cheaply than is otherwise possible (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Laland, 2004). As such, for conformist transmission to evolve, it must increase fitness relative to learning on your own (i.e. asocial learning) as well as other forms of social learning.

There is robust theoretical evidence that this is the case for conformist transmission, at least under appropriate circumstances. For example, a model of naive migrant individuals in a spatially variable environment found that upon joining a new group in an unfamiliar environment, conformist transmission was a very effective means by which the migrant individual could accurately learn about their new environment and identify locally adaptive behaviours (Boyd & Richerson, 1985). Expansions upon this work (Nakahashi et al., 2012) found that spatial variation, errors in learning, and the number of options between which individuals choose all favour the evolution of conformist transmission. Other work has compared conformist transmission to other forms of strategic social learning, including payoff-biased transmission (Kendal et al., 2009). In this case it was found that environmental variation favoured payoff-biased transmission, while a more stable environment favoured conformist transmission.

The adaptive value of conformist transmission comes from its ability to aggregate the information produced by multiple individuals into a single decision. Other work has confirmed that simply doing what the majority do is a highly successful way to respond to the decisions of multiple individuals (Hastie & Kameda, 2005) and that its utility increases with group size (King & Cowlshaw, 2007). Nonetheless, conformist

transmission is not a perfect decision-making process; for instance it performs poorly in an unstable environment (Perreault et al., 2012). The reason for this is that responding to environmental change requires suitable innovations to spread; however, any new innovations start in the minority and so conformist transmission will act against them (Eriksson et al., 2007). Indeed, theory has observed that conformist transmission can become so dominant during periods of stability that it leads to catastrophic population declines when the environment does change (Whitehead & Richerson, 2009). As such, a conformist psychological bias applied across all situations is likely to be weak, such that other factors can drive the spread of rare but valuable behaviours (Kandler & Laland, 2013; Perreault et al., 2012).

Evidence for Conformist Transmission in Humans

Virtually all of the empirical tests of conformist transmission in humans have been laboratory studies conducted with WEIRD (Western, Educated, Industrialized, Rich, and Democratic) populations (Henrich et al., 2010; see Stengelin et al., this volume). In general these have found evidence in favour of conformist transmission across a range of computer-based tasks, including crop choice (McElreath et al., 2005), technology choice (Efferson et al., 2008), quantity estimation and mental rotation (Morgan et al., 2011), and length estimation (Muthukrishna et al., 2016). An experimental study in which young children had to estimate whether an array of dots contained more blue or yellow dots found that the youngest children (three and four years) were anti-conformist but that this developed into a conformist response by around age six (Morgan et al., 2014).

Nonetheless, not all studies have found evidence of conformist transmission. For instance, Eriksson and Coultas (2009) asked participants to agree or disagree with 12 statements (e.g. 'Married people should always wear rings'). While responding, participants could see the (manipulated) decisions of nine other individuals but the results showed very little social influence, and no evidence of conformist transmission. Similarly an experimental study recruiting from subsistence pastoralists in southern Bolivia (a non-WEIRD population) found that individuals mostly relied on their own past experience instead of conformist or payoff-biased transmission (Efferson et al., 2007).

These results can nonetheless be reconciled. Note that (i) theory suggests that any overarching conformist tendency will be weak, and (ii) most theory assumes variant popularity is the only information individuals have to guide their decision, while in these experiments individuals typically come with prior beliefs (Eriksson & Coultas, 2009) or receive additional information as part of the experiment (Morgan et al., 2011). As such, a weak conformist tendency at the psychological level may be masked and not produce a conformist response at the behavioural level. Indeed, Morgan et al. (2011) only detected a conformist psychological tendency by statistically controlling for these other factors, while conformist transmission at the behavioural level required highly specific conditions. Similarly, Efferson et al. (2008) did observe conformist transmission at the behavioural level but used a design such that social learners had access only to information about popularity and so more closely replicated theoretical assumptions.

Another explanation for the inconsistent findings is that a conformist tendency may itself vary in strength across conditions, being potent when popularity is the only information available but much weaker otherwise. For instance, conformist transmission has been observed to increase in strength with the number of options available to choose from, the fitness relevance of the decision, and the fidelity of transmission (Muthukrishna et al., 2016). In addition, there is plenty of evidence that conformist transmission, and social learning more generally, varies across individuals. For instance, Efferson et al. (2008) found that while many participants identified as conformists and behaved accordingly, many others did not, a group characterized as 'mavericks'. Similar inter-individual variation has been documented in

other studies (Morgan et al., 2011; Muthukrishna et al., 2016) and so appears to be a common feature of human social learning.

Evidence for Conformist Transmission in Other Species

The evidence for conformist transmission outside humans is remarkably mixed. This may reflect the wide range of species studied. However, even within a single species there is dramatic variation in the observed behaviour.

While social learning among primates has been extensively studied (see Whiten, this volume, and van de Waal & Canteloup, this volume), few experiments have considered conformist transmission in particular. One possible exception is a study of ‘majority-biased transmission’ in human children, chimpanzees, and orangutans (Haun et al., 2012) in which observers could place a token in one of three receptacles; a popular option (used by three others), an unpopular option (used by one other), and a third option (used by no-one). Chimpanzees exhibited a preference for the popular option, human children were more mixed, and orangutans behaved at random. Nonetheless, the preference among chimpanzees was not strong enough to be considered conformist transmission (Haun et al., 2012). Another relevant paper studied collective movement in wild baboons, finding that, when multiple subgroups initiated movement in different directions, the group as a whole displays a sigmoidal response to the absolute difference in size of the groups (Strandburg-Peshkin et al., 2015). However, this study measured the absolute size difference between the subgroups, not their proportional sizes, and the total size of the subgroups varied. As such, a dedicated analysis testing for conformist transmission may be required.

Less direct evidence comes from a variety of studies finding that in some primate species, seeded behaviours can spread through groups and persist even as alternative behaviours are discovered. Species in which this has been documented include chimpanzees (Hopper et al., 2011; Whiten et al., 2005; for an example with naturally occurring behaviour see van Leeuwen, 2021; van Leeuwen & Hoppitt, 2023) and capuchin monkeys (Dindo et al., 2009; for an example with naturally occurring behaviour see Perry, 2009). Other studies observed that vervet monkeys (van de Waal et al., 2013) and chimpanzees (Watson et al., 2018) would switch to group-typical behaviours when migrating to neighbouring groups, or being amidst large enough groups of group members, respectively. However, while all these studies are broadly consistent with conformist transmission, they are unable to rule out other processes and so cannot provide unambiguous evidence.

Regarding birds, there have been multiple studies of conformist transmission. Paramount among these is a study of free-ranging great tits that found strong evidence of conformist transmission (Aplin et al., 2015; see Aplin, this volume). The birds were provided with a puzzle box that could be solved in two ways, and different populations were seeded with trained birds proficient in one method or the other. The seeded solutions quickly spread and dominated the populations while the unseeded solutions remained unpopular despite being discovered. Using indirect co-presence data to estimate the observations made by each bird, the authors’ analysis also produced a clear sigmoidal curve between the proportional popularity of a behaviour and its probability of adoption, the hallmark of conformist transmission. Further work found that although conformist transmission was present, the birds combined it with information about payoffs such that suboptimal behaviours did not persist (Aplin et al., 2017). Another example of conformist social learning was found in the song learning of swamp sparrows. By analysing the song repertoires of 615 adult male swamp sparrows and comparing syllable frequency distributions to the output of individual-based simulations, researchers found evidence of a conformist bias, with a combination of overproduction and selective attrition proposed as the underlying mechanism (Lachlan et al., 2018).

Not all studies with birds have found similar results. For instance, an experimental study examining conformist transmission in zebra finch foraging decisions (van Leeuwen et al., 2021) provided birds with two feeders, each with a different number of demonstrators, and measured the response of observer birds. In this case, they found that the birds did not appear to attend to the decisions of other birds (i.e. which feeder they were at) but instead were influenced by the intensity of their activity when feeding (i.e. the number of pecks), most likely using it to estimate patch richness, a form of social learning known as ‘public information use’ (Danchin et al., 2004). Moreover, the response to the frequency of pecks at each feeder was anti-conformist rather than conformist.

Among fishes, many studies of social learning have been conducted with sticklebacks (Laland, 2017; see Brown, this volume). Of these, one has specifically tested for conformist transmission (Pike & Laland, 2010). This study presented nine-spined sticklebacks with two feeders, each of which was populated by a group of demonstrators. The sizes of the groups were varied (3 versus 3, 2 versus 4, and 1 versus 5) and the observers’ response measured. The study reports evidence in favour of conformist transmission on the basis that as one feeder became increasingly popular the observers increasingly favoured it, with the influence growing in an accelerating fashion. However, such a response is actually consistent with anti-conformist transmission; under conformist transmission the growth of influence would *decelerate* as the majority size increases because even small majorities have a disproportionate influence and their influence quickly reaches ceiling levels as the majority grows. The decelerating growth of influence results in an S-shaped influence curve whereas accelerating growth of influence with majority size is a feature of anti-conformist transmission (see Figure 1). Nonetheless, another study found that U-turns in swimming schools of rummy-nose tetras propagate from front to back in a conformist fashion allowing the school to move as a cohesive unit (Lecheval et al., 2018). However, the relationship between rapid U-turns while swimming and more deliberative decisions, such as where to forage, may not be simple.

Lastly, among invertebrates, there are two studies of conformist transmission in fruit flies, however they find entirely different results. In one case, flies were provided with two egg-laying substrates (strawberry or banana flavoured) and observed groups of pre-trained demonstrators with varying numbers of demonstrators favouring each substrate. However, while there was clear evidence of social influence (albeit somewhat muted), it did not match conformist transmission (Battesti et al., 2014). The other study presented female flies with males painted green or pink, and a group of six demonstrators each of which mated with either a green or pink male (the composition was varied). The results showed that female flies favoured the majority preference regardless of the majority size, which is broadly consistent with conformist transmission (Danchin et al., 2018; see Danchin et al, this volume), although note that these results have been challenged (Thornquist & Crickmore, 2019). However, even if the results hold, when the majority was unanimous the response fell short of the popularity, which is inconsistent with conformist transmission. The result is a sigmoidal curve that combines elements of conformist transmission (disproportionate influence of small majorities) with anti-conformist transmission (sub-proportionate influence of large majorities). Consequently, the response of flies does not drive popular variants to fixation but instead keeps them around 75 per cent. Among groups as small as those studied, this allows for drift to periodically reverse the direction of the group norm, as was observed experimentally (Danchin et al., 2018).

Future Directions: Theory

The theoretical basis of conformist transmission is quite mature. Many of the foundational contributions (Boyd & Richerson, 1985; Henrich & Boyd, 1998) have been followed up with more recent models that elaborate on some of the underlying assumptions. For instance, examining what happens if observers attend to instances of a behaviour being performed as opposed to the number of individuals performing it (Morgan et al., 2019), or what happens if individuals must estimate the size of the majority from incomplete data (Morgan & Thompson, 2020), as well as a debate over the extent to which sigmoidal curves can be produced by psychological tendencies other than a conformist one (Acerbi et al., 2016; 2018; Smaldino et al., 2018). Nonetheless, there are several major gaps remaining.

Notably, the majority of theory deals solely with a choice between two options or variants. This may be a significant deficiency, because empirical data suggest that the number of variants affects the extent to which humans engage in conformist transmission (Muthukrishna et al., 2016) with it being weakest for two variants. Models by Kandler and Laland (2013), and Nakahashi et al. (2012) allow for more variants but do so by assuming that conformist transmission involves *always* selecting the most popular option, rather than doing so disproportionately.

Another limitation of theory is its assumption that demonstrators will only ever perform one option. However, in reality, demonstrations are often mixed. For instance, the flies trained to lay eggs on a specific substrate only did so around 65 per cent of the time—well over chance but far from perfect consistency (Battesti et al., 2014). Conformist theory has not explored how individuals should respond to such mixed demonstrations, though it does make clear that whether or not observers reduce multiple performances by a single individual to a single preference can change cultural dynamics (Morgan et al., 2019).

Lastly, given that it seems plausible that there might be considerable variation in the presence, absence, and strength of conformist transmission across species, it would be constructive for theory to identify factors that promote or inhibit its evolution. As discussed above, theory already suggests that conformist transmission is favoured in stable environments (Kendal et al., 2009). However, this alone is unlikely to explain the observed diversity, and a more complete account is required.

Future Directions: Experiment

The number of experiments testing for conformist transmission has grown considerably over the past decade and testifies to its perceived importance as a foundational part of cultural inheritance. However, the inconsistency of the results across species is no less striking. Here, we will suggest methodological tweaks that we hope will increase the robustness of any findings.

A major difficulty with conducting studies of conformist transmission among non-human animals is keeping track of (or precisely controlling) who sees which demonstrators/demonstrations. In the case of the great tit study (Aplin et al., 2015), the simplifying assumption was made that observers saw everything taking place at the feeder over a short time leading up to the observer's interaction with the feeder, and nothing beforehand. While an expedient heuristic, it is potentially problematic when different groups share access to the same feeders and switch location across similar time scales (van Leeuwen et al., 2016). In studies of social learning and conformity in chimpanzees, video data have been used to identify who was watching each demonstration (Kendal et al., 2015; van Leeuwen et al., 2013), and such an approach may be valuable in studies of conformist transmission and social learning biases in general.

Furthermore, analyses testing for conformist transmission typically use an analogue of one of the functions described above as part of their model. However, whichever function is chosen, the resulting models are not

totally free to fit any shape and as a result are often asking whether the data are more consistent with a specific formulation of conformist transmission or a linear response (though depending on the specific equation, forms of anti-conformist transmission may be tested as well). This can lead to false positives if the data are not actually a result of conformist transmission but resemble it more so than the other considered responses (Acerbi et al., 2016; 2018; Smaldino et al., 2018). Given this level of uncertainty, a robustness check is to repeat the analysis by binning the data according to the option popularity among demonstrators and then fitting a categorical model. While such an approach decreases statistical power, it is nonetheless free to take any shape, and in the case of data from adult humans, this approach found that the assumed function was underestimating the strength of conformist transmission (Morgan et al., 2011).

As discussed above, one thing that theory has established is that whether individuals attend to the number of demonstrators favouring each option, or whether they attend to the number of demonstrations, can affect cultural evolutionary dynamics and erode popular traditions (Morgan et al., 2019). Nonetheless many animal studies use demonstrations (as opposed to demonstrators) as their measure of popularity (for an example where demonstrators and demonstrations are distinguished, see (Haun et al., 2012)). This is in many ways highly sensible as keeping track of demonstrations may be less demanding than using demonstrators to infer the preferences of your individual group members. Nonetheless, it means these experiments may be testing something other than conformist transmission and so care should be taken with interpretation.

A final issue with current experimental work is that it pays insufficient attention to the distinction between a conformist psychological tendency and conformist cultural evolutionary dynamics. As noted above, a conformist tendency may not lead to tradition stability if other factors influence behaviour to the extent that the conformist tendency is overwhelmed. Nonetheless, many studies conclude that conformist evolutionary dynamics are likely given that evidence for a conformist tendency has been found. This can be seen in a study of adult humans (Morgan et al., 2011) where although evidence for an underlying conformist tendency is clear (and validated with a categorical model), many other variables are at work (like a participant's confidence in their prior beliefs) and as a result of these dynamics participants' behaviour falls far short of that required to stabilize traditions. More care needs to be taken in cases like these. An example of work attempting to bridge the gap from tendency to dynamics is the study of mate choice in fruit flies. Here the authors executed a cultural evolutionary simulation, inserting the flies' observed tendency to conform to the mate choices of their demonstrators (Danchin et al., 2018), and documented the cultural evolutionary dynamics it produced. Such work is a valuable test of whether observed conformist tendencies produce conformist transmission at the population level. Nonetheless, they require significant extrapolation (in the fruit fly study, the simulated population sizes were far larger than those studied experimentally) and cannot account for what might happen were other variables included. A more direct approach is to use large populations and then simply observe tradition stability, as was done in meerkats (Thornton et al., 2010) and chimpanzees (van Leeuwen, 2021), where traditions persisted even after significant population turnover. However, depending on the species, the study duration might be quite short compared to the generation length of the species under consideration and so such an approach may not always be feasible.

Conclusion

The study of conformist transmission has come a great way since its inception almost 50 years ago. Early theoretical work highlighted its importance to cultural evolution and the role it can play in stabilizing arbitrary group norms. More recent theory is adding complexity and caveats to this picture and additional work needs to be done to generalize conformist transmission to cases with more than two options and inconsistent demonstrators. In the past 20 years empirical work has begun to flesh out a picture of conformist transmission within and across species. However, the empirical literature, both human and non-human, is strikingly diverse in its findings making it difficult to draw clear conclusions about the nature, evolution, and distribution of conformist transmission. Empiricists should pay more attention to whether an observed conformist tendency is sufficient to produce conformist evolutionary dynamics, how this interacts with other factors, and the extent to which the conformist tendency itself is context sensitive. Once such a comprehensive account can be achieved there will be clarity concerning the evolution of a conformist tendency, its capacity to shape cultural change and stabilize traditions, and the role it has played in the evolution of culture.

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