Forum

A reappreciation of 'conformity'

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Whiten & van de Waal (this volume) present an answer to a critical account of their conformity interpretations (van Leeuwen et al., 2015). Their target study (van de Waal et al., 2013) evidenced immigrant male vervet monkeys adjusting their food colour preferences to the preference demonstrated by the resident vervets, which was interpreted in terms of conformity. Van Leeuwen and colleagues (2015; also see van Leeuwen & Haun, 2013 and online commentary by Tennie, Fischer, Galef & Haun, 2013, at Sciencemag.org) acknowledged the insight gained from the reported observations for our understanding of social learning processes in wild primates, but criticized van de Waal et al.'s conformity interpretation (2013) as alternative learning biases, other than conformity, could not be ruled out. In their reply to this critique, Whiten & van de Waal (this volume) systematically list their arguments against alternative explanations. Whiten & van de Waal (this volume) also present new data indicating that in their target study (2013) the "majority of individuals" opting to perform a specific behaviour correlated with the "majority of behaviours" performed across the population, thereby adding to a recent debate about how "the majority" should be operationalized in order to study conformist transmission (see Aplin et al., 2015a in response to van Leeuwen et al., 2015). Here, we respond to Whiten & van de Waal (this volume) by i) discussing how their arguments against our alternative explanations for their conformity interpretation (as advanced in van de Waal et al., 2013) may be misguided, ii) defending the position that their presented correlation between the "majority of individuals" and the "majority of behaviours" is tangential to the current debate, iii) presenting evidence in favour of our original suggestion to keep reliance on the "majority of individuals" and the "majority of behaviours" as two separate learning biases, and iv) realigning the debate between Aplin et al. 2015a and van Leeuwen et al. 2015 to focus again on animals' observation records as prerequisite knowledge to interpret their behavioural decisions in terms of learning biases.

Alternative explanations

In line with Whiten & van de Waal (this volume), we define conformity as "abandoning personal preferences or behaviours to match alternatives exhibited by a majority of others" (Haun, van Leeuwen & Edelson, 2013). In their original study (van de Waal et al., 2013), male vervet monkeys who were trained to prefer one of two food colours in their native group immigrated to a new group where the alternative food colour was preferred and adjusted their preferences accordingly (except for one high-ranking male who maintained his native preference). These immigrants were typically confronted with a large group of residents feeding from the alternative food colour, while very few or none of the residents fed from the food colour the immigrants were most familiar with (see illustrations in Whiten & van de Waal, this volume). Van de Waal et al. (2013) interpreted these behavioural adjustments by the immigrants as 'conformity'. In response to this interpretation, van Leeuwen & Haun (2014; also see van Leeuwen et al. 2015) pointed out that although the immigrants might have been guided by inclinations to conform to the majority, alternatively, they might have been guided by other (social) learning biases that are independent of majority considerations. For instance, the immigrants might have been focused on copying particular resident individuals, like visibly dominant individuals, or indeed *any* resident individual, precipitated by their immigration-induced stress, anxiety or general state of uncertainty. Whiten & van de Waal (this volume) replied to this suggestion by arguing that any transmission bias other than 'copy-the-majority' is unlikely to explain the switching behaviour of the immigrants. For instance, they argue that the fact that the immigrants do not have female kin in their new group rules out a kin-based learning rule. Likewise, they propose that male vervets are relatively *poor* in recognizing the social hierarchy of females, ruling out a 'copy high-rankers' learning rule (Whiten & van de Waal, this volume). While these particular proposals may or may not be correct, more generally, we wish to emphasize that although field experiments with wild animals are to be applauded for their ecological validity, they do not have any superior claim on epistemological validity. When confounding effects cannot be controlled for rigorously, interpretation of observed patterns need to be made cautiously.

Whiten & van de Waal (this volume) argue most forcefully against the 'random copying' interpretation of their data, stating that: '…for the immigrant vervets to copy just one individual randomly would seem rather *perverse* in the face of the repeated, extensive and quite consistent scenarios of multiple monkey preferences staring immigrants in the face…' (line 95-98). We disagree. Clearly, the sheer availability of information is no guarantee it will be utilized in expected ways, or, at all. Random copying is as good a predictor of the observed patterns of transmission as conformity: When observer monkeys are consistently confronted with the majority of residents feeding from one particular food colour, while only a few, or none, of the resident monkeys feed from the alternative, copying a random individual would, probabilistically, boil down to observer monkeys tending to use the foraging option demonstrated by the majority rather than that demonstrated by the minority, irrespective of observers' particular preference for copying the majority. We consider this a potentially more parsimonious explanation – if observer monkeys could obtain the locally practiced foraging rule by the mere inclination to copy, there is no need for them to apply a cognitively more demanding rule like 'conform to majorities'.

Typically, an investigation of whether individuals copy the majority with a higher probability than the relative size of the majority (henceforth 'the disproportionate criterion') is applied to ascertain that individuals are indeed *majority*-biased, or at least to exclude the possibility that individuals merely copy randomly (e.g. Laland, 2004; Mesoudi, 2009). We note that the disproportionate criterion can be viewed as rather stringent and unrealistic for cases in which individuals have already obtained a working strategy, where the key behaviour of interest is the foregoing of prior information for an alternative ('conformity'). Indeed, the disproportionate criterion is typically used in the context of naive individuals setting out to obtain a useful strategy by means of social learning; the context in which *conformist transmission* (CT) is studied (e.g. Boyd & Richerson, 1985; Morgan et al., 2014). In the CT context, when individuals are confronted with a balanced population in which only two possible strategies exist, it is assumed that copiers solely rely on social information and thus have a 50% likelihood of obtaining one or the other strategy. Similarly, when strategy A is wielded by 70% of the demonstrators, and strategy B thus only by 30%, copiers have a 70% likelihood of obtaining strategy A by chance, i.e. if they were to apply a *random copying* rule. To show that individuals *preferentially* copy the majority, and not just by chance, the disproportionate criterion should be adhered to, meaning that in this case copiers should have a likelihood of obtaining strategy A that is significantly larger than 70%. However, in this same example, if individuals are *not* naive and thus have already learned to prefer one strategy over the other, e.g. strategy B, the assumption that they will obtain strategy A or B with a 50% likelihood (in the balanced 2-variant population) is unrealistic. Instead, these experienced individuals will most likely stick to their familiar strategy, in this case strategy B. In a similar vein, experienced strategy B users will not have a 70% chance of ending up with strategy A when 70% of the population they could sample from are strategy A users. If these experienced individuals turn out to start using strategy A with a 70% likelihood, in fact, one could consider this to be a strong indication ('disproportionate' in a sense) of majority influence (see Haun, Rekers & Tomasello, 2014). Thus, contrary to the CT setting, when individuals are experienced, it seems less valid to interpret a copying probability in accord with the relative majority size (here: 70%) in terms of *random copying*: past experience must be weighted in and perhaps a lower threshold than the majority display accepted as strong evidence for conformity (see van Leeuwen & Haun, 2014).

For the vervet monkeys (van de Waal et al., 2013), given that i) they were indeed experienced in preferring one food colour over the other when they encountered the opposing demonstrations in the new population, and ii) many of them chose to eat from the food colour in accord with these preference-opposing demonstrations (perhaps in numbers approximately matching the relative majority size, although here, crucially, this cannot be confirmed as the vervets' observation records are missing; see below for more on this topic), this might indicate that 'random copying' could be dismissed as a mechanistic explanation in favour of 'majority copying'. It is important to note, however, that this conclusion rests on the crucial assumption that no other variables were at play in the decision arena of the respective vervets, which is arguably not true. Notably, the immigrant vervets were leaving behind a familiar home range, and social setting, while moving into an unknown territory with unknown conspecifics ('a different habitat': van de Waal et al., 2013, p. 484). We could envisage the very predicament of the migrating vervets as sufficiently potent to induce a motivation to obtain new, locally more attuned behaviours (ecologically and/or socially). Van de Waal and colleagues (2013; also see Whiten & van de Waal, this volume) acknowledge that such drastic changes in the lives of the vervets could have facilitated the so-called 'copy-when-uncertain' rule (Laland, 2004), a social learning heuristic for which evidence has been found across a wide range of taxa (e.g. see Kendal et al., 2009). They explicitly echo our suggestion by writing: "The fitness of foraging decisions made by wild primates like those we studied will be governed by a host of complex factors that are inherently unknown to foragers, ranging from dietary constituents to plant toxins and competing needs such as predator vigilance: Exploiting the prior discoveries of local experts may be an optimal strategy, overriding opposing knowledge gained in a different habitat such as one's original group." (van de Waal et al., 2013, p. 484). Yet, crucially, neither van de Waal et al. (2013) nor Whiten & van de Waal (this volume) consider the possibility that the 'copy-when-uncertain' heuristic *alone* could have caused the immigrants to adjust their foraging preference upon entering their new environment. It is entirely reasonable that the uncertainty of their new environment changed the default information-gathering mode of the immigrants to "copy" anybody (instead of relying on possibly out-dated and locally inadequate personal strategies).

Given the discussion above, and widespread local foraging traditions, the simplest form of copying – random copying – would equip the immigrating vervets with the local "majority" strategy. In other words, the transition from home to unknown territory could have reset the vervet monkeys, rendering prior information irrelevant, turning them effectively into naïve learners. We call this the "reset hypothesis". One possible way to empirically test this hypothesis is to investigate whether immigrants would switch to the local foraging preference upon seeing a small number of residents showing a preference against an even larger background of non-behaving others, or, maybe a simpler case, upon seeing just one single resident's demonstration of this preference (something that may have been opportunistically possible to assess had immigrant observation records been acquired, see below). If these observers would switch their preference, *majorities* would cease to be the single possible object of the immigrants' copying efforts. Indeed, drawing on parsimony again, this finding would indicate that "conformity" is not even necessary to explain the immigrants' behaviour. Note that even if one adheres to the conformity definition of 'a willingness to subjugate one's own countervailing knowledge in matching the majority's choice' – as in van de Waal et al. 2013 supplementary material p. 6 – one is still left with the burden of proof for the claim that 'the majority' is being matched, not just any individual.

Overall, the problem with interpreting the observations made by van de Waal et al. (2013) is the lack of nuance in the data regarding observer monkeys responding to different majority/minority ratios of (inadvertent) demonstrator monkeys. If observers are only presented with one stimulus ("the majority"), which consists of many other stimuli ("general social information", "high-ranking individuals", "low-ranking individuals", "conspicuous individuals", etc.), it is impossible to disentangle the very learning bias that the observers follow, while this is exactly what we want to know (e.g. see Heyes, 2016). For instance, if we were to investigate the evolutionary roots of conformist decision-making and we find that immigrant vervet monkeys, patas monkeys and rhesus macaques all adjust their preferences to the majority of the new group, we would need to know whether they were biased to "the majority" or to any other cue provided by the majority, for without this knowledge, the apparent similarity in decision-making strategies across these species may be purely coincidental.

Majority of individuals versus majority of behaviours

Due to our emphasis (van Leeuwen et al., 2015) upon the need for observation records in interpreting transmission events, we are delighted to find more detailed analysis on the observation records of the vervet monkeys (van de Waal et al., 2013) in their follow-up paper (Whiten & van de Waal (this volume)). Whiten & van de Waal (this volume) present an analysis of how the number of individuals feeding from the locally-preferred food colour correlated with the number of behaviours (handfuls of corn) regarding this same food colour. Specifically, they state: "Indeed the two variables [individuals and behaviours] show a significant correlation across the twelve sample periods ($r = 0.67$, $n = 12$, $p = 0.018$). Accordingly we infer that the migrant males' striking switch from their own to the opposite local preference was an effect of these majority displays, and hence a case of conformity" (Whiten & van de Waal, this volume, L69-73). To clarify, Whiten & van de Waal (this volume) aim to address a subject pertaining to the analysis of *conformist transmission* that was discussed in van Leeuwen et al. (2015) and Aplin et al. (2015a). In summary, where van Leeuwen et al. (2015) argued for keeping separate the biases of following the majority of individuals versus the majority of observed behaviours, and only reserving the term 'conformist transmission' for the former, Aplin et al. (2015a) argued for grouping the biases together under the same term, i.e. 'conformist transmission'. Aplin et al. (2015a) based their argument on the fact that in their original great tit study (Aplin et al. 2015b), the birds did not seem to distinguish between individuals and behaviours (analysed in Aplin et al. 2015a). Following up on this debate, Whiten & van de Waal (this volume) echo Aplin et al.'s position by showing that in their vervet monkey study (van de Waal et al., 2013) the frequency of *individuals* using a certain behavioural option and the frequency of demonstration of this particular behavioural option in total were not affecting the observers differently. In other words, the monkeys were indistinguishably following the majority of individuals and the majority of behaviours (Whiten & van de Waal, this volume).

While we acknowledge the additional analysis and appreciate its intent, we do not find it compelling for several reasons. First and foremost, in line with our previous arguments, Whiten & van de Waal (this volume) neither use the frequency of individuals nor behaviours to test their conformity hypothesis against any other (social) learning bias. Therefore, the reported correlation between the frequency of individuals and behaviours, while representing an affirmation of internal validity, has no power to falsify alternative hypotheses. For instance, Aplin et al. (2015b), though confronted with similar limitations due to working with wild animal populations, obtained detailed records of birds responding to differently-sized majorities and incorporated their majority numbers, in terms of individuals and behaviours, into statistical analyses to provide insight regarding whether the birds actually *used* the majority cue or merely obtained the most common strategy randomly. Without such analysis, our understanding of transmission biases is not furthered by the reporting of a correlation between two possible measures. Note that due to the very nature of "the majority" (i.e. comprising more than half of the sampled individuals) measures of for instance, skilful, conspicuous and high-ranking individuals will also coincide with the majority strategy.

Furthermore, we note that two cases of correlation between the number of individuals and behaviours indicating the use of a particular strategy (Aplin et al., 2015a and Whiten & van de Waal, this volume) do not constitute sufficient evidence in favour of the two measures being 'functionally equivalent'. While scenarios in which the number of individuals and behaviours correlate are straightforward to envision, we could imagine other scenarios in which the two respective measures would diverge, either due to individual differences in performance rates (in conjunction with relative preferences for certain strategies) or population structure (increasing the likelihood of repetitively sampling the same individuals). Moreover, for reasons of informational accuracy, it may well matter if one individual "cries wolf" ten times, or if ten individuals (independently) do so once (e.g. see Wolf et al., 2013). We conjecture that the adaptive value of relying on indiscriminate sampling of behaviours versus relying on the aggregate knowledge of similarly poised, unpredictability-reducing conspecifics will differ to the extent that under certain conditions, one particular bias is expected to evolve (at the expense of the other). Formal modelling would be a constructive way forward in fuelling our understanding and expectations regarding this pending question, which was acknowledged by Aplin et al. (2015a). In the absence of such understanding, we fail to see how grouping two potentially distinct social learning biases (see Haun et al., 2012) under one and the same denominator of "conformist transmission" could be beneficial to the (comparative) study of learning biases.

Methodological concern for using the majority of 'behaviours' instead of 'individuals'

In addition to our conceptual arguments in favour of keeping separate the biases of relying on the majority of individuals versus the majority of behaviours (also see van Leeuwen et al., 2015), we now present a methodological argument in favour of this proposition. Specifically, we note that the gold standard to evidence conformist transmission has been to identify a sigmoidal relation between individuals' probability to copy the majority and the proportional majority size (e.g., see Boyd & Richerson, 1985; Chou & Richerson, 1992; Claidiere et al., 2012; Battesti et al., 2015; Aplin et al., 2015b; but see Acerbi et al., under review). A simple agent-based model may help illustrate one of the problems arising from considering the frequencies of *behaviours*, instead of the frequencies of *individuals*, in detecting this sigmoidal signature of conformist transmission.

Imagine a population of individuals randomly initialised with one of two behaviours, A and B. At each time step, one individual X is randomly selected from the population, and performs its allocated behaviour, and another individual Y is also randomly selected from the population, and then Y always copies the behaviour performed by X. If one plots the relation between the probability of copying a behaviour and the frequency of *individuals* that possess that behaviour at time *t*, the relation is perfectly linear (see Figure 1, left). Each behaviour is, in other words, copied with a probability equal to the frequency of individuals that possess it in the population. This is exactly what we would expect with unbiased – i.e. random – copying (e.g. see Boyd & Richerson, 1985; Henrich & Boyd, 1998; Mesoudi, 2009).

FIGURE 1.

However, if we plot the relation between the probability of copying a behaviour and the frequency of *behaviour* observed in the population, we obtain a sigmoidal relation, that can be mistaken for a signature of conformist transmission (see Figure 1, right). The reason for this result is that, as behaviours where randomly initialised, the total frequency (over all time steps) of the majority behaviour in the population will be, in most cases, lower than the frequency of individuals that possess that behaviour at time *t*. Imagine that behaviour A reaches fixation in the population. The probability to copy A will be 100%, but its cumulative frequency will be somewhat lower, as, at the beginning, at least some individuals performed behaviour B. This behavioural mixture is sufficient to create the effect in the bottom-left and top-right portions of the function, typical of a sigmoidal relation.

This effect is an artefact of how populations are initialised in the model, i.e. starting from a random mixture of the two behaviours, but it clearly shows that different analysis may lead to different results. More specifically, in this case, the analysis based on *individuals* reveals perfect linearity, in keeping with the individual-level random copying default, whereas the analysis based on *behaviours* reveals the sigmoidal relation between copying probability and relative frequency characteristic of conformist transmission (see Aplin et al., 2015b). In other words, the analysis based on *behaviours* leads to a detection of conformist transmission where clearly there is none (because all copying here is *random*).

A slightly more complex model shows an analogous result, without the need to initialise the populations in the above way. In this set-up, populations start naïve, and the two possible behaviours are instead introduced through individual innovations (each behaviour – A or B – with the same probability). Note that this set-up reflects the scenario in which conformist transmission is typically studied (e.g. Boyd & Richerson, 1985; Henrich & Boyd, 1998; Morgan & Laland, 2012; van Leeuwen & Haun, 2014). The guiding copying mechanism is exactly the same as in the previous model, i.e. random copying remains the only form of copying. The only twist in our new model is that innovation rate decreases over time, mimicking individuals gradually converging on a certain variant preference (we believe this to be a realistic scenario). The results are analogous to the previous model: an analysis based on *individuals* shows perfect linearity in keeping with the random copying default, but an analysis based on *behaviours* reveals a sigmoidal relation between copying probability and the variant frequency in the population (see Figure 2). The reason for this result is that an initial innovation rate creates a situation in which both behaviours become present – similar to the random mixture of behaviours with which the populations were initialised in the first model – and, after that, populations again converge on one of the two behaviours, as innovation becomes less influential. Regardless, it is striking that even in the more typically studied scenario of naive individuals exploring a novel cultural landscape (the conformist transmission scenario), the illusion of conformist transmission can still emerge when analysis focuses on *behaviours* instead of *individuals*.

FIGURE 2.

In conclusion, for reasons of conceptual, empirical and methodological clarity, we propose to keep the study of conformity and conformist transmission restricted to the level of *individuals* and pursue the study of the effects of repetitive exposure to stimuli or behaviours, regardless of their executors, in its own right. Accordingly, we note that in the seminal conformity studies "the majority" did not consist of *behaviours* but *individuals*. For instance, in the Asch studies (1956), "the majority" was assembled by a group of confederates each expressing one opinion, not by one confederate expressing his/her opinion multiple times (for studies on the (mere) exposure effect, see e.g. Bornstein, 1989; Zajonc, 1968).

The pivotal role of observation records

Finally, we wish to draw attention to the most prominent matter highlighted by van Leeuwen and colleagues (2015) in reference to the study of conformity in particular and social learning biases in general: observation records. Underlying all previous considerations, e.g. whether or not the social learning rule 'copy high-rankers' could explain the patterns described in van de Waal et al. (2013), lies the implicit assumption that the respective decision-makers have observed all available social information. We challenge this assumption and wish to emphasize that when it comes down to pinpointing (social) learning biases, it is essential that observation records are obtained and used in analysis, especially given that such data are accessible (e.g. see van Leeuwen et al., 2013; Kendal et al., 2015).

Whiten & van de Waal (this volume) respond to our previous criticism that in their original study (van de Waal et al., 2013) it was 'unknown what and whom the immigrating males had observed prior to their preference switching' (van Leeuwen et al., 2015, p.3) by stating that this is true for all studies, including experimental ones like that conducted by Haun and colleagues (2012). However, our criticism did not refer to the actual observations made by individuals – we agree that a certain level of assumption, ultimately even when using eye-tracking or more advanced technologies, is unavoidable. Instead, our criticism pertained to the assumption that the immigrants were somehow able to obtain knowledge of the available social information. The immigrant vervets' observation records were entirely absent in the original study claiming to have identified conformity (van de Waal et al., 2013) and remain too imprecise for the investigation of conformity in the follow-up analysis (Whiten & van de Waal, this volume). In the first instance, we refer to records of what/whom the vervets could have observed because they were *present* when the social information (which would need to be quantified per observation bout) was available. In the second instance, head orientation during the inadvertent demonstrations seems a crucial measure to report. Such measures provide the necessary information to link an individual's observational input (in this case: social information) to an individual's behavioural output (in this case: maintaining or adjusting food colour preference), and thus the relevant information to draw conclusions on individuals' specific learning biases.

Another example of individuals' observation records receiving insufficient consideration concerns the recent great tit study by Aplin and colleagues (2015b). While this study provides detailed analyses of the birds' tendencies to learn socially, including, importantly, their propensities to copy in response to different majority sizes, the very data central to their conformist transmission analyses rest on assumptions rather than observations. The authors derived an external measure of which birds typically flocked together and calculated an average ‘group length’ of flocking (i.e. 245 seconds) that was subsequently used during the experiment in order to *assume* that all birds operating the experimental task in this time-window obtained knowledge of each other’s choices. In other words, the authors did not score which birds were simultaneously present at the experimental task (or which birds observed each other), but instead relied on the assumption that the birds were in the vicinity of the experimental task at the same time as the birds that were considered to be “demonstrators”, and the further assumption that they paid attention to those demonstrations (see Aplin et al., 2015b). We feel this to be an unfortunate caveat in an otherwise excellently conceived and conducted study. Regardless of the plausibility of such assumptions, observational input is the very measure from which we aim to derive conclusions on individual’s (social) learning biases, which, in our view, makes it imperative to be as accurate as possible. We wonder, for instance, whether the birds with the most extreme copying probabilities (0 and 100%) had observed that the entire sub-group of their sub-population had not converged on one particular strategy (see Figure 1 in Aplin et al., 2015a). These data seem crucial for the sigmoidal pattern to emerge, which was used to argue for conformist transmission in the birds’ social learning patterns (Aplin et al., 2015b). Notably, new modelling insights show that this very sigmoidal pattern can emerge in the absence of individuals’ being conformist biased (Acerbi et al., under review), making it even more pertinent to know what the birds observed exactly.

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Figure Legends

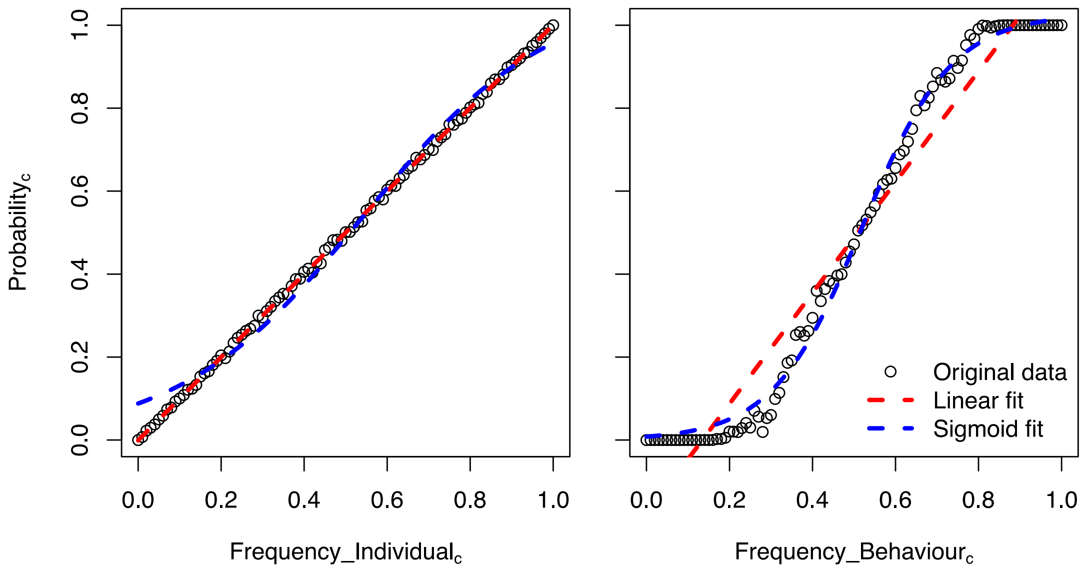

Figure 1. A population of N=100 individuals is randomly initialised with one of two behaviours. At each time step, a model and an observer are randomly extracted from the population, and the observer always copies the model. The simulation ends at 10,000 time steps, i.e. 10,000 possible interactions. Results are based on 1,000 replications of the model. Simulated data are fitted with a linear and a sigmoid model. Copying probability is plotted against frequency of individuals (a), and frequency of behaviours (b).

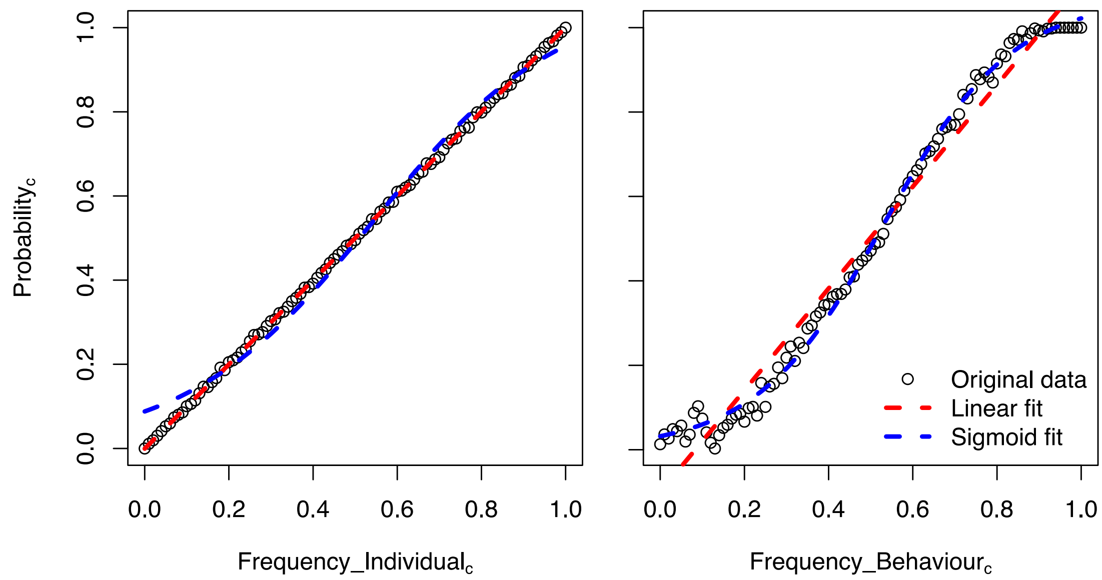

Figure 2. Simulations start with a population of N=100 naïve individuals. At each time step there is a probability that an individual, randomly extracted from the population, will innovate, i.e. will introduce, with equal probability, one of the two possible behaviours. Probability of innovation is initially equal to μ=.1 (one innovation every 10 time steps on average), and decreases exponentially with time, according to $e^{-5t/T}$, where t is the current time step, and T is the maximum amount of time steps. In addition, at each time step, a model and an observer are randomly extracted from the population, and the observer always copies the model. The simulation ends at 10,000 time steps, i.e. 10,000 possible interactions. Results are based on 1,000 replications of the model. Simulated data are fitted with a linear and a sigmoid model. Copying probability is plotted against frequency of individuals (a), and frequency of behaviours (b).