



Review Article

Conformity in nonhuman primates: fad or fact?

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ABSTRACT

Majority influences have long been a subject of great interest for social psychologists and, more recently, for researchers investigating social influences in nonhuman primates. Although this empirical endeavor has culminated in the conclusion that some ape and monkey species show “conformist” tendencies, the current approach seems to suffer from two fundamental limitations: (a) majority influences have not been operationalized in accord with any of the existing definitions, thereby compromising the validity of cross-species comparisons, and (b) the results have not been systematically scrutinized in light of alternative explanations. In this review, we aim to address these limitations theoretically. First, we will demonstrate how the experimental designs used in nonhuman primate studies cannot test for conformity unambiguously and address alternative explanations and potential confounds for the presented results in the form of primacy effects, frequency exposure, and perception ambiguity. Second, we will show how majority influences have been defined differently across disciplines and, therefore, propose a set of definitions in order to streamline majority influence research, where *conformist transmission* and *conformity* will be put forth as operationalizations of the overarching denominator *majority influences*. Finally, we conclude with suggestions to foster the study of majority influences by clarifying the empirical scope of each proposed definition, exploring compatible research designs and highlighting how majority influences are inherently contingent on situational trade-offs.

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1. Introduction

While humans are arguably the most creative and innovative of species, they sometimes seem to give precedence to majorities beyond reason. In a seminal set of studies, Solomon Asch showed that a substantial proportion of the adult subjects would forgo their personal opinion when confronted with an erroneous but unanimous group of peers (Asch, 1956). These findings have been replicated across cultures (Bond & Smith, 1996) and in children as young as 4 years of age (Haun & Tomasello, 2011; Walker & Andrade, 1996). Possible reasons for this seemingly irrational behavior are the benefits of group life, where avoiding social conflict through reducing behavioral dissimilarity plays an important role (Over & Carpenter, 2012), and the benefits of relying on the wisdom of the crowd, where discounting personal preferences in favor of the majority strategy on average reaps safer, more reliable, and more productive information (Boyd & Richerson, 1985; Henrich & Boyd, 1998; King & Cowlishaw, 2007). Where giving precedence to majority strategies can reap both social and informational benefits, it has also been advocated as one of the driving forces behind cultural diversification. In theory, adopting

the behavior displayed by the majority of individuals will produce within-group homogeneity, whereas the between-group heterogeneity will be accentuated (given initial between-group differences). As such, the tendency to “conform” to what most others are doing has been associated with the evolution of human cultures (Boyd & Richerson, 1985; Claidiere & Whiten, 2012; Efferson, Lalive, Richerson, McElreath, & Lubell, 2008; Henrich & Boyd, 1998).

In recent years, researchers have started to address majority influences in nonhuman animals in general (Day, MacDonald, Brown, Laland, & Reader, 2001; Galef & Whiskin, 2008; Pike & Laland, 2010) and nonhuman primates (hereafter called “primates”) in particular (Bonnie, Horner, Whiten, & de Waal, 2007; Dindo, Thierry, & Whiten, 2008; Dindo, Whiten, & de Waal, 2009; Hopper, Schapiro, Lambeth, & Brosnan, 2011; Perry, 2009; Pesendorfer et al., 2009; Whiten, Horner, & de Waal, 2005). The investigation of several primate species enables us to investigate the phylogenetic distribution and history of majority influences, as well as the processes that may have driven their evolution, thus shedding light on the evolutionary roots of this perplexing human behavior (MacLean et al., 2012; Haun, Jordan, Vallortigara & Clayton, 2010). The endeavor to validly study majority influences and compare the extent to which humans and primates are affected by majorities, however, seems in need of clarification (Galef & Whiskin, 2008; Pesendorfer et al., 2009). For instance, whereas social psychologists have used the term “conformity” to

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describe the tendency to forgo individual information in favor of the majority opinion (Asch, 1956; Bond & Smith, 1996; Sherif, 1936), cultural evolutionary models have operationalized “conformity” as the disproportionate tendency to copy the behavior that is most frequent in a given population (Boyd & Richerson, 1985; Henrich & Boyd, 1998). In this review, we evaluate the validity of the operationalizations used in the recent primate studies and aim to calibrate the study of majority influences by providing a conceptual and methodological framework.

2. Is primates' behavior affected by majorities?

While not originally set out to investigate majority influences, recent primate studies (Bonnie et al., 2007; Dindo et al., 2008; Dindo et al., 2009; Hopper et al., 2011; Whiten et al., 2005) have culminated in the conclusion that primates show “conformist” behavior (Claidiere & Whiten, 2012). The shared ground on which these studies build their conclusions is the observation that subjects tend to revert back to their socially learned solution of a “two-action problem” after discovering an equally effective alternative individually (the design used in these studies will hereafter be referred to as “reversion design”). Since their first solution was also acquired by most group members, the subjects seemingly revert back from a new innovation to the majority strategy. The critical problem, however, is that by seeding only one method in an isolated group of naïve primates, the subjects lack the crucial choice between the majority and minority strategy needed to investigate majority influences. One could argue that the “corruptions” from the first learned behavior may function as minority demonstrations for opportunistic bystanders; yet, these demonstrations will have to compete with an established and reliably reinforced behavioral contingency, deeming any conclusions on majority influences confounded with maintaining familiar and reliable information.

In the following paragraphs, we will present an alternative explanation for the observation that primates revert back to the majority behavior (§2.1) and show how the interpretation of “conformist” behavior is confounded by frequency exposure (§2.2), perception ambiguity (§2.3), and inherent study design limitations (§2.4). Subsequently, we will show that the usage of majority influence definitions across research disciplines is currently inconsistent and propose a set of definitions in order to streamline majority influence research—*conformist transmission* and *conformity*—where we will stay close to the definitions as they have emerged within the respective research traditions and outline the empirical scope of each definition by means of thought experiments (§3.1). Finally, we will address study designs that would test for the different kinds of majority influences accordingly (§3.2) and explore some further considerations to advance the study of majority influences more generally (§3.3). In conjunction, this scrutiny should allow for a more valid interpretation of primates' behavior in the used reversion designs and offer conceptual and methodological tools for studying majority influences across species more commensurably.

2.1. Primacy effects

One of the most crucial difficulties in the current study of majority influences in primates is the possible confounding influence of primacy effects. When primates first become familiar with the method that later becomes the majority strategy and do not discover the equally effective alternative strategy until the first method has become fairly well ingrained, it seems impossible to reliably attribute their “re-convergence with the majority strategy” (Whiten & Schaik, 2007) to a majority influence. First of all, in certain studies, the discovery of the alternative strategy could be accidental as the two available strategies to solve the two-action problem could arguably be conceived of as structurally similar (Dindo et al., 2008;

Dindo et al., 2009). This means that the subjects might not actually learn the alternative strategy, which in turn means that instead of “reverting back,” the subjects *continue* using their first learned behavior. Second, even if the subjects do learn to use the alternative strategy, the first learned strategy will be more ingrained through repetitive and reliable reinforcement, which precludes any valid interpretation of preferring one strategy over the other in terms of social influences. Moreover, in the respective studies, the subjects that learned to use both strategies most likely did so in a qualitatively different way: the first strategy socially and the alternative strategy individually [e.g., in (Bonnie et al., 2007; Dindo et al., 2009; Whiten et al., 2005)]. Since research has shown that animals can weigh socially acquired information differently than individually acquired information [for reviews, see (Kendal, Coolen, van Bergen, & Laland, 2005; Kendal, Coolen, & Laland, 2009)], this aspect too needs to be balanced between strategies in order to be able to attribute the behavioral choices of subjects in terms of majority influences. Finally, at least in chimpanzees (Hrubesch, Preuschoft, & van Schaik, 2009; Marshall-Pescini & Whiten, 2008) and marmosets (Pesendorfer et al., 2009), preferring the strategy that first entered the behavioral repertoire over subsequently discovered strategies might be more parsimoniously explained by a high level of conservatism. While conservatism has been rejected as explanation for the observed within-group homogeneity of behavioral strategies in favor of conformity in chimpanzees (Hopper et al., 2011), we believe that the extent to which conservatism can exert effect on behavior should be revisited. Based on the premise that the frequency and intensity of previous experiences impact individuals' future decisions, in our view, *conservatism* entails any mechanism that, after mastering a strategy, decreases the likelihood of performing a novel behavior in the same stimulus–response domain, where the learning curve for the acquisition of the first strategy should be the benchmark to judge this likelihood. Importantly, this definition leaves open the possibility of prior knowledge impeding the adoption of a new behavioral strategy *even after this strategy has been explored*, deeming the rejection of conservatism in favor of “conformity” in the primate studies premature (Hopper et al., 2011) (The relation between the impact of previous knowledge on future behavior and majority influences will be discussed in paragraph 3.3). An early social learning study in chimpanzees seems to illustrate this matter succinctly, while at the same time indicating that conclusions on majority influences require proper caution. In this study, chimpanzees preferentially used their first learned action pattern that was demonstrated to them by a human experimenter, even after discovering that other sequences worked equally well [(Whiten, 1998), see also (Whiten & van Schaik, 2007)]. In our view, this study shows that chimpanzees will also retain their first learned behavior in the absence of a majority (of conspecifics) and that their conservatism is not necessitated by an inability to perform alternative actions [just like in the reversion designs, see (Bonnie et al., 2007; Dindo et al., 2008; Dindo et al., 2009; Hopper et al., 2011; Whiten et al., 2005)].

2.2. Frequency exposure

Another important matter for the study of majority influences is the nature of the strategy distribution within the population. In principle, the overall *frequency* by which strategies are being used is independent from the number of *individuals* using the same strategy. Since both variables can serve as information source for others, it remains an empirical challenge to infer which social learning bias subjects use in the process of adopting cultural variants. Whereas Perry (2009) used the absolute frequency exposure as a measure to advocate “conformism” in capuchin monkeys, a recent study in chimpanzees separated the effects of *frequency* and *individuals*, finding that the majority of individuals, but not the equivalent

frequency, predicted naïve subjects' tendency to adopt the demonstrated cultural variant (Haun, Rekers, & Tomasello, 2012). For conceptual and empirical reasons, hence, we propose to separate majority influences (in terms of individuals) from effects that might be exerted through absolute frequency exposure [cf. (Claidiere & Whiten, 2012)].

2.3. Perception ambiguity

As a prerequisite for any majority consideration, subjects need information on the behavioral distribution within their group. Since instantly obtaining knowledge of the overall distribution seems unlikely outside the experimental setting, subjects will either sample subsets of the group instantly or engage in sequential sampling. Importantly, both these sampling methods are prone to distortions from the overall (objective) strategy distribution, necessitating a more individually based approach to the study of majority influences. In most primate studies, however, the objective knowledge of the strategy distribution seems to be falsely equated with the subjects' perception records. One recent study in chimpanzees does report the average number of observations per study group (Hopper et al., 2011). However, while this study sets the right example, it remains unclear *which* strategies the subjects had observed and whether their observations tallied up to the perception of the same strategy distribution as the authors have assumed in their conclusions. In other words, while some subjects might have been influenced by a *perceived* majority, others might have copied a minority yielding the same end result.

2.4. Further limitations of the “reversion” design

The observation that individuals are inclined to revert back to their first learned behavior after discovering an equally effective alternative does not justify the claim that those individuals are conformists. Besides the above-mentioned confounds, the reversion design does not seem to test for majority influences in any conventional way: First, the individuals that are designated “conformists” in this paradigm are the only ones that *diverge* from the “group norm” at some point in time, and second, rather than having to *change* their behavior in order to match the majority, the designated “conformists” need to *maintain* their most familiar strategy (Bonnie et al., 2007; Dindo et al., 2008; Dindo et al., 2009; Hopper et al., 2011; Whiten et al., 2005). Furthermore, and perhaps even more essential to the study of majority influences, in designs where only one strategy gets demonstrated (like in the reversion designs), it is impossible to infer that the majority per se was responsible for any modifications in behavior. First, a majority by definition needs a minority (and thus an alternative strategy demonstration), and second, distinguishing between adopting the strategy that gets demonstrated *socially* and the bias toward copying the social information that gets demonstrated by the *majority* of individuals requires comparisons between the extent to which different numbers of demonstrators affect the observers' behavioral decisions (see paragraph 3.2). Contrary to being futile, these considerations may be pivotal in demarcating majority influences from other social influences, thereby aiding both the study of species-typical social learning behavior and the cross-species comparison of conformist tendencies. Finally, in the reversion scenario, any claim of “conformity” as it has been advanced in the cultural evolution literature (Boyd & Richerson, 1985; Henrich & Boyd, 1998; Mesoudi, 2009) would be problematic since, with only one strategy seeded, there is no way to test whether the tendency to copy the majority is *disproportionate* to the relative size of the majority. As will become clear in the next section on (the scope of) the different majority influence operationalizations, without such a stringent criterion, it is impossible to conclude that individuals *preferentially* do so [see (Mesoudi, 2009)].

In order to elucidate what we can possibly learn from primates' behavior in the reversion designs and streamline the cross-species comparison of conformist behavior in general, we will now turn to the operational definitions of majority influences. Subsequently, we will propose designs that would test for the different majority influences more validly.

3. Comparing apples and oranges: a proposal for calibration

As several scholars have pointed out, the study of “conformity” is currently convoluted (Claidiere & Whiten, 2012; Efferson et al., 2008; Galef & Whiskin, 2008; Mesoudi, 2009; Pesendorfer et al., 2009). For example, while originally used to describe the adjustment of one's conviction to a majority position (Asch, 1956), conformity was more recently invoked to describe the tendency to revert back to the first learned behavior after discovering an equally effective alternative (Whiten et al., 2005). Misguided by such operational mismatches, researchers have investigated different processes under the same banner of “conformity,” not only leading to preliminary conclusions on species' behavioral repertoires but also clouding the perspective on the evolutionary roots of conformist behavior (Claidiere & Whiten, 2012). Hence, in order to assess animals' behavioral tendencies more validly, we propose a set of definitions with the aim to delineate majority influences from other learning effects and dissect the different ways in which majorities can affect the behavior of observers.

3.1. Majority influence definitions

We propose to use the term “majority influence” to refer to all instances where the very presence of a majority affects the behavior of observers. Importantly, here, we define these effects in terms of behavioral end results, not mechanisms. We argue that the confusion in majority influence terminology at least in part stems from the convolution of mechanisms and end results.

Where the mechanism under study is the bias to *copy the majority* (Laland, 2004), the means to investigate this bias have typically been operationalized as different magnitudes on the probability continuum of adopting the majority strategy. For instance, majority influence has been defined in terms of “an increased likelihood to adopt the majority strategy compared to the expectation in absence of any inherent or social biases for one cultural variant over the other” [see “linear imitation” in (McElreath et al., 2005), “weak- and linear-conformity” in (Claidiere & Whiten, 2012), and “majority-biased transmission” in (Haun et al., 2012)]. One possible mechanism that would lead up to this end result is where individuals copy one of multiple demonstrators at random: in the presence of a majority, these individuals will be more likely to end up with the cultural variant that is shared by most group members [see (Mesoudi, 2009)]. Similarly, when the relative size of the majority is significantly bigger than the probability of adopting a cultural variant in the absence of any biases (e.g., majority proportion=0.8, unbiased adoption probability=0.5), the presence of a majority may even increase the likelihood to adopt the majority strategy of individuals that learn by accommodating and persevering in the first observed behavior (see paragraph 2.1 on primacy effects). Albeit seemingly trivial, without a majority, these individuals would have been less likely to adopt the respective majority strategy and thus acquire the cultural variant that has been postulated to be relatively adaptive (Boyd & Richerson, 1985; Henrich & Boyd, 1998; King & Cowlshaw, 2007).

A more stringent effect of the presence of a majority has been operationalized by adhering to the criterion of a *disproportionate* likelihood to adopt the majority strategy. In this case, the probability for an individual to end up with the majority strategy is not only higher than expected in the absence of any inherent or social biases for one cultural variant over the other but also higher than the relative

size of the majority in the population (this scenario is called “conformist transmission,” see below). In principle, these differently operationalized majority influences do not presuppose any specific mechanism(s): since the *majority* by definition comprises most individuals and in a given group, and thus likely affords a multitude of (social) learning strategies to be triggered (e.g., ‘copy the most skillful individual’) (see Kendal et al., 2005, 2009; Laland, 2004), ending up with the majority strategy can be caused by different (interacting) mechanisms. However, even though the increased likelihood to adopt the majority strategy is interesting in its own right [see (Haun et al., 2012)], the identification of the underlying mechanism(s) is important for reasons of pinpointing the source of behavioral modification and thus individuals’ capacities and/or inclinations. Moreover, knowledge of the underlying mechanism would be necessary for any valid cross-species comparison and thus for investigating the evolutionary roots of majority influences (MacLean et al., 2012). Therefore, in the remainder of this review, we outline the majority influence operationalizations that have typically been used to assess the existence of a copy-the-majority heuristic, investigate the extent to which the behavioral end results delineated by these operationalizations relate to the potential underlying mechanisms, and explore ways to further augment the study of the copy-the-majority heuristic.

Conformist transmission refers to the disproportionate tendency of naïve individuals to copy the behavior of the majority (Boyd & Richerson, 1985; Efferson et al., 2008; Henrich & Boyd, 1998; Mesoudi, 2009). Thus, in the case of conformist transmission, the probability for an individual to end up with a certain cultural variant is not only higher than expected in the absence of any inherent or social biases for one variant over the other but also higher than the relative size of the majority in the population, thereby excluding the possibility that individuals are “merely” copying others at random (Mesoudi, 2009). For instance, if we consider a population where a majority of individuals perform behavior A ($N=17$) and a minority behavior B ($N=3$), we would only refer to conformist transmission when the probability for a naïve immigrant to adopt behavior A would be significantly higher than $p=0.85$ ($17/20$) [for an empirical example in humans, see (Morgan, Rendell, Ehn, Hoppitt, & Laland, 2011)]. Note however that this definition refers to a behavioral end result, not to a mechanism. Where the copy-the-majority strategy would yield this particular behavioral outcome, other learning heuristics that are consistently afforded by the majority may equally well explain the observed effect. For instance, under the assumption that the majority strategy is relatively adaptive because it is an aggregate of individual learning outcomes, it is not untenable to postulate that the majority is consistently comprised of the most proficient individual learners. Hence, the strategy to copy the most skillful individual could potentially superimpose the strategy to copy the majority. Thus, even though random copying can be excluded by adhering to the criterion of *disproportionate* copying, the actual mechanism by which naïve individuals end up with the majority strategy remains unclear. In our view, this consideration should be pivotal to the study of majority influences: Do individuals copy the majority strategy *because* it is the majority strategy, or do they copy the majority for some other reason that is consistently afforded by the majority? We will elaborate on this quandary in paragraph 3.2.

Conformity refers to the tendency to forgo personal information by adopting the cultural variant that is used by the majority (Asch, 1956; Haun & Tomasello, 2011; Whiten & van Schaik, 2007). This term has emerged in the realm of human social psychology and has been used to describe the process in which human adults adjust their personal conviction to the unanimously expressed yet conspicuously erroneous conviction of the majority (Asch, 1956). While conformity entails the same adoption of the majority strategy as in the scenarios described above, it pertains to a different behavioral process in the sense that a familiar cultural variant needs to be abandoned in favor of

another cultural variant. The criterion of adopting the majority strategy with a probability higher than chance or the relative size of the majority does therefore not apply to conformity: under the premise of equal cultural variant affordance (equally effective, intuitively appealing, etc.) and controlling for individual differences in exploration tendencies, every *change* in behavior can be attributed to the social context. For instance, when an individual has acquired solution A to a two-action problem, one could investigate its tendency to conform by calculating the difference in probability to forgo solution A for solution B between the situation in which the individual has no knowledge of the other group members’ solutions versus the situation in which the individual has been exposed to a majority of group members using solution B. While the primate studies using the reversion designs base their conclusions on those individuals that acquire both of the available strategies, they fail to show how the subjects would respond in a nonsocial environment [see (Bonnie et al., 2007; Dindo et al., 2008; Dindo et al., 2009; Hopper et al., 2011; Whiten et al., 2005)]. Especially in the aforementioned studies where the two available solutions might be perceived as structurally similar (Dindo et al., 2008; Dindo et al., 2009), this nonsocial control condition would be additionally necessary to be able to attribute the observed behavioral patterns in terms of majority influences [see also (Morgan & Laland, 2012)].

Similar to the case of conformist transmission, however, the mechanism behind the behavioral change should be additionally scrutinized in light of the plethora of potential (social) learning biases [see (Claidiere & Whiten, 2012; Kendal et al., 2005, 2009; Laland, 2004; Rendell et al., 2011)]: Where majorities could be influential in their own right, the individual members comprising the majority could equally likely exert effect on observers’ decision-making processes. By adhering to the criterion of disproportionately copying the majority, at least “random copying” can be excluded from the possible underlying mechanisms [for “conformity,” see (Pike & Laland, 2010); for “conformist transmission,” see (Morgan et al., 2011)]. In the next paragraph, we will propose ways to further circumvent the mechanism ambiguity revolving around majority influences and investigate the copy-the-majority bias more precisely.

3.2. Study design proposals

In this paragraph, we will present study designs that would test for majority influences more validly, following the proposed set of operational definitions. Subsequently, in the next paragraph, we will explore some further considerations that may help to improve the study of majority influences across species.

First, in order to study conformist transmission in primates more validly, we propose to adjust the designs in accord with some recent animal studies [sticklebacks: (Pike & Laland, 2010; Webster & Hart, 2006); great apes: (Haun et al., 2012)]. In these studies, focal individuals are presented with equivalent foraging patches, one demonstrated by the majority and one by a minority, and subsequently tested for their foraging preferences. Crucially, the choice availability in this design allows for a more direct investigation of majority influences than the reversion designs, in which only one of the two possible strategies is seeded and hence demonstrated to the focal individuals. As long as focal individuals do not have a choice between a majority and minority strategy, and the demonstration and subsequent acquisition of available alternatives are not fairly balanced in time and thus in perception records, results will remain hard to interpret in terms of majority influences.

Similarly, in order to study conformity validly and hence facilitate the cross-species comparison, the primate studies could improve by mimicking the human designs more closely. Instead of letting the conformity choice coincide with the strategy that the focal individuals learn first [see (Bonnie et al., 2007; Dindo et al., 2008; Dindo et al., 2009; Hopper et al., 2011; Perry 2009; Pesendorfer et al., 2009);

Whiten et al., 2005)), the improved designs should investigate whether the focal primates would forgo their initial knowledge and/or preference in order to match the majority behavior [see (Asch, 1956; Bond & Smith, 1996)]. This way of operationalizing “conformity” has also been integrated in the stickleback studies, where knowledgeable subjects were presented with majority vs. minority demonstrations, yielding strong indications that at least nine-spined sticklebacks show tendencies reminiscent of conformity as found in human subjects [see (Pike & Laland, 2010)]. Strictly speaking, the evidence for preferentially copying the majority is stronger in the stickleback study than in the human studies since the former presents evidence of subjects adopting the majority strategy *disproportionately*, while the latter are typically conducted using a unanimous “majority,” deeming it impossible to disentangle whether the focal individuals copy the majority or an (random) individual of the majority [see Asch (1956) and Bond and Smith (1996); for recent evidence of preferentially copying the majority in humans, see Morgan et al. (2011)]. Note however that, up till now, *personal knowledge* has not been dissected in terms of reinforcement histories or preferences. The importance of this dissection for understanding conformity behavior will be addressed in paragraph 3.3.

Finally, in order to be able to draw valid conclusions on the actual *preference* to copy the majority, one needs to take into account that a majority bias would almost inevitably coincide with other social learning biases that are predicted to be beneficial for social animals, like copy kin, copy prestigious individuals, or copy the most skillful individual (Laland, 2004). Therefore, in order to make sure that the focal individuals copy the majority per se and not the individuals in it (similar reasoning for a possible minority bias), the designs should incorporate repeated measures of differently composed subgroups, where all the meaningful characteristics and relations of the involved individuals (like age, gender, bonds of affiliation, etc.) should be counterbalanced over trials. (Since characteristics like age, gender, and demeanor could similarly exert effects through imagery, to a certain degree, the same reasoning would hold for video demonstrations). This consideration additionally exposes the empirical question as to what extent the relative size of the majority impacts the focal individual's behavior; ranging from unanimous “majorities” (Asch, 1956) to subgroups comprising the highest number of individuals without being the majority [i.e., “pluralities,” see (Hastie & Kameda, 2005)], majorities can differently affect decision-making processes in subtle yet crucial ways [see studies in humans: (Coultas, 2004; Morgan et al., 2011); and sticklebacks: (Pike & Laland, 2010)].

3.3. Further considerations for the study of majority influences

Another important aspect to consider in studying majority influences—one that is generally overlooked—is the character of the situation under study. For instance, in situations where individuals need to compete over *known* food resources, one might not expect majority influences at all, or if anything, the opposite effect: individuals would optimize their gains by avoiding foraging with the majority [the opposite might be true for exploring *new* foraging patches, see, e.g., (Day et al., 2001)]. Alternatively, in situations in which individuals need to coordinate their behavior in order to gain benefits or avoid costs, one might expect majority influences to be highly present or at least likely [see (Eriksson, Enquist, & Ghirlanda, 2007)]. By taking into account the (nature of the) situational pressures that individuals are under, one could more reliably assess the relative importance for individuals to copy the majority. For instance, the incentive to follow the majority might be more pronounced for animals under high predation risk [e.g., nine-spined sticklebacks; see (Pike & Laland 2010)] than for animals living in a relatively predictable environment, having acquired a perfectly safe and reliable strategy on their own, like in the reversion designs [see (Bonnie et al., 2007; Dindo

et al., 2008; Dindo et al., 2009; Hopper et al., 2011; Pesendorfer et al., 2009; Whiten et al., 2005)].

Similarly, the nature of the focal behavior might differentially impact the extent to which majorities affect observers' behavior. Where behaviors like foraging or prey avoidance can yield substantial fitness benefits if executed adequately, and thus bear costs if executed inadequately, behaviors like playing or grooming might be less strictly regimented by the anticipation of survival. In the former case, one could expect a majority bias to be highly rewarding in light of the fact that the majority strategies are aggregate responses of individuals sampling the environment with their unique toolkits (physical and psychological instruments), thus amounting up to relatively adequate strategies (Boyd & Richerson, 1985; Henrich & Boyd, 1998). On the other hand, even with behaviors that pertain less directly to fitness benefits, like in the latter case, one could expect individuals to preferentially copy the majority of individuals: under the assumption that a social life merits benefits, the threat of ostracism can be a strong incentive for group members to imitate the behavior of the subgroup with the most power, i.e., the majority (Over & Carpenter, 2012). Therefore, in any study investigating majority influences, it would be fruitful to elaborate on both the instrumental and social trade-offs that might pertain to the focal behavior of the species under study. For instance, in a compatible token-design study, one should contemplate the relative incentive for chimpanzees to switch from using their first learned token contingency to using the majority's token contingency in terms of strategy efficiency and social acceptance and/or punishment. Perhaps, in this particular situation, the equation of incentives (instrumental and social) would yield the prediction that sticking to the first learned strategy would be the most adaptive strategy [e.g., both strategies work equally well, no uncertainty/risk pertaining to the outcome of using either strategy, relatively little opportunity for social control; see (Morgan et al., 2011) for an example of identifying the circumstances under which humans are most likely to copy the social information provided by the majority]. Not merely an explorative option, this consideration could prevent researchers from investigating majority influences under circumstances that do not predict forgoing personal information or adopting the majority strategy for behavioral optimization. Moreover, the framework in which situation and behaviors are scrutinized in light of instrumental and social trade-offs would prove fruitful in identifying species-typical inclinations and hence in the realm of cross-species comparisons.

Finally, one of the critical features in predicting and determining the magnitude of conformity might be the psychological distance between the subject's familiar behavior and the majority strategy. In line with factors related to environmental oscillations [see (Boyd & Richerson, 2005)] or to the relative advantage of using one strategy over the other [see (Kendal et al., 2005)], the extent to which personal information is *ingrained* (reliably reinforced) and *preferred* might be additionally important in light of conformity processes. For instance, to induce conformity in subjects, the majority would need to represent a stronger social cue for an individual who has reached a stable behavioral pattern through frequent exposure than for an individual who has only recently learned his baseline cultural variant. Similarly, the majority would need to be more persuasive for an individual with a clear preference than for an individual who is already in doubt. Although potentially challenging to quantify, researchers should take into account this psychological distance in order to be able to interpret behavioral decisions more accurately.

4. Conclusions and future directions

Based on the considerations outlined in this review, we conclude that it is currently impossible to state whether primates' are biased toward copying the majority. While the reviewed studies might indicate a certain reliance on majority strategies, the reversion designs allow for too many alternative explanations to warrant

interpretation of the observed behavioral patterns in terms of majority influences [cf. (Claudiere & Whiten, 2012)]. The only primate study, to our knowledge, that validly investigated majority influences reported evidence of “majority-biased transmission” in chimpanzees, but not in orangutans (Haun et al., 2012). In general, it is our opinion that the study of majority influences in animals, and particularly in primates, could benefit from taking into account the following considerations: First, specifying the employed operationalization and situating it within the here proposed framework would aid the cross-species comparison substantially. Moreover, it would be informative to scrutinize a species' inclination to copy the majority across both naïve and knowledgeable individuals, where the assumption that naïve individuals are more likely to use social information needs to be investigated under different trade-offs (e.g., uncertain outcomes, varying acquisition costs). Second, albeit practically challenging, it would be constructive to explore more refined ways of measuring the perception records of the subjects under study. Only by knowing the subjects' observed strategy distributions can we discuss the behavioral outcomes in terms of majority influences. Third, the study of majority influences would advance by incorporating situational characteristics. Formal models have yielded different predictions based on aspects like the relative cost of individual sampling, the predictability of the environment and whether the situation requires competition or coordination to optimize fitness (Eriksson et al., 2007; Kameda & Nakanishi, 2002; Wakano & Aoki, 2007). Similarly, the instrumental and social gains of the behavior under study are likely to influence the adaptiveness of copying the majority. By integrating both these situational and behavioral characteristics into detailed trade-off equations, we will be able to formulate more specific hypotheses about the expected form and function of the different ways in which majorities can affect behavior. Finally, it might be worth to adopt an approach in which individual differences are the subject of analysis, rather than the study group as a whole [see e.g., (McElreath et al., 2005; Efferson et al., 2008)]. Analysis on the group level might complicate the interpretation of effects, whereas the conception that individuals might differ in their inclination to adopt the majority strategy is not inconceivable, perhaps especially not in primates.

It remains an important endeavor to single out the underlying mechanisms that drive groups to behavioral homogeneity across species. While the existence of majority influences can at most provide an indication of majority considerations in behavioral decision-making, carefully crafted designs could tease apart the plethora of mechanisms that could lead to behavioral homogeneity and assess the relative importance of actual majority preferences across a multitude of situations. Only by knowing the mechanism behind majority influences will we be able to shed light on the evolutionary roots of preferring the majority over minorities and/or personal information. Moreover, pinpointing the underlying mechanism could provide valuable insights into species-specific learning capacities given that not every mechanism bears the same potential to adaptively navigate individuals through their (changing) environments.

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