Integrating the Study of Conformity and Culture in Humans and Nonhuman Animals

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Conformity—defined here by the fact that an individual displays a particular behavior because it is the most frequent the individual witnessed in others—has long been recognized by social psychologists as one of the main categories of social influence. Surprisingly, it is only recently that conformity has become an active topic in animal and comparative biology. As in any new and rapidly growing field, however, definitions, hypotheses, and protocols are diverse, not easy to organize in a coherent way, and sometimes seriously in conflict with one another. Here we pursue greater coherence by reviewing the newer literature on conformity in behavioral ecology and evolutionary biology in light of the foundational work in social psychology. We suggest that the knowledge accumulated in social psychology can be exploited by behavioral ecologists and evolutionary biologists to bring conceptual clarity to the field, avoid some experimental pitfalls, and help design new and challenging experiments. In particular, we propose that the notions of *informational* and *normative* conformity that, until now, have been little recognized in recent literature can resolve some important controversies. In turn, research on animal culture should be of great interest to social scientists, because understanding human culture and human uniqueness requires an evolutionary analysis of our cognitive capacities and their evolutionary origins. Our review suggests excellent opportunities for social and natural scientists to join forces in building an interdisciplinary and integrative approach to the pervasive phenomenon of conformity.

Keywords: animal culture, cultural evolution, social learning, imitation, learning strategy

The study of animal culture has recently received considerable attention, largely because of the expectation that understanding the simpler forms of social learning and traditions in nature can enhance our understanding of the nature and origins of human culture (Laland & Galef, 2009). Most of these recent studies have been concerned either with documenting behavioral variations in the wild (e.g., Krützen et al., 2005; Perry et al., 2003; Rendell & Whitehead, 2001; van Schaik et al., 2003; Whiten et al., 1999) or with studying social learning mechanisms underlying the interindividual transmission of culture (for recent reviews, see Hoppitt & Laland, 2008; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004). Both steps are fundamental in establishing the very existence of animal culture, showing that (a) behaviors in nonhuman animals (henceforth simply animals) differ from community to community within the same species, just as human behaviors differ from place to place, and (b) many animals have the capacity to learn from one another such community-specific skills, as humans do. Much of the recent debate has naturally focused on whether animals have culture in some sense. The weight of evidence accumulated over the last 30 years shows that many do; in particular, socially learned traditions are documented in fish, birds, and mammals (Boesch, 2003; Box & Gibson, 1999; Fragaszy & Perry, 2003; Galef, 1992; Heyes & Galef, 1996; Laland & Galef, 2009; Laland & Janik, 2006; Tomasello, 1994; Whiten & van Schaik, 2007; Zentall & Galef, 1988), albeit in obviously simpler forms than in humans.

Although most of these research efforts have focused on the acquisition of new behaviors through social learning, other important processes involved in the emergence and evolution of culture have received considerably less attention. Now that research on animal culture is well established, we propose it is time to move toward a richer, more complex analysis (see also Whiten & van Schaik, 2007). Social learning cannot explain, on its own, the stability and diversity of animal culture that we observe in the wild; other factors, environmental or psychological, have to be involved (Claidière & Sperber, 2010).

This review seeks to take a significant step in this direction by reviewing evidence for conformity in animals in the light of research in social psychology. Conformity—defined here by the fact that an individual displays a particular behavior because it is the most frequent the individual witnessed in others—has begun to emerge as a topic of active research in animal social learning as well as in cultural evolutionary modeling. Research on conformity in animals should also be of great interest to social scientists, because understanding human culture and human uniqueness requires an evolutionary analysis of our cognitive capacities and

their evolutionary origins (Whiten, Hinde, Laland, & Stringer, 2011). This has typically been pursued through comparative research—the study of similar cognitive capacities in different species. Such comparative analyses reveal cognitive analogies and homologies and therefore help formulate precise hypotheses about the selection regimes that shaped evolutionary pathways (van Schaik, et al., 2003; Whiten, 2009). However, comparative analysis can only succeed if the cognitive capacities under study can be precisely identified in different species. Clear definitions and standard protocols are a necessity; otherwise the possibility that different capacities are compared across species undermines the entire enterprise.

In the case of conformity in animals, as in any new and rapidly growing field, definitions, hypotheses, and protocols are diverse, not easy to organize in a coherent way, and sometimes even in serious conflict with one another. Whiten, Horner, and de Waal (2005), for instance, in studying the acquisition of traditions in chimpanzees, described conformity as "a powerful tendency to discount personal experience in favour of adopting perceived community norms" (p. 738) consistent with "an intrinsic motivation to copy others, guided by social bonds rather than material rewards such as food" (p. 739). By contrast, Lachlan, Janik, and Slater (2004) saw conformity as a spatial property of behavioral distribution: "Cultural conformity occurs when individuals are more likely to share variants of a cultural trait with nearby individuals than with more distant ones" (p. 561). Perry (2009) stated that conformity is

> the tendency for individuals to preferentially exhibit behavioral alternatives that they witness most frequently in their peers, or to exhibit the behaviors that are performed by peers who are considered most prestigious or successful, or those peers with whom they have the highest quality social relationships (however that might be defined). [Conformity] can involve the adoption of new behaviors, but it can also involve an acquired preference of the use of behaviors that are already in an individual's behavioral repertoire and/or the suppression of some other behavior formerly used in a particular context. (p. 706)

This formulation itself includes several criteria that might in principle operate separately. Given such a broad array of definitions, it is difficult to know whether different studies really address the same cognitive capacity. Galef and Whiskin (2008), for instance, expressed skepticism regarding a homology of conformity in guppies and conformity in primates. Meanwhile, Pesendorfer et al. (2009) have argued that Whiten et al.'s (2005) chimpanzee study was not specifically designed to test conformity and that the relatively weak effect found, although statistically significant, might have resulted from unstudied factors. The authors have also argued that Galef and Whiskin (2008) cannot demonstrate the presence of conformity because the setting involved one-to-one interactions only.

We believe that much of the confusion suggested by these examples results from the broad range of definitions proliferating and the lack of a coherently integrated literature. A principal objective of this article is to provide a specification and analysis of conformity that can productively span comparative studies of human and nonhuman animals. Such a specification may be logically anchored in the field of human social psychology, since conformity has been an important topic of research in this field for more than half a century.

Furthermore, the idea of conformity is in some ways inseparable from anticonformity and nonconformity. Anticonforming individuals are usually noticed when other individuals conform. For instance, when everybody is dressed casually, anticonforming individuals arrive in suits, and when everybody is in suits, anticonformists arrive casually dressed (Griskevicius, Goldstein, Mortensen, Cialdini, & Kenrick, 2006). Anticonformity can further be distinguished from nonconformity. Nonconforming individuals are simply not sensitive to group pressure; they are not motivated to be similar (conformity), or different (anticonformity), from others. Assessing the existence of anti- and nonconformity in animals will be difficult unless conformity is clearly identified; we therefore limit our review to conformity only, but note that anti- and nonconformity represent interesting avenues for future research that should be followed once the existence of conformity is clearly established.

In pursuing this objective, we note that a particularly influential distinction drawn in social psychology is between *informational* and *normative* conformity. Informational conformity is concerned with accuracy and the search for information about reality, whereas normative conformity is concerned with social interactions. For instance, when faced with a choice of unknown music, a good strategy to find the best songs is to listen to the one that has been downloaded the most (Salganik, Dodds, & Watts, 2006). This would correspond to informational conformity because one conforms in order to find information about reality (i.e., the best songs). On the contrary, Maeda (1975) described how the importance that Japanese rural communities attribute to group belonging and group identity makes them more likely to conform than Malays, for whom group identity and belonging are much more flexible. In this example of normative conformity, individuals conform to social rules to maintain and develop their group identity. This fundamental distinction between informative and normative conformity plays a crucial role in social psychology but has generally been little mentioned in behavioral ecology and evolutionary biology.

In the second section of this article, we suggest that much of the confusion that has arisen in the behavioral sciences can be resolved with the informational–normative distinction. Using this distinction, we review studies of conformity in animals and conclude that the existence of both types of conformity receives some support from the current literature. Future experiments aiming at testing specifically one or the other form of conformity, by avoiding contexts in which they are intermingled, should provide definitive evidence for, or against, these kinds of conformity in animals.

Another set of studies against which the existence of conformity in animals can be assessed comes from the field of evolutionary biology. In the third and last section of this article, we discuss the consequences of conformity for cultural evolution and the evolution of conformity by natural selection. Using the informational–normative distinction, we develop a new hypothesis regarding the relationship between informational and normative conformity and the response curve of individuals to the frequency of behaviors they witness. The informational kind, we propose, should be associated with weak or linear conformity, whereas the normative kind should be associated with hyperconformity. This hypothesis provides a clearer and simpler explanation for the evolution of conformity and points toward new directions for future research.

In this review our goals are thus threefold: (a) to provide a precise and operational definition of conformity that can be useful in comparative research, (b) to present the main protocols and criteria that can be used to assess the presence and degree of conformity present in different species, and (c) to describe the main hypotheses concerning the evolution of conformity by natural selection and the expected effects of conformity on cultural evolution.

What Is Conformity?

The study of conformity in animals is a relatively recent development by comparison with social psychology. Accordingly, we here pursue a definition of conformity inspired by the large corpus of work in social psychology, yet compatible with the behavioral sciences and evolutionary biology. In particular we highlight and justify the importance of the distinction between informational and normative conformity. Before turning to the application of this distinction in animal studies, we provide a concise overview of important studies in social psychology for researchers not familiar with the field.

The Concept of Conformity in Social Psychology

Building on the work of Sherif (1935, 1936, 1937), Asch (1955, 1956) set the stage for the study of conformity in humans by showing that individuals have difficulties maintaining their own opinion in the face of a unanimous majority of others expressing a contradictory opinion. In one version of a now classical experiment, Asch (1955) asked groups of seven to nine psychology students to participate in a visual judgment task. The individuals were shown two cards, one presenting a standard line and another presenting three test lines. They were asked to say in front of other members of the group which line among the three test ones was equal to the standard. Among the students, all except one were confederates of the experimenter. Confederates would start by giving the right answer, but on predefined test trials they would all give a (patently) wrong answer. Asch recorded the number of times the participant would conform by giving the same answer as the confederates despite its glaring incorrectness. In a control condition, without confederates, participants gave wrong answers on less than 1% of trials. With more than three confederates involved, this error rate rose above 30%. Asch concluded:

> That we have found the tendency to conformity in our society so strong that reasonably intelligent and well-meaning young people are willing to call white black is a matter of concern. It raises questions about our ways of education and about the values that guide our conduct. (p. 34)

Asch's approach presents several advantages when it comes to defining conformity comparatively, because it relies almost exclusively on the behavior of the participant and not on the motivations underlying the participant's behavior. By contrast, more refined definitions of conformity have tended to focus on the secondary question of what makes the individual conform, rather than on what constitutes conformity at the behavioral level (Cialdini & Goldstein, 2004; Deutsch & Gerard, 1955; Kelman, 1958; Tanford & Penrod, 1984). What motivates behavior is certainly important, but ascribing motivations to conformity represents a more advanced stage of analysis that can only be achieved once the identification of conformity is realized. Given that the study of conformity in animals

is just beginning, it seems logical to start with a definition of conformity based on behavior that can progress and be refined by distinctions such as those concerning motivations.

Asch (1955), however, does not give an explicit definition of conformity, but we can deduce from his experiments three necessary conditions. A participant is said to conform when he or she (a) has to choose between several alternative behaviors, (b) chooses the one displayed by a majority of other individuals, and (c) does so because it is the option chosen by the majority (and not for alternative reasons). Thus participants must weigh alternative possibilities and not give more weight to their own opinion than to the opinion of the majority.[1]

Crucially, conformity so defined differs from social learning per se and from other forms of social influence. Social learning requires the individual to learn something new from other individuals, whereas conformity can be based on behaviors already known. For example, we might conform when choosing between eating with our fingers or with cutlery, both being options we already know well. To an extent, this depends on what we mean by "learning," for even in this example, if conformity in using cutlery in certain contexts comes to dominate an individual's habits, we might say they have socially learned this; however, cutlery use was already in their repertoire and not itself socially learned. Once social learning and conformity effects are conceptually separated in this way, we can acknowledge that they may interact, as when an individual does learn a novel action displayed by a majority of the community, rather than one displayed by a minority.

Conformity also diverges from other forms of social influence, such as a potential model's authority, reputation, or performance, because it refers to the influence of a group of individuals as a group of individuals. Metaphorically speaking, conformity is often thought of as a form of group pressure in which the size of the group and the proportion of the majority may be influential factors, not the identity of the individuals or their social relationship with the participant. Compare, for instance, the person who buys a particular vehicle because her favorite football player drives a similar car with the person who does the same because most people she knows drive such a car. In the first instance, prestige drives the change in behavior, and a single person provides this influence. In the second case, conformity to a group drives the change in behavior.

However, the notion of majority can sometimes be misleading. In Asch's (1955, 1956) experiments, as in many other studies on conformity, each individual had the opportunity to display a single behavior per trial. In any one trial, the frequency of a particular

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[1] In the literature it is sometimes difficult to know exactly to which individuals the terms *majority* and *minority* refer. Asch's experiments, for instance, are usually interpreted as showing the influence of a unanimous majority on one individual. The participant under study is therefore excluded from the calculus of the majority (Asch, 1955, 1956). Latané's model also excludes the focal individual from the calculus of the size of the majority (Latané, 1981). But in Tanford and Penrod's model, the focal individual is included as part of the majority, or as part of the minority (Tanford & Penrod, 1984). To avoid potential confusion, we define *conformity* as the influence of others on one's own behavior and therefore exclude the focal individual from the calculus of majority and minority. Likewise we shall call the influence group the ensemble of all individuals except the one under study.

behavior was therefore equal to the proportion of individuals displaying that behavior. As a consequence, it is not possible to tell whether it is the frequency of behaviors or the proportion of individuals that has influenced the participant. In Asch's experiments, our intuitive understanding of the situation suggests that it is the proportion of individuals and not the frequency of behaviors that is responsible for the observed effect, hence the classical interpretation in terms of majority influence. In other situations, however, when individuals are not consistently displaying the same behavior, it is the most frequent behavior, and not the proportion of individuals, that may be the relevant factor driving conformity (see Perry, 2009, for a recent nonhuman primate example). Indeed, conformity in the mathematical modeling literature is often couched in terms of the influence of the most frequent behavior in a group, rather than in terms of the majority of individuals (Boyd & Richerson, 1985; Henrich & Boyd, 1998): "According to our definition, frequency-dependent bias occurs whenever a naive individual uses the frequency of a variant to evaluate the merit of the variants" (Boyd & Richerson, 1985, p. 206; conformity is a type of frequency-dependent bias). In this literature it is therefore often unclear whether it is assumed that individuals behave in a consistent manner such that behavioral frequencies are reflected in proportions of individuals behaving in different ways.

Ultimately, the question of whether individuals are sensitive to the proportion of individuals and/or the frequency of alternative behaviors is an empirical issue. Therefore, whether it is preferable to restrict the definition of conformity to one or the other measure ought to be based on empirical evidence rather than mere speculation. Given that at present such evidence is lacking, we propose a definition of conformity that leaves open the object of the frequency calculation (whether the frequency represents a proportion of individuals or a frequency of behaviors).

On the basis of these considerations, we propose the following definition of conformity:

> *Conformity:* A behavior is said to conform when an individual in a group displays that behavior because it is the most frequent the individual witnessed in others.

Note that we attribute conformity to a behavior in this definition, rather than to an individual. Conformity, in our view, is a graded property; a behavior can be more or less conformist depending on the contribution of the frequency relative to the contribution of other factors (such as individual preferences, dominance, competence, etc.). Compare, for instance, the influence exerted by a group of unknown students on a participant in an Asch experiment with the influence exerted by a group of friends on the same participant. In the first case, the frequency of the behavior is the main factor accounting for the change in behavior of the participant, whereas when a group of friends is present, both the relationship between the participant and the confederates and the frequency of the behavior may influence the participant. However, if the same effect is observed in both conditions, the behavior is more conformist in the "unknown" case than in the "friend" case because the influence of the frequency plays a greater role in explaining the behavior of the focal participant in the former.

Further studies in social psychology show that some individuals are more likely to conform than others. In Asch (1955), for instance, some participants gave the majority's answer nearly all the time, whereas others never did so. Accordingly, we also define a conformist tendency at the level of the individual:

> *Conformist tendency:* a disposition to be conformist, that is, a disposition to be influenced by the most frequent behavior witnessed in others.

Such a tendency can also be graded relative to the rest of the population and might also vary across behavioral domains such as mate choice and foraging decisions.

Interestingly, when Asch (1955) compared the response of participants confronted with a unanimous majority with the response of participants who had one ally (a person who disagreed with the majority), he noticed that conformity decreased markedly (this result might be an effect of the presence of confederates, however; see Mori & Arai, 2010). Conformity was therefore most evident in a unanimous situation and not with other proportions of the majority (which also shows that conformity can be nonlinear, as discussed in the last section of this article). Later studies varied the proportion of the majority and showed that unanimity is not always necessary for conformity (see Campbell & Fairey, 1989, and below). The effect of unanimity reported by Asch is therefore probably linked to the details of the situation in which the participants found themselves, with an obvious conflict between their senses and the answers given by their peers. Changes in the confidence of the participants in their judgment, or the size of the influence group, revealed interesting effects on conformity, to which we now turn.

Different Kinds of Conformity

Asch's (1955, 1956) studies had an important and lasting impact in social psychology and stimulated numerous studies on conformity in adults (for a review of recent work, see Cialdini & Goldstein, 2004) and children (Corriveau, Fusaro, & Harris, 2009; Corriveau & Harris, 2010; Harris & Corriveau, 2011; Walker & Andrade, 1996). Most of Asch's results were confirmed by other studies, but the influence of the size of the majority provoked debate. Asch found that conformity increased when the size of the majority increased from one to three but remained approximately constant for larger group sizes. Later studies provided mixed support for this finding, with some studies finding an increase of conformity beyond a majority of three (e.g., Gerard, Wilhelmy, & Conolley, 1968). These conflicting results supported two opposing models of social influence (of which conformity is only a part).

First, in agreement with Asch's early findings, Tanford and Penrod (1984) developed the social influence model based on computer simulations of jury decision making. This model postulates that the shape of the group size function follows a Gompertz law (an S-shaped curve). The influence of the majority is of the form[2]

$$p(n) = 1 - \left[.5 - \left(.5 \left(1 - \frac{2}{n} \right) \right)^{2.5} \right]^{\frac{n}{12}}, \qquad (1)$$

where $p(n)$ is the probability that one individual adopts the behavior of the majority and n is the size of the reference group. In this

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[2] This is an adaptation of Tanford and Penrod's general model to the Asch experimental situation.

model, the marginal effect, $p(n + 1) - p(n)$, increases with group size when the group size is small and decreases with group size when the group size is large (the effect is S shaped; see figure 1).

Opposing the social influence model, Latane's social impact theory postulates a decrease in marginal effect with an increase in the size of the influence group (Latané, 1981; Latané & Wolf, 1981). For instance, the increase in conformity should be larger when the size of the majority goes from two to three than from three to four. Latané (1981) proposed the following psychological law to account for the observed tendency:

$$SI(N) = \alpha N^{\frac{1}{\beta}} \text{ with } \beta > 1, \qquad (2)$$

where SI(N) is the social impact resulting from the influence group, N is the size of the group, and α and β are scaling constants. With β being larger than 1, the social impact increases as the root of the group size and the marginal effect, $SI(N + 1) - SI(N)$, decreases with N.

Both social impact theory and social influence models received support from conformity studies and other studies of social influence (Eriksson & Coultas, 2009; Latané, 1981; Tanford & Penrod, 1984). Campbell and Fairey (1989), however, suggested that the conflict between the models can be at least partly explained by a distinction between informational and normative conformity, a distinction originally introduced by Deutsch and Gerard (1955). Deutsch and Gerard recognized that participants can conform for either of two reasons: one is to gain information about reality (informational motivation), and the other is to manage social interactions (normative motivation). They defined "a normative social influence as an influence to conform with the positive expectations of another" and "an informational social influence . . . as an influence to accept information obtained from another as evidence about reality" (Deutsch & Gerard, 1955, p. 629).

Additionally, according to Campbell and Fairey (1989):

> Informational influence is based on the desire to be accurate; others' responses are used as a source of information about reality, and people conform because they believe that the others may be correct. Normative influence is based on the desire to maximize social outcomes. Even when people believe the others are wrong, they may conform in order to gain the rewards or avoid the punishments that such agreement and disagreement mediate. (p. 458)

These characterizations were elaborated in the context of human adult research, and as stated, they are likely to have limited direct applicability to the context of animal or even child research. It would be difficult to know, for instance, whether fish, chimpanzees, or young children have positive expectations of another, or entertain a desire to maximize social outcomes. From a comparative perspective, the value of this distinction lies not so much in the way the different forms of conformity are implemented but rather in their having different cultural consequences, as we explore below.

For our purposes, the primary conception of the informational–normative distinction is at the functional level: What matters is that informational conformity functions to gain useful information about reality, and normative conformity functions to manage social interactions, whatever the specifics of the underlying causal processes. Of course, there may well be cognitive differences underlying the two alternative functions, but that is a secondary question here.

Informational conformity functions to gain nonsocial information and adapt one's behavior to the nonsocial environment. It is not influenced by the other's awareness of the individual's behavior and can exist in the absence of social feedback on one's behavior. For example, one might assume that it is safe to swim in an area if a good proportion of individuals are swimming there.
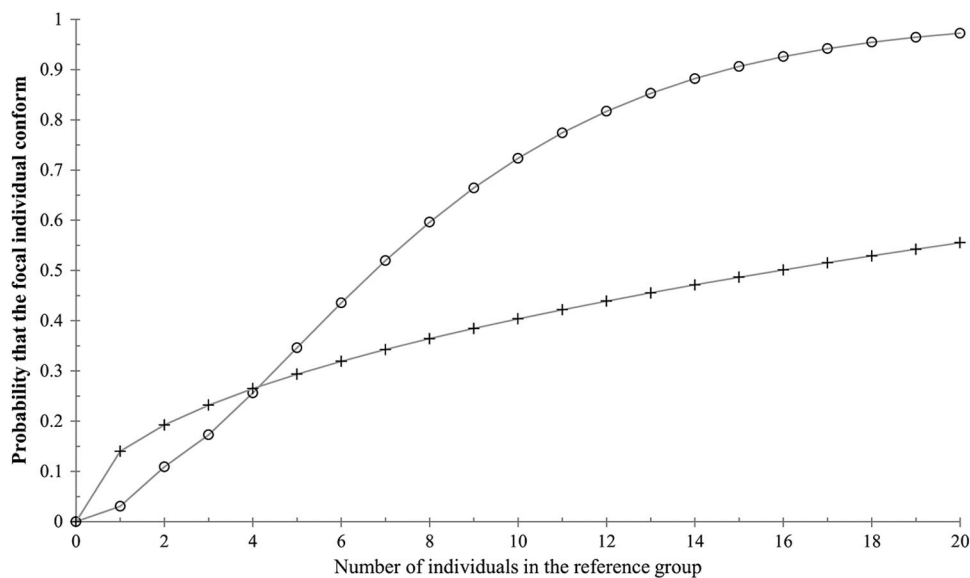
Figure 1. Comparison between the social influence model and the social impact theory model. The social influence model proposed by Tanford and Penrod (1984) suggests an S-shaped relationship between the size of the influence group and the probability that the focal individual conforms (circled line; see Equation 1). By contrast, Latane's (1981) social impact theory suggests that this relationship is concave only (crossed line; see Equation 2; $\alpha = 14$ and $\beta = 0.48$; α and β are from Latané, 1981, Figure 2b).

The number and proportion of individuals who swim there gives information regarding the safety of the location; this is informational conformity. The other's awareness of one's behavior (swim or do not swim) is not affecting that individual's decision to swim.

Normative conformity functions to gain social information and adapt to one's social environment. It is generally linked with the social consequences of one's behavior. For instance, even if one knows that smoking has important health consequences and one does not find smoking particularly pleasant, one might still be motivated to smoke if others do so. In that case, the social consequences of not smoking in a group of smokers can outweigh one's own preference, knowledge, and experience.

Of course, complex interplays between the two forms of conformity are possible and perhaps even likely, so that showing the contribution of each form of conformity in practice will require careful experiments. For instance, one might conform for both normative and informational reasons at the same time (Kelley & Shapiro, 1954). One might also first conform for normative reasons, only later to find that this brings important information about reality. Sometimes, informational conformity can foster normative conformity too; what was first done for informational reasons is later socially approved, for instance.

Many cases of conformity may reflect both functions, and the contribution of normative and informational conformity is likely to vary between different instances of conformity and between individuals. For the purpose of comparative research, however, it is important to identify situations in which one or the other alternative is in play, to address the existence or absence of each form of conformity.

Campbell and Fairey (1989) remarked that if informational conformity is dominant, the change in the amount of information involved with an increase in group size decreases with group size, as predicted by Latane's model. For instance, when the group size changes from one to two, the additional individual provides a larger amount of information than when the group size changes from two to three. This is because the information provided by the third individual is redundant with the information provided by the second individual. By contrast, when normative conformity is dominant, if the size of the group is small, the marginal effect of an increase in group size increases with the size of the group, as predicted by the Tanford and Penrod model. Thus, when group size changes from one to two, the additional individual has less effect than when the group size changes from two to three. This is because three individuals provide much stronger evidence for a group norm than two individuals. When normative conformity is dominant, it is also the case that when the group size is large, the marginal effect decreases with an increase in group size. The evidence for the existence of a group norm increases less when the group size increases from, say, 99 to 100 than when it increases from nine to 10.

Campbell and Fairey (1989) therefore argued for a correspondence between the types of conformity and the models of social influence. Normative conformity corresponds with Tanford and Penrod's model, whereas informational conformity corresponds with Latane's.

Following this line of reasoning, Campbell and Fairey (1989) noted that informational conformity and Latane's model should prevail in contexts in which participants' psychological uncertainty[3] is high, whereas normative conformity and Tanford and Penrod's model should dominate situations in which psychological uncertainty is low. Imagine, for instance, that you have a job interview and have to decide whether to dress formally. If it is your first interview of this kind, psychological uncertainty is high. You do not know which behavior is most appropriate, but others' behavior can reduce this uncertainty and indicate the most appropriate behavior. If conformity is in play, informational conformity is more likely in this case. If you are familiar with job interviews, psychological uncertainty is low. You already know the appropriate behavior, and others should be less useful as a source of information. If there is any conformity, normative conformity is more likely in that case.

To test such predictions, Campbell and Fairey (1989) used a visual discrimination task in which participants were asked to judge whether two dot patterns had a similar number of dots. The uncertainty of the participants was manipulated by changing the number of times they had visual access to the dot patterns before answering and by changing the difference between the patterns (one pattern always had 25 dots, and the other pattern had a number of dots varying from 26 to 54). Campbell and Fairey manipulated the size of the majority by showing participants either one answer from another participant or three answers from three other participants (i.e., the size of the influence group was either one or three). The results supported the authors' predictions and have since been confirmed by a large number of experiments showing that informational and normative conformity are different phenomena. For instance, Cialdini and colleagues (Cialdini & Goldstein, 2004; Cialdini & Trost, 1998) have shown the relevance of this distinction when interpreting situations in which participants are trying to achieve effective action, to build and maintain social interactions, and to maintain a positive evaluation of themselves. The informational–normative distinction has also led to significant advances in research on the effectiveness of messages in influencing individuals' behaviors (Cialdini, 2003; Schultz, Nolan, Cialdini, Goldstein, & Griskevicius, 2007).

Other refined subdivisions among different aspects of conformity have been proposed. Kelman's (1958) classical distinction between compliance, identification, and internalization, for instance, has been very influential. Kelman recognized that at least three processes can result in conformity:

• compliance ("when an individual accepts influence because he hopes to achieve a favorable reaction from another person or group. He adopts the induced behavior not because he believes in its content but because he expects to gain specific rewards or

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[3] The term *uncertainty* is used in this article in two contexts. To avoid confusion, we call "psychological uncertainty" the fact that one individual is uncertain in a particular context, as in "Shall I wear a tie or a bow tie?" "Is it in the living room or the kitchen?" etc. In contrast, "environmental uncertainty" refers to the stability of the environment. Environmental uncertainty is an evolutionary notion independent of the psychological state of the individual. When the environment is uncertain, it might rain or snow, be hot or cold, provide many resources or few, etc. Logically, there should be a relationship between the two types of uncertainty: Environmental uncertainty should trigger psychological uncertainty. If it might rain or snow, one might wonder which jacket to put on, for instance. This relationship need not be perfect, however.

approval and avoid specific punishments or disapproval by con-
forming," p. 53),

• identification ("when an individual accepts influence because
he wants to establish or maintain a satisfying self-defining rela-
tionship to another person or a group," p. 53), and

• internalization ("when an individual accepts influence be-
cause the content of the induced behavior—the ideas and actions
of which it is composed—is intrinsically rewarding," p. 53).

Kelman's distinctions have been influential in human psychology
but may be challenging to identify in other species. We propose
that the informational–normative distinction offers a first funda-
mental step in analyzing conformity across species.

Furthermore, from a comparative perspective, the distinction
presents several important advantages. First, as we have seen, it
rests on solid empirical and theoretical grounds. Second, informa-
tional and normative conformity make different experimental pre-
dictions, and although both processes are likely to be involved to
some extent in many settings, some contexts are more likely to put
weight on one or the other process. Third, if normative and
informational conformity do involve different cognitive processes,
it is important to analyze their evolutionary origins and their
consequences for cultural evolution separately. Finally, much of an
earlier confusion in social psychology about conformity derived
from the lack of distinction between these two kinds of conformity.
Recent controversy over the presence and scope of conformity in
animals might stem from this unrecognized distinction. As we
argue in the next section, the distinction between informational and
normative conformity might be as much help in making sense of
the animal literature as it has been in the social psychological
literature.

Evidence for Conformity in Animals

Studies in social psychology suggest that (a) conformity results
from the influence of the frequency of behaviors individuals wit-
ness in others and (b) there is a fundamental difference between
informational and normative conformity. In this section, we use
these conclusions to critically review studies of conformity in
nonhuman animals. Our review provides support for the existence
of conformity in animals and highlights the importance of consid-
ering the informational–normative distinction. We conclude that
evidence for conformity could be much stronger if experiments
were to address more precisely the existence of either normative or
informational conformity and avoid contexts in which they might
be intermingled.

Informational Conformity and Foraging Strategies

Early results on conformity came as a surprise to social psy-
chologists because it was discovered that confronting a participant
with a majority of individuals behaving in a curious way, that is,
in a way the participant would not normally engage in, was often
enough to make the participant behave in the same curious way.
The most surprising results came from experiments in which the
participant was confronted with other individuals making an ob-
viously wrong judgment, as in the Asch (1955, 1956) experiments.
To our knowledge, Konopasky and colleagues (Catano &
Konopasky, 1975; Catano, Konopasky, & Mazmanian, 1980;
Konopasky & Catano, 1974; Konopasky & Telegdy, 1977) were

the first to use a similar method to test for the presence of
conformity in animals. Their studies appear to have been far ahead
of their time and to have been neglected in the proliferating new
animal literature. The authors developed an analogue of Asch's
paradigm that could be used with rats. Konopasky and Telegdy
(1977) used a Y maze with a white door in one arm and a black one
in the other. Models[4] were trained to use these door colors to
retrieve food hidden at the extremity of the maze. During the first,
training phase, observer rats were paired with one model that
would always use the same door color to retrieve food. If the
observer followed the model toward the same door, the observer
was rewarded too. During the test phase, observer rats were
divided into three groups. In the first group, observers could see
and follow the model but could not see the door color selected by
the model. In the second group, observers were tested in the
absence of a model and could see the door colors. Finally, in the
third, "conformity" group, observers could see the door colors, but
they were paired with models that always chose the previously
unrewarding door color. The results for the first and second groups
showed that during training, rats learned that the reward was
associated with a specific door color and that following the model
led to the reward. The results for the third group showed that rats
tended to follow the model toward the previously unrewarding
door, rather than use the door color cue. Konopasky and Telegdy
concluded that in their experiment rats gave more weight to social
information than to individual information, in a way analogous to
what has been observed in humans in Asch's experiments.[5]

A recent experiment by Galef and Whiskin (2008) strongly
supports this early conclusion. On the 1st day of the second
experiment that these authors described, isolated rats in the test and
social control condition could eat from two food cups either their
normal diet flavored with cocoa or a sugar-enriched diet flavored
with cinnamon. Rats in the third, individual-experience control
condition ate their normal unflavored diet. After eating, test rats
and individual-experience controls individually interacted for 30
min with one model that had just fed on the cocoa flavored diet
only. On the 2nd day, rats of all three conditions could eat from
both the cocoa and the sugar-rich cinnamon diet. As expected, on
the 1st day rats showed a very strong preference for the sugar-rich
diet. After having interacted with the model, however, test rats had

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[4] The terms *model* and *demonstrator* are often used interchangeably in
the literature. We prefer to use the term *model* over *demonstrator*, as
demonstrator can give the impression that the individual is actively trying
to show the other individual how to do something, which is not always the
case.

[5] It could be argued that in the Asch experiments the participant knows
the right answer and gives the wrong one, whereas the rats that had been
trained to follow a conspecific toward a specific door color cannot know
whether it is the selection of the appropriate door color or the fact that they
follow a conspecific that is rewarded. The rats are therefore not exactly in
the same position as the participants in the Asch experiment. However, if
the social information (the direction taken by the model) and the nonsocial
one (door color) were valued equally, we would expect rats to follow the
model on 50% of the trials. The experiment therefore reveals that rats tend
to give more weight to social rather than to nonsocial information, a fact
that could be explained by the high sociality of rats and their tendency to
stay with conspecifics. Also, it should be noted that Asch dealt especially
with the influence of a group and not a single individual.

a much weaker preference for the enriched diet, a preference similar to that of individual-experience control rats that had had no prior experience with the two diets. A 30-min interaction with a conspecific that had just eaten a less palatable food is therefore enough to cancel the preference acquired by the individual while feeding. This, again, suggests that social information can be valued more strongly than individual information.

However, evidence showing that social information can be valued more strongly than individual information is not in itself compelling evidence for the existence of conformity. Here we have defined conformity as the result of the influence of the frequency of behavior witnessed on the behavior of the focal individual, and the previous studies did not directly address this question insofar as the source of the social influence was only one type of behavior performed by a single individual (Galef & Whiskin, 1995, 2008; Konopasky & Telegdy, 1977). Showing that the frequency is the relevant factor that influences the behavior of individuals when they witness a single type of behavior (a frequency of 100%) is of course difficult; other confounding factors could be involved. Rats could be sensitive to the presence of the behavior rather than to its frequency, for instance. Stronger evidence for conformity can be obtained by varying the frequency of alternative behaviors witnessed in others by varying the size of the influence group (the number of individuals), by changing the proportion of individuals displaying alternative behaviors, or by varying the frequency of each behavior in the population.

Another difficulty arises from the fact that the influence of the frequency can be confounded with other factors. In fish, for instance, it has been argued that several experiments have shown that fish conform (C. Brown & Laland, 2002; Day, MacDonald, Brown, Laland, & Reader, 2001; R. L. Kendal, Coolen, & Laland, 2004; Lachlan, Crooks, & Laland, 1998; Laland & Williams, 1997; Webster & Hart, 2006). In these experiments, however, the influence of the frequency is confounded with a tendency to shoal. C. Brown and Laland (2002), for instance, trained model guppies to escape a moving partition using only one of two equivalent routes. Observer guppies given the opportunity to follow a model preferred to use the same route as the model rather than an alternative route when the model was present. When the model was removed from the tank, observer fish did not show any preference for the previously showed route. C. Brown and Laland interpreted their results as providing "strong evidence for the social conformity effect whereby the behavior of the majority compels the minority to conform" (p. 45). Another, more parsimonious explanation, however, involves the well-known tendency of guppies to shoal in groups, lowering predation risk. If guppies have a natural tendency to join groups (especially larger groups) to avoid predators, it is not surprising that they tend to escape with a conspecific rather than alone. More generally, because shoaling fish must take directional decisions as a group, they are not in a position to conform; the decision taken by the focal individual is instead part of a group decision process (see Conradt & List, 2009). To make this clear, imagine, for instance, that we modify the Asch paradigm by asking participants to come up with a single answer for the whole group instead of answering independently of one another. In this new experiment, the group decision process in itself could be studied and might reveal instances of conformity, but the point is that conformity cannot be inferred from the result of that process only because we do not know what happened. The

participants might be swayed by the frequency of alternative opinions, an eloquent participant, or a person they like, or they might not have any role in the group decision process.

In fish, improving on the previous studies described above, Pike and Laland (2010) manipulated the proportion of models that subjects saw. First, isolated nine-spined sticklebacks learned that one of two feeders (the food-rich feeder) contained more food than the other (the food-poor feeder). Then the positions of the rich and poor feeders were swapped, and the test fish watched one group of fish feeding at each feeder. Finally, the groups were removed, and the test fish was given the opportunity to feed at both feeders again. The experimental conditions differed in the proportion of fish feeding at both feeders: three fish at both feeders, two at the poor and four at the rich feeder, or one at the poor and five at the rich feeder. Results showed that test fish tend to be more attracted toward the rich feeder when there have been more fish feeding at that feeder. It should be noted, however, that nine-spined sticklebacks can assess the profitability of food patches by observing the feeding activity (movement speed) of others (Coolen, van Bergen, Day, & Laland, 2003; Coolen, Ward, Hart, & Laland, 2005; J. Kendal, Giraldeau, & Laland, 2009; Pike, Kendal, Rendell, & Laland, 2010; van Bergen, Coolen, & Laland, 2004). Test fish might not have conformed but been simply attracted toward the feeding site where the feeding activity itself was previously high (when groups were of equal size, observer fish tended to forage toward the feeder where feeding activity had been high). Fish might be able to use the activity of other fish as a cue to the amount of food present. If fish move slowly, this could indicate a limited amount of food compared to where fish move faster. So, for instance, if a group of two is feeding at a rich feeder and moving fast, while a group of four is feeding at a poor feeder and moving slowly, would the observer fish forage toward the group of two or toward the group of four? Previous studies suggest that they would not conform and go toward the group of four, but instead would forage toward the group of two (Coolen et al., 2005; Pike et al., 2010).

Beck and Galef (1989) also studied the acquisition of food preference by Norway rats and found that isolated rats choosing among four foods, three of which were protein deficient and one of which was protein rich, failed to learn to prefer the protein-rich diet and lost weight. Conversely, rats that interacted with conspecifics trained to eat the protein-rich diet developed a strong preference for that diet and thrived. The authors also found that increasing the size of the influence group (using zero, one, or three model rats) can increase social influence, an effect akin to what is found in humans. This experiment, however, differs from human studies because it involved rewarding social information (finding the protein-rich diet). Chou and Richerson (1992) also manipulated the proportion of the majority in a food choice task. Food-deprived rats were given the opportunity to eat either cocoa- or cinnamon-flavored food. Five groups of four models were created with a 0:4, 1:3, 2:2, 3:1, or 4:0 ratio of cocoa versus cinnamon. Each naive observer rat interacted during 30 min with one group of models and was then given a food choice test 24 hr later. The authors found evidence of conformity, as we have defined it here, suggesting that in this case the proportion of individuals eating a different food was a relevant factor.

In summary, some of the research on social learning about foraging suggests that conformity might be an important factor. It

does not yet provide definitive evidence because many studies confound the effect of frequency with other factors or because the size and proportion of the majority are usually not systematically varied (but see Beck & Galef, 1989; Chou & Richerson, 1992; Pike & Laland, 2010). Nevertheless, if we assume that the effects we observe result from a genuine influence of the frequency, we may wonder whether this influence is of a more informational or a more normative character. From a theoretical point of view, we expect conformity to be more informational when experiments involve foraging strategies, because in this situation individuals are motivated to find the best possible solution to a particular problem. The social consequences of one's behavior might be less important than finding the most valuable food. Results suggest that this is indeed the case. In a task similar to Konopasky and Telegdy's (1977), when model rats are not consistent and led to the reward on either 70% or 30% of the trials, observer rats progressively abandon the social cue (following the model) for a nonsocial one (Catano et al., 1980). This suggests that rats are not willing to follow the model just for the sake of being with the model (that would suggest normative conformity) but rather to find rewarding food (more compatible with informational conformity). Similarly, in Galef and Whiskin's (2008) study, observer rats interacted with models on Day 1 and were then tested alone on Day 2. We would not expect a strong effect of normative conformity in this case because individuals were tested alone after a delay, so normative effects are limited. If informational conformity is involved, the information acquired previously is still valuable after a delay, and the absence of others should not affect the results. In fish, van Bergen et al. (2004), in a task similar to that of Pike and Laland (2010), showed that nine-spined sticklebacks rely on social information only when their own personal information is not reliable, suggesting that if fish conform, they do so for informational purposes.

Theory and experiments therefore suggest that if conformity is involved in these experiments, it is likely to be more informational than normative conformity. However, this may be a consequence of the task used—a foraging task—rather than a property of the species tested. Other, more social tasks might uncover the presence of normative conformity in animals.

Normative Conformity and Learning New Skills

Evidence for normative conformity in animals is at present scarce and often subject to multiple interpretations. This is in part because it is difficult to show that the function of behavior is to optimize social interactions; accordingly, the studies we present in this section do not provide definitive evidence for normative conformity but rather point in that direction.

One important difference between the following studies and previous ones is that they often involve learning a particular skill from another individual rather than learning a particular strategy. The most thorough analysis in primates is Perry's (2009) 7-year study of the developmental acquisition of scrubbing and pounding food extraction techniques in capuchin monkeys. Perry showed that these two techniques are equally efficient and that during their first 2 years capuchins try a variety of techniques to extract seeds from *Lueha candida* fruits, yet settle on the technique they have most frequently observed. Of course, during their first years monkeys spend a lot of time with their mother, so the technique used

by their mother is an important factor, but Perry also found that the technique used by other members of the group with whom young monkeys spend time in proximity is also a significant predictor of the technique used by the individual. This suggests that it is the frequency of alternative behaviors that influences the acquisition of one or the other technique.[6] Furthermore, Paukner, Suomi, Visalberghi, and Ferrari (2009) showed that capuchins, like humans (Chartrand & Bargh, 1999), prefer individuals that imitate them rather than nonimitative ones. They concluded: "These experimental results demonstrate that imitation significantly affects the behavior of capuchin monkeys: They look longer at imitators, spend more time in proximity to imitators, and prefer to interact with imitators in a token exchange task" (p. 882). Therefore, adopting the most frequent behavior in one's group could be a way to manage one's social relationships (see also Rudolf von Rohr, Burkart, & van Schaik, 2011). Normative conformity in that case could explain why, despite the fact that both techniques were almost equally efficient in Perry's study, there was significant variability between groups regarding the frequency of use of these techniques (Perry, 2009).

Nelson and Poesel's (2009) study of white-crowned sparrows suggests that something similar might happen during song learning in this species. The authors showed that although yearlings produce a variety of songs, most individuals later selectively retain only one song that matches those that their neighbors sing (a phenomenon described as overproduction followed by selective attrition in the birdsong learning literature; see Cully Nordby, Campbell, Burt, & Beecher, 2000; Marler & Peters, 1982; Nelson, 1992, 2000). The process of song overproduction followed by selective attrition corresponds to our definition of conformity: A young bird produces a variety of songs and chooses the one most frequently sung because it is the most frequent song sung.

Song overproduction followed by selective attrition results in what is more generally known as "song sharing," the fact that bird songs are sometimes shared in part, or entirely, between several individuals. Conformity will, by definition, always result in song sharing, but song sharing is not always the result of conformity. In the case of bird songs, song similarity between individuals can reflect adaptation to local environments; it can also result from a high degree of copying fidelity that is not influenced by the frequency of alternative possibilities or from a tendency to copy the individual with the greatest reproductive success, for instance (summarized in Catchpole & Slater, 2008).

The fact that several mechanisms can result in similar population-level patterns of behavior makes it difficult to infer conformity from such patterns. In *Vidua chalybeata*, for instance, unsuccessful breeding males tend to adopt the song of the most successful one, giving rise to within-group homogeneity and

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[6] Perry (2009) pooled the observation of individuals other than the mother into a single category and therefore did not incorporate a social status variable in her model. She showed, however, that the technique used by individuals is largely predicted by the frequency of observation of that technique during infancy. In capuchins, young individuals are frequently associated with a broad range of individuals with very different social status (mother, peers, and alloparents that are mainly other adult females and subadults males and females; see Fragaszy, Visalberghi, & Fedigan, 2004). Therefore, although the study cannot rule out the effect of social status entirely, it is very unlikely.

between-group diversity without conformity (R. B. Payne, 1985; see also Kohler, VanBuskirk, & Ruscavage-Barz, 2004, for an example in archeology). However, recent models such as that of Mesoudi and Lycett (2009) seek a characteristic signature of conformity at the population level, which might provide a solution to this problem (see also Henrich, 2001). We note that the difference between normative and informational conformity is more likely to appear in the context of the spread or disappearance of behaviors. Normative conformity induces a resistance to change that does not appear with informational conformity: If individuals are normative conformists and learn a new behavior, they should refrain from displaying it in the presence of conspecifics. The spread of the behavior should therefore be slower than with non-conformity or informational conformity.

Interestingly, in the song learning literature there is a long tradition of discussing hypotheses regarding the evolutionary origin of song learning (for review, see Beecher & Brenowitz, 2005; Catchpole & Slater, 2008; Slater, 1986). One hypothesis regarding the likely origin of song sharing is that songs can be used as a marker of group identity (E. D. Brown, 1985; E. D. Brown & Farabaugh, 1997; Lachlan et al., 2004). In particular, in territorial systems, nonneighbors who are trying to establish themselves are a greater threat than neighbors who are already established. Territory neighbors can therefore avoid costly and unnecessary fighting by recognizing and responding less aggressively to one another (R. B. Payne, 1982, 1983; R. B. Payne & Payne, 1997; R. B. Payne, Payne, & Doehlert, 1988) and might also benefit from the joint defense of their territory against intruders (Beecher et al., 1997). This phenomenon is referred to as the "dear enemy" effect (Temeles, 1994; Wilson & Vehrencamp, 2001). In other species, song sharing has been linked to long-term association between individuals in species with complex social relationships; it is thought to increase affiliation between sharing individuals (E. D. Brown, 1985; E. D. Brown & Farabaugh, 1997). These two possibilities provide an interesting parallel with normative conformity in humans, which is also assumed to be linked to group identity and affiliation between individuals.

Studies also suggest that something similar can exist in mammals and more precisely in greater spear-nosed bats (Boughman, 1998; Boughman & Wilkinson, 1998; Wilkinson & Boughman, 1998) and humpback whales (Garland et al., 2011; Noad, Cato, Bryden, Jenner, & Jenner, 2000; K. Payne & Payne, 1985). Garland et al. (2011), for instance, did a 10-year study of the propagation of humpback whale song types across the South Pacific Ocean that revealed that at any one time, males of the same population sing very similar songs, but these songs change through time by the progressive replacement of song types that propagate across populations. The function of the songs and the mechanism of their transmission are unknown, but one possibility, modeled on our discussion of bird songs and motivated by the fact that vocal learning in mammals and birds shares many interesting properties (Janik & Slater, 1997, 2000), is that songs are displays of group identity and that males conform and use the same song in order to show their group membership.

These examples suggest normative rather than informational conformity because the individuals are in a familiar context, use known behaviors, and settle on the one that is simply most frequent among surrounding individuals. In a human example, you might have learned several shoe-lacing techniques when you were young

and you might even be able to use more than one at present. Yet, at some point you had to settle on some dominant technique that you now use most of the time. If we were to show that you learn two techniques equally well and then settle on the more frequent technique in your vicinity, this would be evidence of normative conformity.

These results echo other findings in which learners are found to experiment with several techniques before settling on the technique most commonly used in their group. Whiten et al. (2005), for instance, taught the dominant females of each of two groups of chimpanzees to use one of two techniques to retrieve food from a complex apparatus. After learning, each female was returned to her own group, and the apparatus was presented to the whole group. The authors observed the spread of the technique learned by the dominant females to other members of their respective groups. Some individuals also discovered the alternative technique and used it, but 2 months later, the apparatus was presented again to the two groups, and there was a significant tendency for individuals who had been using the alternative technique in the first session to abandon it to use the one more common in their group. Although the effect described by Whiten et al. is weak (Pesendorfer et al., 2009), a similar phenomenon has been documented in two other experiments using similar protocols with capuchin monkeys (Dindo, Thierry, & Whiten, 2008; Dindo, Whiten, & de Waal, 2009).

More recently, Hopper, Schapiro, Lambeth, and Brosnan (2011) have also found evidence of conformity in a food exchange task. Chimpanzees could exchange one of two types of tokens for a different food reward: One type was associated with a highly preferred food (grape) and the other with a less preferred food (carrot). Individuals first observed a demonstrator from their group exchange one of the two types of tokens. In one group, this token earned a small reward, whereas in the other group it earned a large reward. The results showed that in both groups, and over 10 sessions of 1 hr, chimpanzees continued to exchange mostly the token the model previously used, despite the fact that two chimpanzees in the small-reward group successfully exchanged tokens corresponding to large rewards. A possible confound in this experiment is the use of a dominant female as a demonstrator; it could be that dominance and not frequency of alternative behavior is driving the behavior of individuals (Horner, Proctor, Bonnie, Whiten, & de Waal, 2010). The same experiment, with a nondominant demonstrator, would control for that confound. Additionally, if chimpanzees are normative conformists, they should exchange the token associated with the large reward when they are on their own. This would provide strong support for normative rather than informational conformity.

Indirect evidence for normative conformity also comes from the study of what Perry et al. (2003) have called "social conventions" in capuchin monkeys. Broadly conceived, social conventions are group-specific customs. In humans, for instance, examples include nodding in agreement, shaking hands, and cheek kissing when meeting. Importantly, typically normative conformity will result in social conventions because this tends to stabilize patterns of social interactions, but the converse is not always true; social conventions do not always come from normative conformity. Stopping at a red light, for instance, is a convention, yet drivers do not stop because it is the most frequent behavior they witness in others; they stop either because they understand the risk involved in not stopping or

because it is a convention enforced by an institution. Evidence for social conventions in animals therefore only suggests that normative conformity could have been involved in their production.

The discovery of a pacific culture in one group of wild baboons is one such example (Sapolsky & Share, 2004). In the early 1980s, in unusual circumstances, 46% of the males in a troop of wild baboons died from bovine tuberculosis. Males affected by the disease were mostly dominant and aggressive, and their death produced a profound change in the level of aggression among members of the troop. Sapolsky and Share (2004) showed that this decrease in aggressiveness was associated with a decrease in glucocorticoids and persisted in the troop even when all males that had been present during the outbreak of the disease were replaced by new migrating males. Surprisingly, new males coming from neighboring troops where the level of aggression was high therefore progressively adapted to the reduced level of aggression in the study group. Normative conformity could be a factor explaining the persistence of a reduced level of aggression—if individuals are sensitive to the frequency of aggressive interactions in their group, for instance, and if they tend to adapt their own level of aggressiveness to that of others.

Perry et al. (2003) also described the diffusion of unexpected social conventions in wild white-faced capuchin monkeys (*Cebus capucinus*). In the "handsniffing" convention, for instance,

> One monkey takes the hand of another monkey and either covers its own nose and mouth with it, as if putting on a gas mask, or else inserts the other monkey's fingers up its own nostrils. This is often a mutual behavior, with each monkey simultaneously having the other's hand on or in its own nose. (p. 247)

Perry et al. described several such conventions and showed that their distribution is limited in space (to one or a few groups) and in time (from a few months to several years). Perry et al. pointed out that one important factor explaining the spread and sometimes disappearance of these social conventions is the presence or absence of key individuals who tend to perform these behaviors very frequently. The presence of one or two individuals who perform the original behavior at a high rate seems to make other members of the group more likely to perform the same behavior, hence the spread of these original behaviors. Normative conformity here would correspond to the fact that the frequency at which the behavior is performed increases the likelihood that an individual performs it. Similarly, in humans, if one or two individuals in a group are very keen on performing some behaviors, say, playing chess, other members of the group may join in even if they are not as keen. If the two members are removed from the group, however, the "convention" might disappear quickly. Therefore, although this would require a more detailed analysis to be confirmed, it also suggests that normative conformity could be involved in the propagation of these social conventions.

When taken together, all these studies suggest that normative conformity could be more common in animals than previously thought, but this last example highlights the importance of conducting experiments addressing specifically the existence of normative conformity to provide definitive evidence. Several experiments could be carried out in the field and in the wild to test the existence of normative conformity in animals. In the wild, evidence could come from long-term studies assessing the influence of the frequency of behavior on its probability of occurrence.

Following Perry (2009), we would recommend using focal follows focusing on social interactions (e.g., opportunities for observation of the behavior, affiliative and antagonistic behaviors) and the behavior under study (e.g., foraging technique) and scan sampling to collect data on the population under study. From these data, a social network analysis and a dominance hierarchy could be established and the results incorporated in a statistical model using dominance, social proximity, affiliation and frequency as predictors for the behavior of each monkey. This model would provide evidence for or against the importance of frequency compared with other social factors such as dominance and affiliation. Another type of evidence could come from the study of individuals who migrate from one group to another and adopt, or not, the behavior of their new group. Evidence from the wild could be supported by laboratory experiments where it is easier to control for social variables such as dominance. For instance, one could teach individuals to perform two equivalent behaviors and expose them to unfamiliar others who would perform the two behaviors in variable proportions. If the individuals tend to perform the behavior they see more frequently, this would constitute evidence of normative conformity. Another possible experiment would look at resistance to change in behaviors. Normative conformity should prevent individuals from adopting new, more efficient behaviors in the presence of others, but not when separate from the group. An experiment could address this issue by measuring the likelihood that individuals change their behavior in a group versus an isolated setting.

Notice also the important differences between these studies and the ones we reviewed in the preceding section. Studies in the informational conformity category have been concerned with optimal foraging strategies; the question they address is of the form, in this particular context what strategies do individuals use to find the most efficient behavior? One possible answer is informational conformity; individuals might use observed behavioral frequency as a proxy for efficiency. Individuals are typically in a new, uncertain situation (facing some new kinds of food, for instance); the context is often linked to food preference or foraging decisions; the effects are often short term (individuals rapidly find the most efficient behavior), persist when the tested individual is isolated from conspecifics (after the individual sees a model, it is then tested in isolation), and disappear when the conspecifics are not reliable.

In contrast, studies under the normative conformity category are concerned with social interactions between individuals insofar as the question is, do members of this group tend to have the same behavior just because they are members of the same group? One possible answer is normative conformity; individuals might conform because this helps them manage social interactions with other members of the group. Importantly, studies investigating the existence of normative effects must rule out the possibility that individuals are using optimal foraging strategies, because otherwise the fact that individuals use the same behavior can be explained by the fact that it is the optimal one. As a consequence experiments are frequently concerned with skill acquisition; individuals are typically in a relatively familiar context (with known conspecifics, for instance), are shown to be able to use several equally efficient alternative behaviors, and nevertheless settle on the one used by other individuals.

Interestingly, there is as yet little evolutionary explanation of normative conformity, but the convergent evolution of normative conformity in birds, bats, whales, and primates might aid the discovery of its function and represent an interesting avenue for future empirical and theoretical research.

Finally, whether or not one believes that the evidence for normative conformity in animals is strong, it still makes sense to distinguish between experiments aiming at understanding optimal foraging strategies and the ones aiming at understanding social interactions. The distinction between the informational and the normative situation is natural; it reflects contexts in which individuals have different priorities.

Predictions in Future Studies of Conformity

The existence of conformity in animals receives some support from the literature, but to date few studies have specifically set out to address this issue (for exceptions, see, e.g., Galef & Whiskin, 1995, 2008; Hopper et al., 2011; Konopasky & Telegdy, 1977; Pike & Laland, 2010). Conformity has more often emerged as a potential and incidental explanation of results obtained. Furthermore, until now the distinction between normative and informational conformity has not been recognized in the animal literature

and has therefore not been addressed. Using this distinction, we have been able to organize the literature on conformity in animals and spot difficulties that can be dealt with in future experiments. Here we summarize under which conditions we can expect the presence of informational and normative conformity (see also Table 1).

Informational conformity is expected when psychological uncertainty is high and individuals are trying to behave efficiently. When an individual faces a new situation, relying on the most frequent behavior witnessed to find the most advantageous option can be an adaptive strategy. Experimentally, informational conformity can be revealed when the effect of an increase in the size of the influence group decreases with the size of the group. Other factors supporting the informational interpretation are the persistence of the effect when the individual is tested alone, a decreased effect when social information is inaccurate or unreliable, and conversely an increased effect when personal information is inaccurate or unreliable.

Normative conformity can be revealed experimentally when the effect of an increase in the size of the influence group increases with the size of the group. Other factors supporting the normative interpretation are the fact that the individual still conforms when

Table 1

Summary of Theoretical and Empirical Differences Between Informational and Normative Conformity

Condition	Informational conformity	Normative conformity
	Theoretical differences	
Function	Functions to gain nonsocial information and adapt one's behavior to the nonsocial environment.	Functions to gain social information and adapt to one's social environment.
Context	Individuals are motivated to find the best possible solution to a particular problem (e.g., foraging strategy).	Individuals are motivated to build and maintain social interactions and to maintain a positive evaluation of themselves (e.g., display group membership).
Evolutionary origin	Informational conformity could help adapt to uncertain environments: It is used as a proxy for finding the most appropriate behavior in an uncertain situation.	Normative conformity could help manage social interactions: It can be used as an honest signal of group membership.
	Experimental differences	
Psychological uncertainty	Individuals face an unknown situation with unknown individuals.	Individuals are in a known situation with familiar individuals.
The other's awareness of one's behavior	The behavior continues in the absence of the group.	The behavior stops in the absence of the group.
Conflict between the individual and the group	The individual relies on social information only when his or her personal information is not reliable.	The individual relies on social information even when it is not reliable.
	The individual displays the most frequent behavior only when it is also optimal.	The individual displays the most frequent behavior even when it is not optimal.
	Having one ally has a limited effect on the influence of the group.	Having one ally can disrupt the influence of the group.
Effect of varying the size of the influence group	Marginal effect decreases with group size for small group sizes.	Marginal effect increases with group size for small group sizes.
Frequency of alternative behaviors	Linear or weak conformity.	Hyperconformity.
Diversity of behavioral repertoire	Individuals learn and perform only one option.	Individuals learn and use several options and settle on one afterward.
Evolution of diversity within group	Diversity of behavior within group can remain stable over time.	Diversity of behavior within group progressively disappears over time.
Resistance to the introduction of new behavior	Weak because individuals who discover new, more efficient behaviors readily display them.	Strong because individuals who discover new, more efficient behaviors are unlikely to display them in the presence of the group.
Migration	If an individual with a different behavior migrates in a group, the individual retains his or her initial behavior.	If an individual with a different behavior migrates in a group, the individual adopts the behavior of the group.

he or she has experienced that the most frequent alternative is not the most efficient option and yet stops conforming when alone.

Finally, one crucial aspect of any study on conformity must be the systematic manipulation of the frequency of behaviors and of the proportion of individuals displaying alternative behaviors, without which the hypothesis that the most frequent behavior influences an individual remains speculative only. Conformity can be shown particularly by manipulating the least efficient option to be the most frequent, but this in itself cannot disentangle informative and normative conformity. Evidence discriminating normative and informational conformity in animals will necessarily come from a diverse array of studies, which should enable us to compare the relative importance of normative and informational conformity in different domains (feeding behaviors, mating behaviors, etc.) and across several species (fish, birds, primates, etc.), with the aim of better understanding the consequences of conformity for cultural evolution and ultimately the factors governing the evolution of conformity by natural selection.

Conformity and Evolutionary Theory

Boyd and Richerson (1982) were the first to study the effects of conformity on cultural evolution and propose plausible evolutionary scenarios that might account for the evolution of conformity in humans. This work is part of a larger and influential research program. Boyd and Richerson (1985; Richerson & Boyd, 2005), together with Cavalli-Sforza and Feldman (1981), have advocated the use of population genetics models to understand how psychological mechanisms shape cultural evolution and at the same time are shaped by natural selection (so-called dual inheritance theory, the inheritance of genes, and culture and their interactions; see Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Richerson & Boyd, 2005). In this third section we review results from population genetics models and experiments with humans aimed at testing these models because they bring yet another perspective to the discussion of the existence of conformity in animals and humans. Indeed, depending on the conditions under which conformity evolved in humans, we might predict in which species we could expect conformity to exist.

One original aspect of this body of literature is that conformity has been defined in this field along a dimension almost orthogonal to its definition in social psychology. This is because in evolutionary biology the focus is on the ultimate consequences of behavior, whereas in social psychology the focus is on the proximate mechanisms. More precisely, the term *conformity*, in this literature, is used to refer to positive frequency dependence, and other possibilities are usually less studied.

Because our aim is to go beyond disciplinary boundaries and lay the ground for an integrative approach to the study of conformity, we have renamed as *hyperconformity* (Claidière, 2009) what is usually simply called conformity in modeling studies (we also use "weak" and "linear" conformity to designate other response curves; see below). This terminological change brings into focus an interesting hypothesis concerning the relationship between studies in social psychology and studies in evolutionary biology. Informational conformity, we propose, might be associated with weak or linear conformity, whereas normative conformity might be associated with hyperconformity.

## The Consequences of Conformity for Cultural Evolution

Conformity is often viewed as an important factor explaining the spread and stability of group-specific behaviors: Individuals who conform adopt the behavior most frequent in their group and thereby increase the frequency of this behavior. As the frequency of the most frequent behavior increases, alternative behaviors should thus progressively disappear from the population, ultimately leaving only one behavior. Conformity is also said to lead to stable between-group differences: If the frequency of different alternatives differs between groups, conformity will increase the difference between them by reducing the diversity inside each group. In short, conformity is thought to increase in-group homogeneity and between-group diversity.[7]

As noted by Boyd and Richerson (1985), this reasoning is valid under some specific form of conformity influence only (see also Efferson, Lalive, Richerson, McElreath, & Lubell, 2008; Henrich & Boyd, 1998). Imagine, for instance, the following situation. Suppose that individuals can wear a baseball cap in only two ways, with the peak at the front ("front" behavior) or with the peak at the back ("back" behavior). Further imagine that these are perfectly equivalent in every respect except their frequency (call p_0 the probability that an individual uses front when there is no social influence; if both alternatives are equivalent, then $p_0 = 0.5$). Now suppose that front is used 60% of the time and back is used only 40% of the time (call F the relative frequency of front inside the population, $F = 0.6$). If an individual does not conform, his or her behavior is not influenced by the most frequent alternative, and therefore the individual's probability to use either form will be identical (call p_i the probability that a particular individual i uses front; when conformity is null, $p_i = p_0$). If conformity is not null, however, the probability that an individual uses the most frequent position will be greater than the probability of the individual's using the less frequent one ($p_i > p_0$ if $F > 0.5$, $p_i < p_0$ if $F < 0.5$), and the stronger conformity is, the larger this probability will be. Figure 2 represents the conformity domain in the case just discussed.

In the conformity domain (shaded area in Figure 2), three dynamics are possible:

1. Weak conformity (dotted domain in Figure 2): The probability that an individual displays the behavior most frequent in the group is less than the frequency of that behavior in the group. In that case the frequencies of both behaviors thus converge toward their probability when there is no social influence (F converges toward p_0).

2. Linear conformity (dash-dotted line in Figure 2): The probability that an individual displays the behavior most

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[7] The factors that explain the origin, spread, and persistence of behaviors are not generally the same (Claidière & Sperber, 2010; Galef, 1995). Here, note that on this account conformity cannot explain how a behavior becomes frequent in the first place; it can only explain its spread and its stability once it is frequent. Several factors could explain the initial spread of a behavior: One could be performance, such as when one behavior is better than another; another could be authority, where a dominant individual adopts. Also, in humans institutions, authority and policing could impose a change in behavior that can later be sustained via conformity.
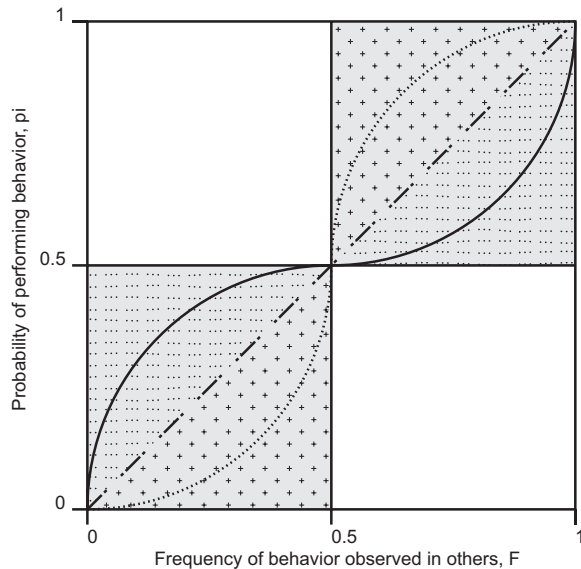
Figure 2. In the conformity domain (shaded in gray) three dynamics are possible: weak conformity (dotted domain; an example is the solid line), linear conformity (dash-dotted line), and hyperconformity (crossed domain; an example is the dotted line). Anticonformity is represented by the nonshaded domains and nonconformity by the straight horizontal line with a probability of performing behavior set at .5. In the example given in the text, F is the frequency of front versus back observed by one individual, and p_i is the probability that this individual displays front versus back given the observed frequency F.

frequent in the population is equal to the frequency of that behavior in the population. The frequency of both behaviors thus remains constant over time (F is constant).

3. Hyperconformity (crossed domain in Figure 2): The probability that an individual displays the behavior most frequent in the population is greater than the frequency of that behavior in the population. The frequency of the most frequent behavior thus converges toward 1 (F converges toward 1 or 0).

In the case of weak conformity, the influence of observed frequency is subtle; individuals are only slightly more likely to display the most frequent alternative rather than the other alternative. Imagine that without social influence, when you are on your own in your home, for instance, you are equally likely to drink tea or coffee for breakfast. Further imagine that you sometimes buy breakfast from a takeout and queue to place your order. If you are weakly conformist in that situation, your probability of ordering tea or coffee is affected by the orders of persons in front of you, but only slightly. So, for instance, if four out of six order tea, you are slightly more likely to order tea (i.e., above 50%) but still less likely than the actual percentage you just witnessed (i.e., 66%). From a dynamic point of view, the frequency of both behaviors will converge toward their probability when there is no social influence, and differences between groups will therefore disappear through time.

In the case of linear conformity, the probability that an individual displays a behavior is equal to the frequency of that behavior

in the population. At the behavioral level, this process gives a result similar to random copying, in which an individual picks another individual at random and then copies that person's behavior (*random copying* usually refers to the dash-dotted line in Figure 2 in modeling studies; Boyd & Richerson, 1985). Despite the fact that random copying and linear conformity give similar outcomes, they are psychologically different. Random copying is useful in modeling studies as a null hypothesis (Bentley, Hahn, & Shennan, 2004; Bentley, Lipo, Herzog, & Hahn, 2007; Bentley & Shennan, 2005; Goodfellow & Slater, 1986; Shennan & Wilkinson, 2001); however, it finds little empirical support in the psychological literature. On the other hand, we know that individuals are sensitive to the frequency of information in different contexts (Kirkham, Slemmer, & Johnson, 2002; Perruchet & Pacton, 2006; Saffran, 2003; Saffran, Aslin, & Newport, 1996; Saffran, Johnson, Aslin, & Newport, 1999) and that even children do not choose "teachers" randomly but based on their preferences, habits, expertise, benevolence, charisma, etc. (Corriveau et al., 2009; Harris & Corriveau, 2011; Mascaro & Sperber, 2009). We would therefore argue that linear conformity is probably more likely than random copying. However, random copying can also result from certain heuristic strategies (Gigerenzer & Selten, 2001; Gigerenzer & Todd, 1999). If individuals copy the first individual they see, for instance, in a well-mixed population where encounters are at random this could give rise to random copying. In such a case, an experiment controlling for the order of presentation of different behaviors should reveal which of the two mechanisms, linear conformity or random copying, is at work.

In the modeling literature, what we here call weak and linear conformity are usually not recognized as kinds of conformity (but see Skyrms, 2005, for a model with linear conformity). This is because the focus is on the forces explaining the persistence of group-specific behaviors, and weak and linear conformity cannot sustain group-specific behaviors on their own. We introduce this distinction because experimental studies of conformity, whether in the social sciences or the behavioral sciences, are not exclusively concerned with group differences but more generally with group influence. From a proximate perspective, it makes sense to call conformist the influence of frequency we have just described, whether this influence is weak, linear, or hyperconformist (Claidière, 2009; Whiten & Flynn, 2010).

Only hyperconformity (or simply conformity in the modeling literature), however, can systematically lead to the erosion of different alternatives and to the fixation of the most frequent alternative (Boyd & Richerson, 1985; Efferson et al., 2008). For this reason hyperconformity has received considerable attention in the modeling literature. The modeling literature has suggested that by increasing the behavioral homogeneity inside groups, hyperconformity can (a) provoke cumulative cultural evolution, (b) explain the existence of maladaptive cultural behaviors, and (c) stabilize cooperation in large groups and potentiate group selection (summarized in Richerson & Boyd, 2005). These theoretical analyses therefore suggest that hyperconformity might be one important factor explaining the divergence between human culture and animal culture. Empirically, however, evidence for hyperconformity in humans remains controversial.

A general approach pioneered by McElreath et al. (2005) to test the existence of a hyperconformist tendency in humans has been to ask participants to play a virtual game in which they could access

various kinds of social information. Hyperconformist participants would do better on average than other participants. However, McElreath et al. found that in their game, most participants do not use social information at all and, among the few who do, only a small minority are hyperconformist. Subsequent studies have not found a clear hyperconformist tendency in humans (Coultas, 2004; Efferson et al., 2008, 2007; Eriksson & Coultas, 2009; Eriksson, Enquist, & Ghirlanda, 2007; McElreath et al., 2008, 2005; Whiten & Flynn, 2010), leading Eriksson et al. (2007) to conclude: "Based on our theoretical arguments and simulations, we do not expect any strong selection pressure for a conformist bias, and we found no satisfactory evidence as yet that such a bias actually exists within human psychology" (p. 85; conformist bias sensu hyperconformity, as we have defined it).

This conclusion is in sharp contrast with the results concerning plain conformity in social psychology and in the animal behavior literature we have reviewed above. The discussion of (hyper)conformity in the modeling literature, however, rarely draws the distinction between informational and normative conformity (Henrich & McElreath, 2007), and the experiments just described suggest that making this distinction might help explain where the discrepancy arises. In McElreath et al. (2005) and others, individuals are trying to find the most efficient decision in a new, psychologically uncertain situation. As we have argued previously, when participants try to find the most efficient behavior, informational conformity but not normative conformity is expected. The results of McElreath et al. and others suggest that hyperconformity is unlikely to be associated with informational conformity, but it might, however, still be associated with normative conformity. This would be consistent with the fact that the persistence of maladaptive behavior and group norms, the stabilization of cooperation, and the evolution of group selection are domains linked to social interactions and might therefore be linked to normative conformity.

The idea that normative rather than informational conformity is likely to be associated with hyperconformity is also consistent with the fact that normative rather than informational conformity should lead to in-group homogeneity and between-groups diversity. Informational conformity is a heuristic to find the best behavior when one is uncertain, but if the situation arises frequently, psychological uncertainty will decrease, and the influence of informational conformity should decrease correspondingly. In most situations in which informational conformity is involved, we expect individuals with different preferences to display different behaviors. For instance, although left-handed individuals may tend to conform first by adopting the behavior of the more frequent right-handed persons, they soon discover that it is more difficult for them to use their right rather than their left hand, and in the absence of other constraints, left-handed persons readily change hands and learn to perform with their left hand. Although at first left-handed individuals conform, at equilibrium there is a stable proportion of both right and left behaviors. In most cases informational conformity should therefore lead to a stable diversity of behaviors inside groups and to the erosion of between-group differences.

By contrast, most of the time normative conformity should give rise to in-group homogeneity and intergroup differences because under normative conformity individual preferences are discarded for the most frequent behavior. At the intergroup level, if all members of a group display the same behavior because it is the most frequent behavior, initially small group differences might get amplified by normative conformity, increasing intergroup differences.

Thus normative conformity and hyperconformity, but not informational conformity and weak or linear conformity, can best explain in-group homogeneity and intergroup differences; hence the suggestion that normative conformity is associated with hyperconformity and that informational conformity is associated with weak and linear conformity.

This hypothesis has important consequences for our current understanding of the evolution of conformity through natural selection. It has usually been assumed that hyperconformity can readily evolve by natural selection to help individuals behave optimally in uncertain situations. This seems to contradict the idea that informational conformity could be associated only with weak or linear conformity. In the following section, however, we review recent results on the evolution of conformity and conclude that the evolution of hyperconformity is less likely than what was previously thought. We conclude that our suggestion that normative conformity is associated with hyperconformity and that informational conformity is associated with weak or linear conformity is not in contradiction with the current literature.

The Evolution of Conformity by Natural Selection

Boyd and Richerson (1985) were the first to propose a model of the evolution of hyperconformity in humans. Boyd and Richerson reasoned that if individuals were facing a complex environment in which it was difficult to find on one's own the most appropriate behavior, relying on others and using a hyperconformist strategy might evolve by natural selection. Their modeling revealed that when the environment is relatively uncertain (this environmental uncertainty is usually represented either by spatial variations or by temporal variations), hyperconformity can evolve. Boyd and Richerson gave the following example to illustrate the principle. Imagine farmers can use two types of the same crop and are trying to grow the one with the better yield. Crop yield might vary with a large number of parameters, such as rainfall, temperature, soil, etc., and might therefore be quite difficult to estimate on one's own. If one crop is better than the other, however, farmers are on average more likely to grow that crop than its alternative. A hyperconformist farmer, who would settle for the crop more frequently grown by other farmers, would therefore be more likely to find the better crop than a farmer who would not use this strategy. Although Boyd and Richerson themselves do not use the distinction between informational and normative conformity, in our terms it is clear that informational conformity but not normative conformity is the subject of their model. In our terminology, Boyd and Richerson's model shows that informational conformity evolves to be hyperconformist. This would seem to argue against the idea that informational conformity is not associated with hyperconformity.

The evolution of hyperconformity, however, is dependent on the degree of environmental uncertainty, and although the evolution of hyperconformity in Boyd and Richerson's model is possible, the likelihood of their evolutionary scenario remains to be determined. To estimate the plausibility of the evolution of hyperconformity, Henrich and Boyd (1998) have examined a model in which the environment is subject to temporal and spatial variations and

where individuals can either learn on their own (individual learning) or rely on others (social learning), being either hyperconformist or not. They found that hyperconformity always evolves to be maximal unless the environment is highly variable. Henrich and Boyd concluded that hyperconformity is likely to evolve under a broad range of environmental conditions:

> The analysis of this model indicates that conformist transmission is favored under a very broad range of conditions, broader in fact than the range of conditions that favor a substantial reliance on social learning. The analysis also suggests that there is a synergistic relationship between the evolution of imitation and the evolution of conformism. (p. 215; conformism sensu hyperconformity)

The results of Henrich and Boyd are, however, somewhat counterintuitive: If hyperconformity is very strong, it will prevent the spread of alternative behavior that might be better adapted to the situation. This might not be an important problem when the environment is quite stable, but it should have a negative impact when the environment keeps changing. Intuitively, we might just as well expect the opposite of what Henrich and Boyd have shown: a decrease in hyperconformity with an increase in environmental variability.

Further analysis indeed revealed that Henrich and Boyd's (1998) results, that hyperconformity can evolve under a broad range of conditions and is favored when the environment is variable, is a consequence of their particular method of numerical analysis (Kameda & Nakanishi, 2002; Nakahashi, 2007; Wakano & Aoki, 2007). To understand why, consider the following simplified scenario (based on Wakano and Aoki's model). Imagine individuals first have two possibilities: learn on their own (individual learning) or learn from others (social learning). Individual learning is based on the information gathered from the environment (you find on your own the most appropriate behavior), and social learning can be either straight imitation (copy a model's behavior) or hyperconformist (use the most frequent alternative). Consider the following two extreme cases.

At one extreme, when the environment changes very quickly, in such a way that it is almost unpredictable, individual learning is more fit than social learning because potential models are likely to have an outdated behavior that might not be the best in the present environment. Among the few social learners, however, those who use a hyperconformist strategy are fitter than those who use a simple imitation rule. This is because most individuals are individual learners and find the most appropriate behavior, in which case relying on the most frequent behavior is always more accurate than simple imitation. In short, when the environment changes quickly, individual learning is common, social learning is rare, but all social learners should become hyperconformists.

At the other extreme, when the environment changes infrequently, social learning is more fit than individual learning because others are a valuable and reliable source of information. However, among social learners, those with a strong hyperconformist tendency are at a disadvantage compared with imitators because in the rare cases when the environment changes, hyperconformists continue to use the more frequent but less efficient behavior, whereas imitators are more likely to copy an individual displaying a better adapted one. In short, when the environment changes infrequently, social learning is common, individual learning is rare, and among

social learners, imitators become more frequent than hyperconformists.

In between the two extreme positions a mixed equilibrium exists, and eventually the precise strength of hyperconformity remains an empirical matter. But the fundamental conclusion is that in these models hyperconformity never evolves to be so strong as to prevent the population from adapting to new conditions in the environment because it would then be counterselected. If hyperconformity evolves to cope with gaining adaptive information in uncertain environments, it cannot explain on its own the persistence of between-group differences, or provoke cumulative cultural evolution, or explain the existence of maladaptive cultural behaviors, or stabilize cooperation in large groups, or potentiate group selection. It is also important to note that there is an inverse relationship between the evolution of social learning and that of hyperconformity. The more stable the environment is, the more individuals rely on social learning, the less hyperconformist they are.

This does not mean that hyperconformity does not exist, but it suggests that a different evolutionary scenario could explain the presence of hyperconformity, and on the basis of our analysis of the literature, we propose that hyperconformity might have evolved with normative conformity to manage social interactions.

In summary, evolutionary analyses reveal that among the various forms that conformity can take, only hyperconformity can stabilize between-group differences and increase in-group homogeneity. Hyperconformity has traditionally been studied in a context where informational conformity should dominate, but more recent experiments and models have revealed that the evolution of hyperconformity is in fact more restricted than what was previously thought. Our proposal of an association between informational conformity and weak or linear conformity on the one hand and normative conformity and hyperconformity on the other hand therefore merits further exploration.

Conclusion and Perspectives

Social scientists in the 1950s and 1960s were struck by the influence that other people can have on one's own behavior (Asch, 1955; Milgram, 1974; Milgram, Bickman, & Berkowitz, 1969), and among the different forms that social influence can take, conformity appeared as one of the most important and most obvious influences. The study of conformity rapidly became a major topic of social research, and a large body of both empirical and theoretical work has been growing ever since. Yet, apart from a few studies, it is only recently that behavioral ecologists and evolutionary biologists have shown interest in the topic. This is a great opportunity for social and natural scientists to join forces in building an interdisciplinary and integrative approach to conformity, but at the same time one must lament the lack of mutual understanding and communication that characterize work on conformity. This review is an attempt to bridge this gap by providing common ground on which the foundation of what we believe would be a very stimulating and productive array of research can be laid. Accordingly, we have tried to render the present article as useful as possible to both social and natural scientists. We have tried to make accessible to others the main results, difficulties, and questions facing conformity research in each field, and by way of conclusion, we briefly summarize them here and in Table 1.

Studies in social psychology show that conformity, the fact that individuals are influenced by the most frequent behavior they witness in others, results from two fundamentally different mechanisms. On the one hand, informational conformity dominates context in which psychological uncertainty is high and individuals are trying to behave accurately. On the other hand, normative conformity is expected in contexts in which individuals need to manage social interactions.

This fundamental distinction in social psychology has been little discussed in behavioral sciences and evolutionary biology. We have endeavored to show that it can help us make sense of the literature in these fields, solve some current controversies, and raise new challenging questions for all disciplines.

In the behavioral sciences, studies of conformity can be organized along the informational–normative distinction to show that what has traditionally been considered as conflicting results is in fact attempts to study different forms of conformity. What appeared as mixed support for conformity in animals can now be understood as evidence of the existence of two forms of conformity. Taking the perspective of the social sciences, however, also reveals a number of weaknesses in animal studies and suggests new ways of addressing them in the future.

In evolutionary biology, the informational–normative distinction also suggests a way out of a conflict between our understanding of the consequences of conformity for cultural evolution and the evolution of conformity by natural selection. Recent experiments and modeling show that hyperconformity, the only form of conformity that can give rise to stable group differences, evolves only in a restricted range of environmental conditions and is not involved in experiments in which the participants are asked to behave accurately. As some have argued, it could be that hyperconformity does not exist at all, but it could also be that the context in which hyperconformity has been investigated is not appropriate. More precisely, we suggest that in informational contexts individuals might be only weakly or linearly conformist and that they might be hyperconformist in normative contexts. In that case the evolution of hyperconformity would be linked to the management of social interactions and not to individuals trying to behave accurately. This hypothesis deserves further experimental and theoretical analysis.

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