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Adaptive cultural transmission biases in children and nonhuman primates

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Abstract

Comparative and evolutionary developmental analyses seek to discover the similarities and differences between humans and non-human species that illuminate both the evolutionary foundations of our nature that we share with other animals, and the distinctive characteristics that make human development unique. As our closest animal relatives, with whom we last shared common ancestry, non-human primates have been particularly important in this endeavour. Such studies that have focused on social learning, traditions, and culture have discovered much about the ‘how’ of social learning, concerned with key underlying processes such as imitation and emulation. One of the core discoveries is that the adaptive adjustment of social learning options to different contexts is not unique to human infants, therefore multiple new strands of research have begun to focus on more subtle questions about when, from whom, and why such learning occurs. Here we review illustrative studies on both human infants and young children and on non-human primates to identify the similarities shared more broadly across the primate order, and the apparent specialisms that distinguish human development. Adaptive biases in social learning discussed include those modulated by task comprehension, experience, conformity to majorities, and the age, skill, proficiency and familiarity of potential alternative cultural models.

Key words: cultural transmission; social learning; model biases; children; infants; nonhuman primates

1. Introduction

The adaptive benefits of social learning are well-established and the ability is widespread among a diverse range of vertebrate and invertebrate species. Social learning is fundamental to the maintenance and spread of animal 'cultures' or behavioural traditions, and we have extensive observational and experimental evidence for these in animals (Price, Caldwell, & Whiten, 2010). However to date, there exists no strong evidence of significant cumulative culture - cultures that become increasingly complex over time as they do in humans - in other species (Dean, Vale, Laland, Flynn, & Kendal, 2014).

Comparative cultural cognition research typically focuses on differences in the social learning mechanisms underlying culture in human and nonhuman animals. One prominent theory suggests that differences in the specific means by which information is spread between individuals might help explain the lack of cumulative culture in species other than our own (Tennie, Call, & Tomasello, 2009; Tomasello, 1996). The suggestion is that humans tend to copy or imitate with higher fidelity than other species, copying actions, end results, and goals. In contrast, other animals are limited by a tendency to copy only some aspects of a behaviour, or only the results of actions (emulation), and precise information regarding actions is not so readily transmitted, leading to cultural "slippage" effects (i.e. the loss of cultural information over time).

Whilst there is certainly evidence to support higher fidelity copying in human children compared to other apes (most typically chimpanzees, e.g. Call, Carpenter, & Tomasello, 2005; Nagell, Olguin, & Tomasello, 1993), both children and chimpanzees have been shown to employ a suite of social learning mechanisms (Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). Other animals sometimes exhibit imitation (e.g.

(Voelkl & Huber, 2000; Zentall, Sutton, & Sherburne, 1996), and children can be seen both to selectively imitate in some contexts (e.g. Gergely, Bekkering, & Kiraly, 2002), and ‘overimitate’, copying even causally irrelevant actions in others (e.g. Lyons, Young, & Keil, 2007; McGuigan, Whiten, Flynn, & Horner, 2007).

Thus, a given individual (or species) does not always apply a single social learning mechanism; rather, they may apply different psychological rules that govern when and from whom to acquire information, and how much of the available information to copy. Such processes have been labeled social learning strategies (Laland, 2004) or cultural transmission biases (Boyd & Richerson, 1985), and may allow an individual to counteract the risk of potentially outdated or maladaptive information (Kendal, Coolen, van Bergen, & Laland, 2005). These biases also likely play a crucial role in determining how behavioural variants are spread and maintained at population levels (Haun, van Leeuwen, & Edelson, 2013).

Comparative research seeking to pinpoint differences underlying cultural transmission biases in humans and other animals has thus risen in prominence. But while transmission biases have been explored separately in both animals (Laland, 2004) and children (Wood, Kendal, & Flynn, 2013), the comparative exploration of these factors, employing similar procedures in humans and nonhumans, is lacking. Given the rapidly growing scale of recent research, we cannot here provide a comprehensive review of cultural transmission biases; rather, we highlight those that we believe to be particularly good candidates for the exploration of similarities and differences between humans and other primates. Although we note that comparisons between diverse species are essential for a full understanding of how cognition evolves, here we focus on human infants and

nonhuman primates (hereafter primates) specifically, because of their central relevance in illuminating the most recent phases of hominin cognitive and cultural evolution. We examine how the context of the learning environment, coupled with the psychological rules the observer is following, helps us better understand the different types of cultural transmission processes observed in human children and primates. Now that we have a substantial corpus of comparative studies focusing on the "how" of social learning with regard to mechanisms, it is important to consider the social and psychological contexts under which different mechanisms are employed, or the "when", "who", and "why" of social learning.

2. When to copy

In some cases, it might not be the most adaptive option to learn from watching others, particularly when information gained asocially by one's own efforts may be more relevant or accurate. Information gleaned from others may be out of date or misleading for a variety of reasons. Choosing between social and asocial learning in any one context can be modulated by the observer's understanding of the problem, experience, or proficiency. Alternatively, the perceived skill of the model or the number of models displaying a particular behaviour may influence when an individual chooses to copy, as outlined below.

2.1. Task comprehension and experience

A given task may be opaque with respect to the actions needed to complete it, for example because the internal mechanisms are occluded. In such cases, it may be

beneficial to apply a "copy-everything" bias to reach a solution. Both preschool-aged children and young chimpanzees have been found to copy all actions, including irrelevant actions, from adult humans when the processes involved in task completion are opaque (Horner & Whiten, 2005).

Children also seem to evaluate a task in relation to a model's particular actions and efficacy with the task. When faced with a model who performs an action with an unexpected body part without a plausible reason (e.g. turns a light switch on with her head, rather than hand), both 14-month-old infants (Gergely, Bekkering, & Király, 2002) and enculturated chimpanzees (Buttelmann, Carpenter, Call, & Tomasello, 2007) copy the specific method used. When there is an evident reason for the seemingly odd action (e.g. arms are wrapped up or hands occupied), both species copy 'rationally', achieving the goal through the more regular means (i.e. manually, in this example). Similarly, (Carr, Kendal, & Flynn, 2015) children are more likely to seek innovative solutions to a task as the efficacy of a demonstration decreases (Carr et al., 2015) and older children are more likely to reject a model's demonstration with a non-appropriate tool in favour of a functional tool (diYanni & Kelemen, 2008); diYanni & Kelemen (2008) suggest that this was due to older children's increased knowledge of artefact design.

The difficulty of the task and the cognitive savvy or experience of the observer can both influence the type of social learning mechanism employed. For example, in simpler tasks (e.g. breaking open a tube, or raking in a reward), chimpanzees tend to perform equally well on witnessing information about actions or about end-results only, whereas children require information about actions to perform best (Call et al., 2005; Nagell et al., 1993). In more difficult tasks (e.g. tool construction), chimpanzees may

require action information to perform better than controls deprived of information (Price, Lambeth, Schapiro, & Whiten, 2009).

Prior experience or familiarity with a given task also influences when or how much information to copy. For example, if social information conflicts with personally-gained information, preschool-aged children may favour personal information (Clément, Koenig, & Harris, 2004; Ma & Ganea, 2010). When five-year-old children have previously successfully solved a task on their own, they are motivated to copy subsequent socially demonstrated solutions but are less likely to copy actions that appear causally irrelevant (Wood et al., 2013). Similarly, if children have a difficult prior experience achieving a goal, they are more likely to copy an adult demonstration precisely than those with an easier prior experience (Williamson, Meltzoff, & Markman, 2008).

Primates' attention to social information can also be affected by prior experience, with young callitrichid monkeys seeking social information about novel over familiar food items (Kendal et al., 2005; Rapaport, 1999). Interestingly, in foraging tasks, previous knowledge of one method can also lead to so-called 'conservatism', wherein a given individual sticks to an individually learned method, even when an alternative, more efficient or better rewarded, method is presented. This has been suggested to be a limiting factor in cultural learning in chimpanzees, with individuals unable or unwilling to adopt new methods, preferring to stick to their asocially learned techniques (Hopper, Schapiro, Lambeth, & Brosnan, 2011; Hrubesch, Preuschof, & Van Schaik, 2008). To date, experimental evidence that specifically explores how individual knowledge of a task influences copying fidelity in primates is lacking and could help inform differences in social learning mechanisms employed by children and chimpanzees, seen in earlier tests.

156

157 2.2. Majority-biased transmission and conformity

158 Comparative research into conformity must cope with somewhat differing definitions
159 deriving from different disciplinary origins (Claidière & Whiten, 2012). Comprehensive
160 reviews of the field can be found elsewhere (Claidière & Whiten, 2012; Haun et al.,
161 2013); for the purpose of this review we restrict ‘conformity’ to when a given individual
162 forgoes an existing behaviour in favour of the behaviour of a majority of others. The
163 broader phenomenon of majority-biased transmission occurs when individuals show an
164 exaggerated tendency to adopt behaviour they witness most frequently, or is
165 demonstrated by most other individuals (a distinction is sometimes made between these
166 two types of observations, (Haun, Rekers, & Tomasello, 2012), but for simplicity we treat
167 them together here).

168 Perry (2009) traced the development of food extraction techniques in capuchin
169 monkeys over seven years and found that after a period of exploring equally efficient
170 techniques, monkeys typically settled on the technique they had witnessed most often in
171 infancy. Experimental evidence for primates comes mainly from studies employing a
172 two-action methodology, wherein one of two equally beneficial solutions is seeded into a
173 social group via a trained demonstrator. The group members' subsequent adoption of the
174 technique is then traced. In some instances, group members will discover the alternative,
175 equally rewarding technique, but then revert back to the technique exhibited by the
176 majority of the group. Such behaviour has been seen in children (Flynn, 2008; Flynn &
177 Whiten, 2008), a range of captive primates (Bonnie, Horner, Whiten, & de Waal, 2007;
178 Dindo, De Waal, & Whiten, 2009; Price & Caldwell, 2007; Stoinski, Drayton, & Price,

2011) and in wild vervet monkeys (van de Waal, Borgeaud, & Whiten, 2013). Similar results have been reported using an exchange paradigm in chimpanzees (i.e. chimpanzees exchanged inedible tokens for varying food rewards, Hopper et al., 2011).

Without experimental manipulation it is difficult to determine if these animals are eschewing minority information or are instead conservatively relying on the technique they learned first, or that has been most frequently reinforced (Hrubesch et al., 2008; Marshall-Pescini & Whiten, 2008; van Leeuwen & Haun, 2013). Haun et al. (2012) directly tested preferences for majority over minority information and found that both children and chimpanzees, but not orangutans, were more likely to copy an action performed by three individuals than by one, controlling for the number of times the action was seen. With reference to conformity specifically, defined as individuals rejecting personal experience in favour of a majority bias, children as young as 4 years have been found to reject correct personal information in favour of incorrect information offered by a majority of adults (Corriveau & Harris, 2010; Ma & Ganea, 2010) and peers (Haun & Tomasello, 2011), albeit only under certain conditions.

Differences between normative and informational conformity further complicate interpretations. Normative conformity is socially motivated, whereas informational conformity functions to gain more information about reality (Deutsch & Gerard, 1955). In the above instances with children, conforming to incorrect information was either only in the presence of those who modeled the behaviour, or was restricted to perceptual tasks (Corriveau & Harris, 2010). When children were alone, or presented with a practical problem, correct personal information was relied upon (Haun & Tomasello, 2011).

Recent use of experimental procedures in field settings has provided compelling evidence of animal conformity (e.g. great tits, Aplin et al. 2015; vervet monkeys, van de Waal et al. 2013, although see van Leuwen, Kendal, Tennie, & Haun, 2015, for a critique of this interpretation and Aplin et al. 2015 for an instructive response). More probing experimental evidence is needed. Tests with primates where comparisons are made between individuals operating a task both in the presence of and away from their groupmates might help shed light on this, as has been done recently with children (McGuigan & Robertson, 2015).

3. Whom to copy

This area has perhaps received the most attention in the literature, with a wealth of information suggesting that children prefer and selectively attend to and copy certain types of models, as outlined below. To date, we have less information pertaining to primates, but emerging data from both wild and captive populations of primates suggest that some similar preferences may be in place. We focus on the model attributes of perceived skill/age/proficiency, social status, and familiarity or social bonding.

3.1. Model skill, age, and status

From a young age, infants are able to discriminate between competent and incompetent models (Zmyj, Buttelman, Carpenter, & Daum, 2010) and children will preferentially copy proficient models in a variety of contexts (e.g. Birch, Vauthier, & Bloom, 2008; Brooker & Poulin-Dubois, 2013; Koenig & Harris, 2005; Metzoff & Moore, 1992, although see Wood, Kendal & Flynn, 2015) . Importantly, children's theory

of mind ability has recently been linked to their ability to copy accurate over inaccurate speakers (Brosseau-Liard, Penney, & Poulin-Dubois, 2015).

Age is an indication of experience with the environment, so copying older individuals is also a potentially beneficial strategy. From infancy, children are more likely to copy actions presented by adults over children (Rakoczy, Hamann, Warneken, & Tomasello, 2010; Seehagen & Herbert, 2011). Children are also more likely to copy visibly, causally irrelevant actions if presented by an adult as opposed to a similarly-aged peer (Flynn, 2008; McGuigan, 2012; Wood, Kendal, & Flynn, 2012). These copying strategies also seem to depend on context, with children more likely to copy adults than peers when information is novel (Zmyj, Daum, Prinz, Nielsen, & Aschersleben, 2012) or related to motor skills (Kuczynski, Zahn-Waxler, & Radke-Yarrow, 1987) and to copy peers when information is familiar or related to play (Ryalls, Gul, & Ryalls, 2000).

Copying high status individuals is another potentially adaptive strategy, since those individuals might be more successful and thus better equipped to deal with the social or physical environment. When a novel puzzle is presented to children to solve in a group, dominant and popular children were attended to more often than their less dominant and popular peers (Flynn & Whiten, 2012). Children also copy more irrelevant actions made by a higher status adult (e.g. head teacher) as compared to a lower status adult (McGuigan, 2013) .

In free-ranging primates, chimpanzees pay more attention to older individuals than younger individuals (Biro et al., 2003; Lonsdorf, 2006) and capuchin monkeys attend more to proficient individuals (Ottoni, de Resende, & Izar, 2005). Van de Waal, Renevey, Favre, and Bshary (2010) found that vervet monkeys selectively attended to

female models over male models. The authors suggest that females, as the philopatric sex, might be better sources of information than immigrant males.

Experimental evidence in captivity is limited, though there is some evidence to suggest a preference in chimpanzees for older, dominant, and previously successful individuals as models (Horner, Proctor, Bonnie, Whiten, & de Waal, 2010) and alternative methods discovered by low ranking individuals do not spread through groups (Bonnie et al., 2007). Similar trends have been found in capuchins on novel foraging tasks (Dindo, Thierry, & Whiten, 2008); however, in a different study, infant capuchins were not more likely to choose food preferred by older or more experienced individuals (Fragaszy, Visalberghi, & Galloway, 1997). Given the nature of many captive tests, dominant individuals are frequently used as models to limit opportunities for individual learning prior to viewing model demonstrations. In the absence of relevant controls, it is therefore difficult to distinguish whether individuals are relying on the first learned method or preferentially attending to these individuals, although recent statistical modeling suggests that chimpanzees operating a foraging device are biased to copy knowledgeable individuals (Kendal et al., 2015).

3.2. Familiarity and social bonds

Copying individuals who are similar to yourself can serve two purposes: first it can be instrumentally fruitful because those individuals are more likely to live in a similar environment and have relevant experience, and second it can help you learn the social customs necessary to integrate and live successfully in a social group (Over & Carpenter, 2014). Infants and children preferentially copy familiar over less familiar models

(Buttelmann, Zmyj, Daum, & Carpenter, 2013; Learmonth, Lamberth, & Rovee-Collier, 2005; Shutts, Kinzler, McKee, & Spelke, 2009).

Children also tend to copy more actions demonstrated by engaging, interactive models, over televised or aloof models (McGuigan et al., 2007; Nielsen, Simcock, & Jenkins, 2008). This ‘video deficit’ perhaps exists partly because children might have difficulty understanding the correspondence between televised information and reality (Anderson & Pempek, 2005; Troseth & DeLoache, 1998), but also because social cues are reduced. When children have the opportunity to engage with a televised model prior to a demonstration through a live video feed, the video deficit effect is reduced (Nielsen et al., 2008). Children seem predisposed towards ostensive signals, such as eye contact, and pointing, that indicate that the model is trying to communicate relevant information (Csibra & Gergely, 2009). For example children copy a model more when s/he stoops to the child’s level, leans in, makes eye contact and talks engagingly (Brugger, Lariviere, Mumme, & Bushnell, 2007).

Learning techniques from others is facilitated by close proximity and some degree of social tolerance (Coussi-Korbel & Fragazy, 1995; van Schaik, 2003) and thus might be expected to occur more frequently between close affiliates, typically defined as those who spend the most time in close spatial proximity (Van Schaik & Aureli, 2000). In fact, the way in which behaviours spread throughout wild populations of primates is often used to infer whether social learning is occurring. For example, if a novel behaviour spreads from an individual to his or her close associates first, it is deemed more likely to be learned via observation than asocial learning, as has been described in several primate species (Hobaiter, Poisot, Zuberbühler, Hoppitt, & Gruber, 2014; Huffman & Quiatt,

1986; Itani & Nishimura, 1973; Kawai, 1965; Kendal et al., 2010; Leca, Gunst, & Huffman, 2007; Nishida, 1987). Similarly, the amount of time individuals spend in close proximity with others is related to the number of cultural variants they display (van Schaik et al. 2003), the similarity of the foraging techniques they use (Agostini & Visalberghi, 2005; Panger et al., 2002) or the actions they copy (Claidière, Messer, Hoppitt, & Whiten, 2013; Russon & Galdikas, 1995). New techniques, including social network analysis can help determine how social bonds influence the spread of information in both wild and captive populations (e.g. chimpanzees, Hobaiter et al., 2014; Kendal et al., 2015).

Controlled experiments comparable to those in the developmental literature are difficult to implement. For logistical reasons, models are typically selected from the social group without the possibility of comparisons between familiar and unfamiliar individuals, so such experiments are typically limited to species whose group composition can be more easily manipulated (see Swaney, Kendal, Capon, Brown, & Laland, 2001 for examples with guppies). Video demonstrations offer one avenue to explore these potential biases in primates. For example, chimpanzees copied demonstrated behaviour in video displays of an unfamiliar model on both a tool modification task (Price et al., 2009) and a two-action task (Hopper, Lambeth, & Schapiro, 2012). Colobus monkeys (*Colobus guereza kikuyuensis*) also copied the modeled solution of a two-action task by watching video footage of a different species (*Colobus polykomos*, Price & Caldwell, 2007) although in the latter instance the monkeys had had previous visual contact with those animals. Mixed species groups are becoming

increasingly common in captivity and offer an excellent opportunity to test for preferences to copy genetically similar individuals in a shared environment.

Considering the latter point, some comparative studies of social learning have been criticized for using human demonstrators with both chimpanzees and children, potentially putting chimpanzees at a disadvantage (De Waal, Boesch, Horner, & Whiten, 2008; Price & Whiten, 2012). Conspecific models are now used more frequently; however, another, equally relevant point to consider is that in the majority of comparative studies, children are presented with unfamiliar models, whereas primates are typically presented with familiar group-mates as models. Given the known role of model type in children's social learning, and the likely similar role in primates, this is an important consideration.

4. Why copy?

Copying can help a naive observer learn new skills or deal with the physical environment, but it can also serve a social function (Uzgiris, 1981). As discussed, cultural transmission biases can vary based on the characteristics of the model, the observer, and the context the learning occurs in. This then makes determining the motivation underlying copying essential to understanding differences between species.

Copying precise actions, or imitation, may help reinforce similarity between the imitator and the imitated, increasing social cohesion (Meltzoff, 2005; Over & Carpenter, 2012). Infants tend to prefer individuals who mimic them over those who do not (Meltzoff & Beeghly, 1990) and will copy more actions of an experimenter who imitates them over one who does not (Eckerman & Stein, 1990). Children given a goal to affiliate

with another will copy actions more precisely than those not given such a goal (Carpenter & Call, 2009) and children also endorse the preferences of those who have previously mimicked them, over those who have not (Over, Carpenter, Spears, & Gattis, 2013).

One of the most fascinating forms of social learning occurs when causally irrelevant and even inefficient actions are copied: ‘overimitation’. Investigation of this phenomenon in children has burgeoned in recent years, with some evidence to suggest that the behaviour increases with age, even into adulthood (McGuigan, Makinson, & Whiten, 2011), and is present in very different human cultures (Nielsen, Mushin, Tomaselli, & Whiten, 2014; Nielsen & Tomaselli, 2010). Many hypotheses have been put forward to explain overimitation. For example, children might automatically encode actions as causally relevant, thus permitting them to negotiate causally opaque processes or tasks before they have the cognitive savvy to work them out for themselves (Lyons et al., 2007). Alternatively, children may realize that the actions are irrelevant, but copy them because they interpret them as part of a larger cultural convention (Kenward, 2012; Keupp, Behne, Zachow, Kasbohm, & Rakoczy, 2015).

One prominent view stresses the importance of social motivation, specifically that overimitation might stem from a motivation to be seen to be like others and in consequence be liked by them (Over & Carpenter, 2012). The apparent paradox that exists between selective imitation and overimitation in children is thus explained by the underlying goal the child has when performing the task (Over & Carpenter, 2013). For example, if the information sought is purely functional, children may be more likely to omit irrelevant actions (Carpenter, 2006), and there is some evidence to suggest that children are more likely to copy irrelevant actions in the presence of the model who

originally demonstrated them (Nielsen & Blank, 2011). Disentangling social from functional copying contexts is a difficult endeavor, however, particularly given that copying is by its very nature a social activity, and children may be motivated by both functional and social dynamics on a given task (Over & Carpenter, 2012).

Carpenter and Call (2009) argue that it is this social motivation, or the drive to be like others, that distinguishes humans from other animals, yet attempting to study this interaction from a comparative perspective is inherently difficult. Experimentally, there is evidence to suggest that apes are aware when others are imitating them (Haun & Call, 2008; Nielsen, Collier-Baker, Davis, & Suddendorf, 2005) and capuchin monkeys show more affiliative behaviours toward humans who have previously imitated them (Paukner, Suomi, Visalberghi, & Ferrari, 2009). Deciphering the goals or motivations underlying copying is more difficult. In free-ranging primates, some observed cultural traditions are social by their nature, including social customs, games, and stone-handling behaviours (Leca et al., 2007; Panger et al., 2002; Perry et al., 2003; van Leeuwen, Cronin, & Haun, 2014; van Schaik et al., 2003; Whiten et al., 2001). Given their social nature or lack of immediate adaptive value, we can infer that motivations to copy these actions are social, rather than instrumental, but in the absence of controlled experiments, it is difficult to draw firm conclusions.

Experimental studies specifically seeking to isolate underlying motivations are equally difficult. As previously discussed, some comparative studies suggest that chimpanzees only copy irrelevant actions when their irrelevance is masked (by the object being manipulated being opaque, for example; Horner and Whiten, 2005); in situations where the function of an action seems readily determined, only children, and not apes,

persist in copying irrelevant actions (Call et al., 2005; Nagell et al., 1993). However, there is some evidence that chimpanzees might overimitate. For example, after socially learning a particular method of constructing a tool, only those chimpanzees who had seen another chimpanzee construct the tool persisted in using this method after a delay of two-weeks when it was no longer necessary (Price et al., 2009). The results cannot be explained by conservatism, since chimpanzees that had learned via emulation or asocial learning tended only to build tools when necessary.

Comparative research is further limited by tasks that focus specifically on learning about the physical environment, typically achieving a food reward (Watson & Caldwell, 2009) although see (Bonnie & de Waal, 2007). Gaining a preferred food in your home environment (be that in captivity or in the wild) might be very different than gaining a sticker or small toy (as is most frequently used with children) in a school or in a laboratory. This difference alone may mean the child's testing environment is more (or less) inherently social.

5. Conclusions and Future Directions

From an early age humans can moderate what to learn, whom to learn from, and when to learn, in apparently adaptive ways. As understanding of knowledge states, memory, physical cognition, language skills, and other key abilities develop throughout ontogeny, these strategies progress, allowing individuals to optimize the combined knowledge of their own individual problem-solving with that of the information that can be learned from others. While many animals have been shown to exhibit cultural transmission biases, to date, the adaptability and flexibility of these remain to be clarified, along with

407 the potential similarities and differences of these biases to our own. Are other primates
408 able to adapt their copying behaviour under as flexible a set of contexts as humans? Do
409 primates copy for purely instrumental purposes, or also to help affiliate with group
410 members? Do social relationships or understanding of a problem determine how much
411 information is copied? Do multiple biases interact or are some of higher priority and do
412 they over-ride others? Most fundamentally, what determines the relative roles of
413 individual versus social learning?

414 We anticipate that further, rigorous comparative studies will be conducted to
415 answer such questions, as has been achieved previously with social learning mechanisms.
416 We have highlighted several areas warranting further exploration, but comparative
417 psychologists face many challenges when designing experiments to be as similar as
418 possible between species. Meeting these challenges will require designing studies that do
419 not rely heavily on language and can be applied in an ecologically valid fashion across
420 species and contexts.

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423

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