Evolution and Human Behavior 36 (2015) 65–72

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.ehbonline.org

Original Article

Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity

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ARTICLE INFO

Article history:
Initial receipt 21 March 2014
Final revision received 1 September 2014

Keywords:
Transmission biases
Social learning strategies
Chimpanzees
Culture
Cultural diversity

ABSTRACT

Evolutionary theory predicts that natural selection will fashion cognitive biases to guide when, and from whom, individuals acquire social information, but the precise nature of these biases, especially in ecologically valid group contexts, remains unknown. We exposed four captive groups of chimpanzees (*Pan troglodytes*) to a novel extractive foraging device and, by fitting statistical models, isolated four simultaneously operating transmission biases. These include biases to copy (i) higher-ranking and (ii) expert individuals, and to copy others when (iii) uncertain or (iv) of low rank. High-ranking individuals were relatively un-strategic in their use of acquired knowledge, which, combined with the bias for others to observe them, may explain reports that high innovation rates (in juveniles and subordinates) do not generate a correspondingly high frequency of traditions in chimpanzees. Given the typically low rank of immigrants in chimpanzees, a 'copying dominants' bias may contribute to the observed maintenance of distinct cultural repertoires in neighboring communities despite sharing similar ecology and knowledgeable migrants. Thus, a copying dominants strategy may, as often proposed for conformist transmission, and perhaps in concert with it, restrict the accumulation of traditions within chimpanzee communities whilst maintaining cultural diversity.

1. Introduction

Many animals acquire information from their social environment, for example pertaining to foraging, mate choice, and predator avoidance, and such social learning often underlies behavioral traditions in a diverse array of taxa (see Kendal, Galef, & van Schaik, 2010 and references therein; Whiten et al., 1999). The strong link between theoretical and empirical work, and the parallels between the social decision-making of human and non-human animals, has fuelled an explosion of interest in the psychological rules that underpin social learning. As highlighted by Rendell et al.'s (2011) review, interest in the decision-making involved in social learning has increased dramatically in recent years, yet empirical evidence lags behind theory. Social learning is not inherently adaptive, due to the risk of acquiring misinformation, but natural selection has fashioned social learning heuristics that combat this problem. Transmission biases (Boyd & Richerson, 1985; Henrich & McElreath, 2003; also termed 'social learning strategies' by Laland, 2004) guide what, when, and from whom, individuals acquire social information (Kendal, Coolen, & Laland, 2009; Kendal, Coolen, van Bergen, & Laland, 2005; Rendell et al., 2011). For example, model-based biases influence who is copied and relate to traits such as prestige (e.g. Henrich & Gil-White, 2001), age (e.g. Dugatkin & Godin, 1993) and rank (e.g. Horner, Proctor, Bonnie, Whiten, & de Waal, 2010). While it is widely believed that such biases are crucial for understanding both how human cultures evolve and the cultural patterns of our closest primate relatives (Biro, Sousa, & Matsuzawa, 2006; Haun, Rekers, & Tomasello, 2012; Luncz, Mundry, & Boesch, 2012; Nishida, Matsusaka, & McGrew, 2009; Reader & Laland, 2001; Rendell et al., 2011), researchers currently lack clear experimental evidence for such biases (but see Chudek, Heller, Birch, & Henrich, 2012; Horner et al., 2010; van Leeuwen, Cronin, Schütte, Call, & Haun, 2013 for the beginnings of this evidence base). Furthermore, researchers do not know whether transmission

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http://dx.doi.org/10.1016/j.evolhumbehav.2014.09.002
1090-5138/

biases operate separately or together, or, in the latter case, how they are combined.

Our study explored these questions by exposing four groups of captive chimpanzees (two seeded with one trained mid-ranking female model each, and two without such a model) and twelve asocial learning control animals to a novel extractive foraging task in which a small door could be pushed right or left to retrieve a food reward. The study of how social learning operates in chimpanzees is of particular significance. Since Whiten et al.'s (1999) influential paper, reporting multiple traditions among wild chimpanzees, much effort has been expended in understanding chimpanzee culture. Investigation of evolved transmission biases in our closest living relative has the potential to shed new light on the ancestral features of humanity's 'adaptations for culture' (Fessler, 2011) and the selection pressures that shaped them. Such data establish whether certain transmission biases are unique to humans and, potentially, whether these explain humanity's uniquely strong reliance on culture, in particular, cumulative culture (Dean, Kendal, Schapiro, Thierry, & Laland, 2012).

The spread of foraging information between chimpanzees was measured by recording—for every successful task manipulation—who performed it, what method was used, and who observed it. We aimed to build on the recent strides made in exploring social learning processes and transmission biases in relatively naturalistic contexts (Kendal, Galef, & van Schaik, 2010). Thus, in place of standard inferential tests of hypotheses, we employed pioneering new analytical methods (Franz & Nunn, 2009; Hoppitt & Laland, 2011; Kendal, Kendal, Hoppitt, & Laland, 2009; Kendal et al., 2010) and model-fitting approaches (McElreath et al., 2008) to examine which biases influence chimpanzee cultural learning, focusing on 'option' choice (push door left or push door right to retrieve a reward).

We then investigated the implications of the findings for understanding cultural transmission and cultural diversity in wild chimpanzees, and potentially humans. For example, we attempt to shed light on reports that high innovation rates (in juveniles and subordinates, Biro et al., 2006; Reader & Laland, 2001) do not generate a correspondingly high frequency of traditions in chimpanzees (Brosnan & Hopper, 2014; Nishida et al., 2009). Similarly, we discuss how transmission biases might contribute to the observed maintenance of distinct cultural repertoires in neighboring chimpanzee communities despite them sharing similar ecology and knowledgeable migrants (Biro et al., 2006; Luncz & Boesch, 2014; Luncz et al., 2012). Thus far, conformist transmission has been proposed to restrict the accumulation of traditions in non-human (Haun et al., 2012; Luncz et al., 2012; van de Waal, Borgeaud, & Whiten, 2013) and human (Henrich & Boyd, 1998; Pagel & Mace, 2004) primate communities, whilst maintaining cultural diversity. It remains to be seen whether such propositions are valid and whether alternative transmission biases are involved, either singularly or in concert with others. There is, however, reason to expect that transmission biases may partially explain the lack of cross-cultural homogenization, and incredible cultural diversity, observed in modern and prehistoric humans (Pagel & Mace, 2004; Pétrequin, 1993).

2. Methods

2.1. Subjects

Fifty-four chimpanzees, housed in social groups in large enriched enclosures at the Michale E. Keeling Center for Comparative Medicine and Research, UT MD Anderson Cancer Center, USA (KCCMR), were the subjects. Chimpanzees were never food or water deprived, and the research was approved by the Institutional Animal Care and Use Committee (IACUC 07-92-03887) and ethical committees of Durham and St Andrews Universities. KCCMR is accredited by the Association for the Assessment and Accreditation of Laboratory Animal Care-International (AAALAC-I), and the research conformed to guidelines of ASAB/ABS. Four chimpanzee groups were used; two (T1, T2) seeded with trained models and two without (N1, N2). T1 comprised 13 chimpanzees (7 female), average age 25.5 years (range: 7–44); T2 comprised 10 chimpanzees (8 female), average age 19.5 years (range: 9–26); N1 comprised 10 animals (6 female), average age 18.1 years (range: 9–35); N2 comprised 9 chimpanzees (4 female), average age 22.3 years (range: 9–42). The 12 asocial adult controls (six female) were of average age of 27.7 years (range: 15–44).

2.2. Apparatus

A bidirectional extractive foraging task, the 'Slide-box' (Hopper, Holmes, Williams, & Brosnan, 2013; Hopper, Lambeth, Schapiro, & Whiten, 2008), which consisted of a cube (32 cm^3) with a food chute (4 cm diameter) that opened in the center of the front panel was used. A door (8 cm^2) covered the aperture of the chute but could be pushed left or right with equal ease to release a grape from the chute (see Fig. S1, available on the journal's website at www.ehbonline.org). Based on observations of wild chimpanzees (Biro et al., 2003), and our previous research with captive chimpanzees (e.g. Hopper et al., 2007; Hoppitt & Laland, 2011), indicating the relative utility of different classes of individuals for both training and model/demonstrator purposes, a mid-ranking adult female from each T group (T1: CO, 22 years, T2: MU, 26 years) was chosen as the 'trained model.' Observations of wild chimpanzees suggest that it is the relative rank or age of the model to an observer that is important, not necessarily their absolute rank (Biro et al., 2003). Therefore we selected individuals whom were dominant enough to be observed by their peers, but not so dominant that other individuals avoided them (Drea & Wallen, 1999; Hopper et al., 2013). Following this, the specific mid-ranking female models were selected for two reasons. First we wanted a model that could be observed easily by their group mates such that close access to the apparatus was possible while the demonstrator was in action. Secondly, these two females were selected because they were both comfortable being briefly separated from their group for training sessions and were known to be fast learners. Although previous captive studies of social learning with chimpanzees have used dominant females (e.g., Hopper et al., 2007), other studies of social learning in primates have demonstrated that younger, less dominant individuals can also represent reliable models (e.g., Hopper et al., 2013). Each model was trained, individually, over two 15-minute sessions, to push the door (CO: right, MU: left) using positive reinforcement. By the end of the second session both models were considered proficient, having pushed the door in the designated direction 30 times in succession during a single training session.

2.3. Procedure

Groups were presented with the Slide-box on the outside of their 21.3 m diameter enclosures. For T groups, initially only the model chimpanzee could access the apparatus (by reaching through the bars of the enclosure) to enable all group members to observe the Slide-box in use by the model. If non-models attempted to use the task, the experimenter pulled it out of reach. During this observations-phase (two 20-minute sessions over consecutive days), and the subsequent open-diffusion phase, once a chimpanzee retrieved a grape the task was turned through 180° to re-set the door to the central position reducing emission of inadvertent experimenter cues (e.g., stimulus or local enhancement). Once re-set, the Slide-box was repositioned and re-baited in full view of any chimpanzees present. The day following the final observation-phase (T groups) or immediately (N groups), the chimpanzees entered the open-diffusion phase where any chimpanzee could operate the Slide-box. No subjects were called by the experimenter; participation in the study was voluntary such that task interactions proceeded in a pattern natural for the group. This phase continued until all group members retrieved a reward 30 times: T1 (9.5 hours) and T2 (7 hours) in April 2007, N1 (10 hours) and N2 (10.5 hours) in January–February 2008. Using video recordings, identities of those