Evolution and Human Behavior 33 (2012) 387–394

Evolution and Human Behavior

Original Article

Context-dependent model-based biases in cultural transmission: children's imitation is affected by model age over model knowledge state

Lara A. Wood[a,*], Rachel L. Kendal[b], Emma G. Flynn[a]

[a]Department of Psychology, Centre for Coevolution of Biology & Culture, Durham University, Durham, DH1 3LE, UK
[b]Department of Anthropology, Centre for Coevolution of Biology & Culture, Durham University, Durham, DH1 3LE, UK

Initial receipt 18 March 2011; final revision received 17 November 2011

Abstract

Many animals, including humans, acquire information through social learning. Although such information can be acquired easily, its potential unreliability means it should not be used indiscriminately. Cultural 'transmission biases' may allow individuals to weigh their reliance on social information according to a model's characteristics. In one of the first studies to juxtapose two model-based biases, we investigated whether the age and knowledge state of a model affected the fidelity of children's copying. Eighty-five 5-year-old children watched a video demonstration of either an adult or child, who had professed either knowledge or ignorance regarding a tool-use task, extracting a reward from that task using both causally relevant and irrelevant actions. Relevant actions were imitated faithfully by children regardless of the model's characteristics, but children who observed an adult reproduced more irrelevant actions than those who observed a child. The professed knowledge state of the model showed a weaker effect on imitation of irrelevant actions. Overall, children favored the use of a 'copy adults' bias over a 'copy task-knowledgeable individual' bias, even though the latter could potentially have provided more reliable information. The use of such social learning strategies has significant implications for understanding the phenomenon of imitation of irrelevant actions (overimitation), instances of maladaptive information cascades, and cumulative culture.

Keywords: Imitation; Transmission biases; Social learning strategies; Model characteristics; Knowledge state

1. Introduction

The adaptive value of social learning is now evident in a vast range of animals, from humans to insects, increasing our understanding of cultural evolution and social intelligence (Boyd & Richerson, 1985; Tennie, Call, & Tomasello, 2009; Whiten & van Schaik, 2007). When acquiring information, individuals face evolutionary trade-offs between the acquisition of costly but accurate personal information and the use of cheap but potentially less reliable social information (Boyd & Richerson, 1985; Kendal, Coolen, van Bergen, & Laland, 2005). Accordingly, the use of social information should be determined by an evaluation of the content of the information presented and the characteristics of the information provider, the model (e.g., Henrich & Gil-White, 2000; Rendell et al., 2011; van Bergen, Coolen, & Laland, 2004). Nevertheless, the transmission of information from one individual to another has resulted in the accumulation of errors or cascades of misinformation (Rieucau & Giraldeau, 2009; Tanaka, Kendal, & Laland, 2009). For example, humans copy nonfunctional attributes (Mesoudi & O'Brien, 2008), and maladaptive behaviors pass between individuals within groups (McGuigan & Graham, 2009; Whiten & Flynn, 2010).

Furthermore, humans copy actions that, at face value, appear to be causally irrelevant to their goal (Horner & Whiten, 2005). The propensity to copy these irrelevant actions appears in different cultures (Nielsen & Tomaselli, 2010), increases with age (McGuigan, Whiten, Flynn, & Horner, 2007; Nielsen, 2006) into adulthood (McGuigan, Makinson, & Whiten, 2011), and persists despite interventions such as reinforcement for the identification of irrelevant actions and direct instructions to only copy relevant actions (Lyons, Young, & Keil, 2007; Lyons, Damrosch, Lin, Macris, & Keil, 2011). Such pervasiveness has led some to view copying irrelevant actions as "an evolutionary adaption that is fundamental to the development and transmission of

* Corresponding author. Psychology Department, Durham University, Science Laboratories, Durham, DH1 3LE, UK. Tel.: +44 191 334 3240.
E-mail address: l.a.n.wood@dur.ac.uk (L.A. Wood).

1090-5138/$ – see front matter © 2012 Elsevier Inc. All rights reserved.
doi:10.1016/j.evolhumbehav.2011.11.010

human culture" (Nielsen & Tomaselli, 2010, p. 729). For example, imitating apparently causally irrelevant elements of tool use demonstrations may help children acquire means actions before they fully understand their causal role (Hernik & Csibra, 2009). If one does not know whether an action is causally necessary, it may be adaptive to copy this action.

Copying causally irrelevant actions could only be adaptive if individuals develop flexible strategies that dictate the circumstances under which they copy others. Theoretical models have explicitly considered heuristics that may be adopted in social learning, which have been termed 'social learning strategies' (Laland, 2004) and 'cultural transmission biases' (Boyd & Richerson, 1985; Rendell et al., 2011). According to Boyd and Richerson (1985), individuals may employ an *indirect* bias towards learning from a model with specific preferential characteristics. These indirect biases, or *context-dependent* (Henrich & McElreath, 2003) model-based biases, include characteristics such as the model's age. Using such model-based biases allows populations to approach adaptive optima much faster than they otherwise would under individual learning or 'guided variation' (Boyd & Richerson, 1985). For example, Mesoudi and O'Brien (2008) found, by simulating the cultural transmission of prehistoric projectile-points, that the population-level pattern observed in Nevada's archaeological record was consistent with a bias of *wholesale* copying of a successful hunter's projectile-point design, including nonfunctional but selectively neutral aspects (such as color), rather than copying particular projectile-point attributes.

In an argument analogous to that of Laland (2004) regarding the relative abundance of cognitively challenging versus simpler social learning strategies in the animal kingdom, we argue that, within a species, there may be differences in the propensity to use certain model-based biases. Specifically, children may find a 'copy adult over child' strategy relatively easy to implement compared to a 'copy task-knowledgeable individual' strategy (Henrich & Broesch, 2011) for a number of reasons. First, an understanding of age develops earlier than an understanding of knowledge (Edwards, 1984; Wellman, Cross, & Watson, 2001), and thus, related biases may also develop earlier. Second, age may be a more salient characteristic and thus involve less cognitive processing. Third, children may understand that self-declared knowledge states may be less reliable than age. In the current study, 5-year-old children received demonstrations of observably relevant and irrelevant actions in relation to the goal of extracting a reward from an artificial fruit, and we investigated whether the observing child's subsequent behavior was influenced by the model's age and/or knowledge state.

Kirkpatrick and Dugatkin (1994) found the strategy of 'copy older individuals' to be a prominent heuristic. There is evidence that older models elicit more social learning than younger models in many species (e.g., seals, Sanvito, Galimberti, & Miller, 2007; mice, Choleris, Guo, Liu, Mainardi, & Valsecchi, 1997; guppies, Amlacher & Dugatkin 2005, Dugatkin & Godin, 1993; chimpanzees, Biro et al., 2003; Horner, Proctor, Bonnie, Whiten, & de Waal, 2010). Likewise, human developmental research has considered model age as a determining factor in social learning for some time. Observational studies have shown that younger (1- to 2-year-old) siblings imitated their older (3- to 5-year-old) siblings far more than the other way around regardless of age gap or sex differences (Abramovitch, Corter, & Pepler, 1980; Pepler, Abramovitch, & Corter, 1981). When presented with two models of differing ages (2 years younger, same age, or 2 years older) simultaneously, 8-year-olds imitate the food preference choice of older and same-age peers over younger peers (Brody & Stoneman, 1981). Similarly, when the two models presented were a child and an adult, 3- and 4-year-olds preferentially used information provided by an adult over a child for word learning (Jaswal & Neely, 2006) and simple rule games, interpreting the adult's behavior as normative (Rakoczy, Hamann, Warneken, & Tomasello, 2010)

The effect of a model's age on children's social learning is modulated by the content of the to-be-copied behavior. Two-action, artificial fruits tasks have shown that 14-month-old infants (Hanna & Meltzoff, 1993) and 3-, 4-, and 5-year-old children (Flynn & Whiten, 2008a; Hopper, Lambeth, Schapiro, & Whiten, 2008; Hopper, Flynn, Wood, & Whiten, 2010) imitate relevant actions performed by a peer to the same extent as children in studies with adult models (McGuigan et al., 2007). However, studies looking at the imitation of irrelevant actions show that 2- and 3-year-old children did not copy the irrelevant actions demonstrated by a peer to the same extent as irrelevant actions presented by an adult model (Flynn, 2008; Horner & Whiten, 2005). Subsequently, McGuigan et al. (2011) explicitly investigated the effect of a model's age on the copying of irrelevant actions. Observers of various ages (3- and 5-year-olds and adults) copied significantly more irrelevant actions when they were modeled by an adult as opposed to a 5-year-old child. It remains unclear whether this disposition indicates a bias of 'copy adults' or the more cognitively complex bias of viewing a child model as 'less rational and knowledgeable' than an adult model (Flynn 2008, p. 3549).

The effect of a model's knowledge state on children's social learning strategies is less clear. By 5 years of age, children have a concept of a model's expertise (Azmitia, 1988; Birch, Vauthier, & Bloom, 2008, Birch, Akmal, & Frampton, 2010; Moore, Bryant, & Furrow, 1989), knowledge (Koenig & Harris, 2005; Sabbagh & Baldwin, 2001; Wellman et al., 2001), and intention to teach (Ziv et al., 2008) and infer a model's knowledge state based on his/her age (Taylor, Cartwright, & Bowden, 1991). One might expect observers to rely more heavily on an individual's demonstration when that individual has professed knowledge in the specific task domain (Henrich & Broesch, 2011). Furthermore, although there has been theoretical speculation of the existence of a hierarchy of transmission biases (McElreath et al., 2008), the interaction between biases remains unclear. We are only aware of one study investigating the interaction of copying biases of children of a model's age and competence. In this study, the competence information, exhibited in an unrelated task, outweighed age information such that children (aged 7 to 8 years old), in order of preference, copied a high-competence peer, a high-competence younger model, a low-competence peer, and low-competence younger model (Brody & Stoneman, 1985). To test a task-directed context bias, however, one must manipulate the model's professed knowledge state of the specific task.

The current study explicitly investigated the effect of two model-based biases on children's copying fidelity. We contrasted the model's age (adult versus peer model) with a bias that might require greater assessment, the model's task-directed knowledge state (task-knowledgeable versus task-ignorant model). The completion of a two-action tool-use task (Dawson & Foss, 1965), which included causally relevant and irrelevant components, was demonstrated by one of four models differing with respect to these biases. We predicted the following: (1) An observer who witnessed a model successfully extract a reward from a task would imitate the relevant actions demonstrated using the same means to extract the reward regardless of the model's characteristics. (2) In line with McGuigan et al. (2011), children who witnessed an adult model would exhibit higher levels of imitation of causally irrelevant actions than those who witnessed a child model. (3) Children faced with a task-knowledgeable model would show higher levels of imitation of causally irrelevant actions than those presented with a task-ignorant model. Finally, (4) in line with Brody & Stoneman (1985), there would be a hierarchy of transmission biases, with a task-knowledgeable adult facilitating the highest level of imitation of irrelevant actions and a task-ignorant child producing the lowest levels of imitation of irrelevant actions, with potential differences between the two other models allowing the hierarchy of biases to be examined further.

2. Method

2.1. Participants

Ninety-six 5-year-old children (45 males, M=65 months, S.D.=3.5 months) from schools in County Durham participated. There were no significant differences for sex [χ^2 (8, N=96)=2.29, p =.97] or age ($F_{8,87}$=0.81, p=.60) across the experimental conditions and the no-model control.

2.2. Materials

A two-action task, the transparent version of the 'Glass Ceiling Box' (GCB; see Fig. 1, Flynn, 2008; Horner & Whiten, 2005; McGuigan & Graham, 2009; McGuigan et al., 2007, 2011), was used. The GCB is a transparent box with an opening at the front that can be revealed by sliding or lifting a door. The goal is to retrieve a Velcro-backed sticker reward from a tube located behind the door by inserting a stick tool (a 22-cm rod with Velcro on the end) into the tube. The demonstrated actions directed to the door at the front of the GCB are causally necessary to retrieve the reward. The GCB has a further opening in the roof, covered by a two-bolt defence that can be removed by poking or dragging it from the opening with the stick tool. This hole leads to an empty compartment with a 'glass ceiling' preventing physical access to the reward, so actions directed to the bolts or the upper compartment are observably causally irrelevant to retrieving the reward.

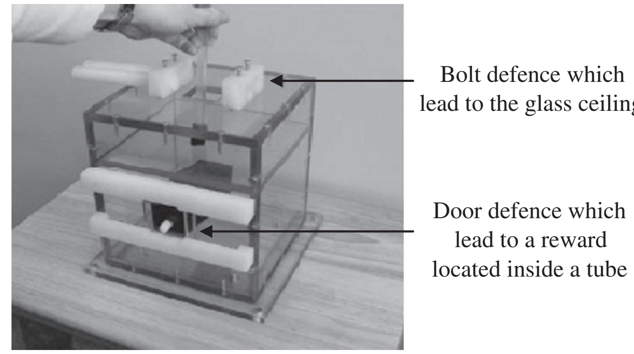

Fig. 1. The GCB showing a model performing one of the irrelevant actions. Photo from Flynn (2008).

2.3. Design

A between-groups design was used, with children randomly allocated to one of four conditions pertaining to the model's characteristics (adult professing knowledge, adult professing ignorance, 5-year-old professing knowledge, and 5-year-old professing ignorance, N=85) or a no-model control (N=11). The control group was relatively small as the GCB has been administered in several experiments (Flynn, 2008; Horner & Whiten, 2005; McGuigan et al., 2007, 2011) with controls showing similar levels of interaction and success as shown in the current experiment. Both models were female and unknown to the participants. After observing a video of the model's initial entrance and profession of knowledge or ignorance about task completion, participants watched one of two video demonstrations of the reward being extracted from the GCB. These clips were identical, regardless of the model's age, and counterbalanced across conditions; the only difference was the depiction of different methods (method 1: poke-bolts-then-slide-door, and method 2: drag-bolts-then-lift-door). As participants had more than one response trial, there was a within-groups variable of trial number (T1 and T2). In the no-model control condition, children were presented with the GCB without witnessing any demonstration.

2.4. Procedure

Children were tested individually in a quiet place in their school. Each child sat at a table in front of a laptop computer with the GCB on an adjoining table. The child was told, “Today I have brought in this toy. This is a video of me showing the toy to Emma. Watch closely and listen carefully.” The child then watched an introduction to one of the video demonstrations in which the model walked into a room, looked at the GCB, and turned to the camera professing either knowledge, “I know this game, I’ve played with it lots of times, I know exactly how to do this” or ignorance, “This is a new game, I have never seen it before, I don’t know how to do it.” Children watched this introduction twice and after each viewing were asked, “Had Emma seen the game before? Did she know how to do it?” By the second viewing, all participants answered correctly.

Then the child was told, “We asked Emma to play with the box and recorded what happened.” Children watched one of two video demonstrations of either the method 1 or method 2 sequences of actions being carried out on the GCB. Unlike McGuigan et al. (2011), these video clips showed only the hands and arms of a petite adult. Thus, any difference in participant’s behavior was due to model characteristics alone and not the physical differences in the demonstration (e.g., motor coordination) or ostensive cues. Twenty adults, blind to the study, watched the video clips and were asked who performed the actions. All labeled the demonstrations as desired, with those seeing a child at the beginning labeling the demonstration as having been performed by a child and those who witnessed an adult at the beginning attributing the actions to an adult.

The sequence of actions was as follows: the tool was used to remove *two* bolts on top of the GCB either by poking or dragging, the tool was inserted into the top hole and the glass ceiling was tapped *three* times (totalling five irrelevant actions), a door at the front of the GCB was moved by either sliding or lifting it, the tool was inserted, and a sticker was removed. Children watched the video demonstration of the sequence of actions twice and were then told, “I would like you to play with the toy. There is no right or wrong way. I just want to see you play.” The child was allowed to interact with the GCB (T1) until (s)he retrieved the reward successfully or 3 min had elapsed. If required, children were given a prompt, “You can play with it as much as you like.” Each child was then shown the demonstration clip a third time and allowed a further attempt (T2).

In the no-model condition, each child was told, “Lots of children have played with this toy today and now I would like you to play with it.” They received 3 min with the GCB and were given the same prompt as the experimental group. All children were rewarded with a sticker for their participation, regardless of their success.

2.5. Analysis

Each participant’s performance was scored on four variables: (a) successful removal of the sticker, (b) method used to open the door, (c) method used to remove the bolts, and (d) how many irrelevant actions were copied. The experimenter coded all children’s behavior, whilst two independent observers, blind to the children’s allocated condition, coded 26% of the sample. All Cronbach’s alpha scores were 0.95 or above, showing an excellent level of rater reliability.

3. Results

All of the dependent variables (a–d above) were compared between conditions (type of model) and within participants (T1 versus T2). Children who observed a demonstration were significantly more successful at retrieving the reward at T1 (success rate=68%, $p<.01$ Fisher’s Exact Test, one tailed) than children in the control condition (18%), with a significant increase in success from T1 to T2 (McNemar $Z_{1,85}=-3.21$, $p<.01$).

3.1. Copying of causally relevant actions

No child in the no-model control condition lifted the door, while 10 slid it. The number of children in the experimental conditions who copied the door-opening method they witnessed was significantly greater than chance, with 71% copying the method at T1 [$\chi^2(1, N=68)=11.53$, $p<.001$] and 72% at T2 [$\chi^2(1, N=74)=13.84$, $p<.001$]. Our first hypothesis was that model characteristics would not affect the copying of causally relevant actions. To test this, we ran a multilevel logistic regression of relevant actions across T1 and T2 with corrected standard errors to account for the dependence between a child’s T1 and T2 behavior. Model age, model knowledge state, and demonstration witnessed (slide or lift) were entered as predictors, and copying of action witnessed was the dependent variable. Age and knowledge state were not significant predictors of the imitation of the relevant actions. The demonstration witnessed (lift or slide) was a significant predictor (see Table 1); children copied the door-slide method more than the door-lift method (97% slide, 46% lift).

3.2. Copying of causally irrelevant actions

Only two children in the control condition produced an action directed to the (causally irrelevant) bolts, both poking them, and no child tapped the tool into the upper

Table 1
The effects of a model’s age and knowledge state and demonstration witnessed on relevant actions copied

Parameters	Estimate (S.E.)
Intercept	1.74 (0.47)*
Model age[a]	0.35 (0.44)[NS]
Model knowledge state[b]	0.46 (0.44)[NS]
Demonstration[c]	1.76 (0.44)*

Logistic regression with standard errors.
[a] Dichotomous variable 0=child 1=adult.
[b] Dichotomous variable 0=ignorant 1=knowledgeable.
[c] Dichotomous variable 0=lift 1=slide.
[NS] $p>.05$; *$p<.001$ (two tailed).

compartment. Baseline behavior comparisons were made between the children in the control group and the experimental children at T1 only, as by T2, the children had experience with the GCB. Children who observed a demonstration performed significantly more irrelevant actions at T1 (M=1.55, S.D.=1.74, t_{34}=−4.72, p<.001.) than control children (M=0.27, S.D.=0.65). In the experimental conditions, the number of children who copied the bolt removal method they witnessed was significantly greater than chance at T1 [χ^2(1, N=48)=16.33, p<.001] and T2 [χ^2(1, N=60)=23.67, p<.001]. As the bolt method witnessed did not affect the total number of irrelevant actions performed at T1 (t_{83}=−1.54, p=.13) or T2 (t_{83}=−1.61, p=.11), the data were collapsed across methods.

It was hypothesized that children would imitate more irrelevant actions when they were presented by an adult as opposed to a child and when presented by a self-reported knowledgeable model as opposed to an ignorant model. To test this, we conducted a Poisson regression analysis of irrelevant actions, using joint modeling with robust standard errors to account for the dependence between a child's T1 and T2 behavior, with model age, model knowledge state, participant age, and participant sex entered as predictors. Participant age and sex were not significant predictors. As expected, model age was a significant predictor (adult model, M=2.26, S.D.=1.81; child model M=1.51, S.D.=1.80; p<.05), but, contrary to expectation, knowledge state was not (see Table 2 and Fig. 2). Thus, whilst children who witnessed an ignorant model produced fewer (M=1.71, S.D.=1.78) irrelevant actions than children who witnessed a knowledgeable model (M=2.05, S.D.=1.89, p=.18), this difference was not significant.

Pairwise comparisons of the four conditions (knowledgeable adult, knowledgeable child, ignorant adult, ignorant child) showed that, whilst children presented with the child-ignorant model performed significantly fewer irrelevant actions compared to children presented with the adult-knowledgeable model (t_{78}=2.66, p<.01), no other differences were significant (see Fig. 2).

Table 2
Effects of a model's age and knowledge state and participant demographics on the number of irrelevant actions performed

Parameters	Estimate (S.E.)
Intercept	0.55 (1.75)[NS]
Trial 2–trial 1	0.35 (0.01)**
Model age[a]	0.41 (0.18)*
Model knowledge state[b]	0.24 (0.18)[NS]
Participant's sex[c]	0.24 (0.18)[NS]
Participant's age	−0.01 (0.03)[NS]

Poisson regression using joint modeling with robust standard errors.
[d]Continuous variable age (months).
[a] Dichotomous variable 0=child 1=adult.
[b] Dichotomous variable 0=ignorant 1=knowledgeable.
[c] Dichotomous variable 0=male 1=female.
[NS] p>.05; *p<.05 (two tailed); **p<.001 (two tailed).

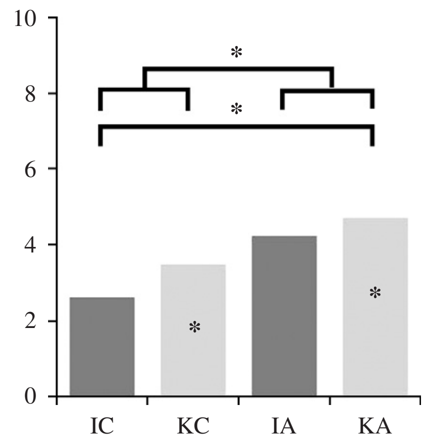

Fig. 2. Mean number of irrelevant actions (out of 10) performed depending on model identity over the two trials. IC: ignorant child, KC: knowledgeable child, IA: ignorant adult, KA: knowledgeable adult. Asterisks indicate a difference in means more than expected between groups (*p<.05). Asterisk within a bar indicates a significant increase in irrelevant actions from T1 to T2 (*p<.05).

3.2.1. Post hoc analysis

Overall, children produced significantly more irrelevant actions at T2 (M=2.21 S.D.=1.89) than T1 (M=1.55, S.D.= 1.74; t_{84}=−3.71, p<.001). This increase was significant for those who observed a knowledgeable adult (paired t test: t_{19}= −2.53, p<.05, Cohen's d=0.56) and a knowledgeable child (t_{22}=−2.08, p<.05, d=0.40) but not for those who observed an ignorant adult (t_{21}=−1.87, p=.08, d=0.28) or an ignorant child (t_{19}=−0.98, p=.34, d=0.28, see Fig. 2), although the power for the latter two tests was low.

4. Discussion

The current study extends research into cultural transmission by explicitly examining the role of, and relation between, two different model-based context-dependent transmission biases: age and professed task-knowledge state. The results confirmed two of our initial predictions: (1) that children would imitate relevant actions regardless of a model's age and knowledge state and (2) that children would imitate more causally irrelevant actions produced by an adult than a peer. Our third and fourth predictions, (3) that children would use a task-directed bias to imitate irrelevant actions produced by a task-knowledgeable, but not task-ignorant, model and (4) that there would be a hierarchy of transmission biases, received comparatively weaker support.

As predicted and in line with previous findings (Flynn, 2008; Flynn & Whiten, 2008a, 2008b; Hopper et al., 2008, 2010), the model's characteristics did not affect the high levels of imitation of the relevant actions. Such faithful imitation of relevant actions appears to be canalization, where the various possibilities for manipulating a task are reduced after a social demonstration (Flynn & Whiten, 2008a; Hopper et al., 2010; Horner, Whiten, Flynn, & de Waal, 2006). This is clearly illustrated by the 46% of children who observed the door of the GCB being lifted and produced a lift action despite the availability of a preferred more salient slide method.

We posit that young children exhibit a social learning strategy (Laland, 2004) of '*faithfully* copy adults' because, whilst children copied relevant actions from both peers and adults, they copied significantly more irrelevant actions when demonstrated by an adult versus a peer. The demonstrations were presented on video, and all children witnessed the same pair of hands manipulating the task, regardless of condition, so the bias we witness for children to copy an adult over a peer was not due to any ostensive cues present in the demonstration. Such a finding is in line with McGuigan et al. (2011), who found similar results with 3- and 5-year-old children. The irrelevant actions in the current study were not neutral (Mesoudi & O'Brien, 2008) but entailed a cost in terms of delaying reward acquisition. This demonstrates the potential power of such transmission biases to establish maladaptive information cascades, sometimes at the population level (Bikhchandani, Hirshleifer, & Welch, 1998; Henrich & McElreath, 2003).

A task-directed bias of 'copy task-knowledgeable individuals' did not override the tendency to copy adults, despite the fact that the children in the current study could correctly identify the model's knowledge state. In contrast, when Brody & Stoneman, (1985) juxtaposed peer age and competence (on an unrelated task), a competence bias outweighed any age bias, such that younger-peer/high-competence models were preferred over same-age peers/low-competence ones. Whether this difference in results is due to the model's ages (adult and child model versus younger and same-age peer model), reputation (knowledge state versus reliability), or medium of competency (self-declared in a video clip versus a description given by an adult experimenter) is unclear but is ripe for further exploration.

Whilst the regression model of irrelevant actions indicated that knowledge state was not a significant predictor, pairwise comparisons (of the four model types) showed that a knowledgeable adult demonstration resulted in more irrelevant actions being produced than an ignorant child demonstration; no other groups differed significantly. Thus, a model's age was weighted over the professed task-knowledge, but task-knowledge was evaluated to some degree, lending some support to the idea that there is a hierarchy of transmission biases as reported by McElreath et al. (2008). Additionally, post hoc analysis revealed that children who witnessed knowledgeable models reproduced significantly more irrelevant actions at their second attempt than children witnessing ignorant models, who showed no change across their attempts. Taken together, these results provide limited support for a knowledge-based strategy.

Our findings provide, to our knowledge, the first evidence in any species (consistent with the analogous prediction of Laland, 2004) that, in decisions pertaining to the cultural transmission of information, easily adopted heuristics, such as age-based biases, may be more readily used than more cognitively challenging biases, such as those involving assessment of another's knowledge state with regard to the task at hand. The question then is whether an age bias is inherently more adaptive than a knowledge state bias or whether it is simply easier to evaluate. Whilst there is an argument that children may understand that self-declared knowledge states may be less reliable than age, we believe it is more likely that the preference for a 'copy adult over child' strategy involves less cognitive processing and is a by-product of its relative ease to implement. An understanding of age develops earlier than an understanding of knowledge (Edwards,1984; Wellman et al., 2001), and thus, related biases may also develop earlier.

This cognitively easier assessment of a model's age may, however, in itself be adaptive because adults, by their increased experience with the world, are generally more proficient and knowledgeable models than children. Children infer a model's knowledge state based on his/her age (Taylor et al., 1991); thus, this correlation may lead to effective social learning strategies. However, when the correlation is contradicted, and there are instances of ignorant adults or knowledgeable children, children still rely on the age bias, resulting in the current study's finding that children are as likely to copy the irrelevant actions of an ignorant adult as a knowledgeable child. This occurred even though every child was able to correctly identify the knowledge state of the model. Thus, it would be informative to conduct future research into children's developing ideas of the interrelation between age and knowledge state.

The relation between these biases also helps us to understand the phenomenon of copying causally irrelevant actions. The children's selective reproduction of causally irrelevant actions suggests that this phenomenon may not be as pervasive as previously thought (Lyons et al., 2007; Nielsen & Tomaselli, 2010) in that the replication of irrelevant actions was modulated in response to a model's characteristics. However, that is not to say that imitation of irrelevant actions can no longer be considered an evolutionary adaptation (Nielsen & Tomaselli, 2010). The copying of causally irrelevant actions may reflect a cognitively complex process within a child, involving assumptions about the 'irrelevance' of particular actions. For example, it would be adaptive for children to evaluate which seemingly causally irrelevant actions may be relevant actions whose causal efficacy they are yet to understand (Hernik & Csibra, 2009) versus those actions which are simply irrelevant. A wise assumption may be that adults are more likely to produce 'irrelevant' actions that actually have an opaque function of social or cultural relevance, whilst irrelevant actions of peer-aged children should be taken at face value. Therefore, an overriding strategy of 'adults should be imitated faithfully, children should be imitated unless their actions seem non-functional' may be extremely adaptive, even though this heuristic may sometimes lead to the copying of irrelevant actions.

High-fidelity copying is a necessary factor underlying the unique capacity of humans for cumulative cultural transmission (Boyd & Richerson, 1985). Faithful imitation is the bedrock of cultural ratcheting (Tennie et al., 2009) as it prevents any loss of knowledge, allowing for potential improvement in subsequent individual development and/or generations. Faithful imitation of causally irrelevant actions, as exhibited in this study, may appear to conflict with our species' capacity for cumulative culture due to its potential to lead to cascades of misinformation. However, the current study has demonstrated that the selective nature of children's social learning, in copying adults over children and potentially assessing the irrelevance of apparently causally irrelevant actions, explains why a more likely result is the advancement of complex, socially learned behaviors.

Acknowledgments

This work was supported by a Durham Doctoral Fellowship to L.A.W. and a Royal Society Dorothy Hodgkin Fellowship to R.L.K. The authors thank Niamh Sykes (the child model); children from schools in County Durham, UK, who participated in the study; Dr. Adetayo Kasim for assistance with Poisson regression with robust standard errors; Andy Long for making the apparatus; Laura Hawkins and Nadia Somers for assistance with interobserver reliability; Dr. Lydia Hopper for helpful comments on an earlier version of the manuscript; and the two anonymous reviewers for their suggested revisions to the manuscript.

References

Abramovitch, R., Corter, C., & Pepler, D. J. (1980). Observations of mixed-sex sibling dyads. *Child Development*, *51*, 1268–1271.

Amlacher, J., & Dugatkin, L. A. (2005). Preference for older over younger models during mate-choice copying in young guppies. *Ethology, Ecology & Evolution*, *17*, 161–169.

Azmitia, M. (1988). Peer interaction and problem solving: when are two heads better than one? *Child Development*, *59*, 87–96.

Bikhchandani, S., Hirshleifer, D., & Welch, I. (1998). Learning from the behavior of others: conformity fads and informational cascades. *Journal of Economic Perspectives*, *12*, 151–170.

Birch, S. A. J., Vauthier, S. A., & Bloom, P. (2008). Three-year-olds spontaneously use other's past performance to guide their learning. *Cognition*, *107*, 1018–1034.

Birch, S. A. J., Akmal, N., & Frampton, K. L. (2010). Two-year-olds are vigilant of others' non verbal cues to credibility. *Developmental Science*, *13*, 363–369.

Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees. *Animal Cognition*, *6*, 213–223.

Boyd, R., & Richerson, P. (1985). Culture and the evolutionary process. Chicago: University of Chicago Press.

Brody, G. H., & Stoneman, Z. (1981). Selective imitation of same-age, older and younger peer models. *Child Development*, *52*, 717–720.

Brody, G. H., & Stoneman, Z. (1985). Peer imitation: an examination of status and competence hypotheses. *Journal of Genetic Psychology*, *146*, 161–170.

Choleris, E., Guo, C., Liu, H. F., Mainardi, M., & Valsecchi, P. (1997). The effect of demonstrator age and number on duration of socially-induced food preferences in the house mouse (*Mus domesticus*). *Behavioural Processes*, *41*, 69–77.

Dawson, B. V., & Foss, B. M. (1965). Observational learning in budgerigars. *Animal Behaviour*, *13*, 470–474.

Dugatkin, L. A., & Godin, J. G. J. (1993). Female mate copying in the guppy (*Poecilia reticulata*): age dependent effects. *Behavioural Ecology*, *4*, 289–292.

Edwards, C. P. (1984). The age group labels and categories of preschool children. *Child Development*, *55*, 440–452.

Flynn, E. (2008). Investigating children as cultural magnets: do young children transmit redundant information along diffusion chains? *Philosophical Transactions of the Royal Society B*, *363*, 3541–3551.

Flynn, E., & Whiten, A. (2008a). Cultural transmission of tool-use in young children: a diffusion chain study. *Social Development*, *17*, 699–718.

Flynn, E., & Whiten, A. (2008b). Imitation of hierarchical structure versus component details of complex actions by 3-and 5-year olds. *Journal of Experimental Child Psychology*, *101*, 228–240.

Hanna, E., & Meltzoff, N. (1993). Peer imitation by toddlers in laboratory, home, and day-care contexts: implications for social learning and memory. *Developmental Psychology*, *29*, 701–710.

Henrich, J., & Broesch, J. (2011). On the nature of cultural transmission networks: evidence from Fijian villages for adaptive learning biases. *Philosophical Transactions of the Royal Society B*, *366*, 1139–1148.

Henrich, J., & Gil-White, G. (2001). The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefit of cultural transmission. *Evolution and Human Behavior*, *22*, 165–196.

Henrich, J., & McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology*, *12*, 123–135.

Hernik, M., & Csibra, G. (2009). Functional understanding facilitates learning about tools in human children. *Current Opinion in Neurobiology*, *19*, 34–38.

Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2008). Observational learning in chimpanzees and children studied through 'ghost' conditions. *Proceedings of the Royal Society B*, *275*, 835–840.

Hopper, L. M., Flynn, E., Wood, L. A. N., & Whiten, A. (2010). Observational learning of tool use in children: investigating cultural spread through diffusion chains and learning mechanisms through ghost displays. *Journal of Experimental Child Psychology*, *106*, 82–97.

Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (*Pan Troglodytes*) and children (*Homo sapiens*). *Animal Cognition*, *8*, 164–181.

Horner, V., Whiten, A., Flynn, E., & de Waal, F. B. M. (2006). Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *Proceedings of the National Academy of Science*, *103*, 13878–13883.

Horner, V., Proctor, D., Bonnie, K. E., Whiten, A., & de Waal, F. B. M. (2010). Prestige affects cultural learning in chimpanzees. *PLoS ONE*, *5*, e10625.

Jaswal, V. K., & Neely, L. A. (2006). Adults don't always know best: preschoolers use past reliability over age when learning new words. *Psychological Science*, *17*, 757–758.

Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. (2005). Trade-offs in the adaptive use of social and asocial learning. *Advances in the Study of Behaviour*, *35*, 333–379.

Kirkpatrick, M., & Dugatkin, L. A. (1994). Sexual selection and the evolutionary effects of copying mate choice. *Behavioral Ecology and Sociobiology*, *34*, 443–449.

Koenig, M. A., & Harris, P. L. (2005). Preschoolers mistrust ignorant and inaccurate speakers. *Child Development*, *76*, 1261–1277.

Laland, K. N. (2004). Social learning strategies. *Learning and Behavior*, *32*, 4–14.

Lyons, D. E., Young, A. G., & Keil, F. C. (2007). The hidden structure of overimitation. *Proceedings in the National Academy of Science*, *104*, 19751–19756.

Lyons, D. E., Damrosch, G. H., Lin, J. K., Macris, D. M., & Keil, F. C. (2011). The scope and limits of overimitation in the transmission of artefact culture. *Philosophical Transactions of the Royal Society B*, *366*, 1158–1167.

McElreath, R., Bell, A. V., Efferson, C., Lubell, M., Richerson, P. J., & Waring, T. (2008). Beyond existence and aiming outside the laboratory: estimating frequency-dependent and pay-off-biased social learning strategies. *Philosophical Transactions of the Royal Society B*, *363*, 3515–3528.

McGuigan, N., & Graham, M. (2009). Cultural transmission of irrelevant tool actions in diffusion chains of 3- and 5-year-old children. *European Journal of Developmental Psychology*.

McGuigan, N., Makinson, J., & Whiten, A. (2011). From over-imitation to super-copying: adults imitate causally irrelevant aspects of tool use with higher fidelity than young children. *British Journal of Psychology*, *102*, 1–18.

McGuigan, N., Whiten, A., Flynn, E., & Horner, V. (2007). Imitation of causally-opaque versus causally transparent tool use by 3- and 5-year-old children. *Cognitive Development*, *22*, 353–364.

Mesoudi, A., & O'Brien, M. J. (2008). The cultural transmission of Great Basin projectile point technology I: an agent-based computer simulation. *American Antiquity*, *73*, 627–644.

Moore, C., Bryant, D., & Furrow, D. (1989). Mental terms and the development of certainty. *Child Development*, *60*, 167–171.

Nielsen, M. (2006). Copying actions and copying outcomes: social learning through the second year. *Developmental Psychology*, *42*, 555–565.

Nielsen, M., & Tomaselli, K. (2010). Overimitation in Kalahari Bushman children and the origins of human cultural cognition. *Psychological Science*, *21*, 729–736.

Pepler, D. J., Abramovitch, R., & Corter, C. (1981). Sibling interaction in the home: a longitudinal study. *Child Development*, *52*, 1344–1347.

Rakoczy, H., Hamann, K., Warneken, F., & Tomasello, M. (2010). Bigger knows better: young children selectively learn rule games from adults rather than from peers. *British Journal of Developmental Psychology*, *28*, 785–798.

Rendell, L., Fogarty, L., Hoppitt, W. J. E., Morgan, T. G. H., Webster, M. M, & Laland, K. N. (2011). Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences*, *15*, 68–76.

Rieucau, G., & Giraldeau, L. A. (2009). Persuasive companions can be wrong: the use of misleading social information in nutmeg manikins. *Behavioral Ecology*, *20*, 1217–1222.

Sabbagh, M. A., & Baldwin, D. A. (2001). Learning words from knowledgeable versus ignorant speakers: links between preschoolers' theory of mind and semantic development. *Child Development*, *72*, 1054–1070.

Sanvito, S., Galimberti, F., & Miller, E. H. (2007). Observational evidences of vocal learning in southern elephant seals: a longitudinal study. *Ethology*, *113*, 137–146.

Tanaka, M. M., Kendal, J. R., & Laland, K. N. (2009). From traditional medicine to witchcraft: why medical treatments are not always efficacious. *PLos ONE*, *4*, e5192.

Taylor, M., Cartwright, B. S., & Bowden, T. (1991). Perspective taking and theory of mind: do children predict interpretive diversity as a function of differences in observer's knowledge. *Child Development*, *63*, 1334–1351.

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B*, *364*, 2405–2415.

van Bergen, Y., Coolen, I., & Laland, K. N. (2004). Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proceedings of the Royal Society of London B*, *271*, 957–962.

Wellman, H. M., Cross, D., & Watson, J. (2001). Meta-analysis of theory-of-mind development: the truth about false belief. *Child Development*, *72*, 655–684.

Whiten, A., & Flynn, E. (2010). The transmission and evolution of experimental microcultures in groups of young children. *Developmental Psychology*, *46*, 1694–1709.

Whiten, A., & van Schaik, C. P. (2007). The evolution of animal cultures and social intelligence. *Philosophical Transition of the Royal Society B*, *862*, 603–620.

Ziv, M., Solomon, A., & Frye, D. (2008). Young children's recognition of the intentionality of teaching. *Child Development*, *79*, 1237–1256.