

Selective copying of the majority suggests children are broadly “optimal-” rather than “over-” imitators

Cara L. Evans^{1,2}  | Kevin N. Laland¹ | Malinda Carpenter^{3,4} | Rachel L. Kendal⁵

¹School of Biology, University of St Andrews, St Andrews, UK

²Department of Linguistic and Cultural Evolution, Max Planck Institute for the Science of Human History, Jena, Germany

³School of Psychology & Neuroscience, University of St Andrews, St Andrews, UK

⁴Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

⁵Centre for Coevolution of Biology & Culture, Anthropology Department, Durham University, UK

Correspondence

Cara L. Evans, Max Planck Institute for the Science of Human History, Kahlaische Straße 10, D-07745 Jena, Germany.
Email: evans@shh.mpg.de; caraevans1@googlemail.com

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Abstract

Human children, in contrast to other species, are frequently cast as prolific “over-imitators”. However, previous studies of “over-imitation” have overlooked many important real-world social dynamics, and may thus provide an inaccurate account of this seemingly puzzling and potentially maladaptive phenomenon. Here we investigate this topic using a cultural evolutionary approach, focusing particularly on the key adaptive learning strategy of majority-biased copying. Most “over-imitation” research has been conducted using consistent demonstrations to the observer, but we systematically varied the frequency of demonstrators that 4- to 6-year-old children observed performing a causally irrelevant action. Children who “over-imitate” inflexibly should copy the majority regardless of whether the majority solution omits or includes a causally irrelevant action. However, we found that children calibrated their tendency to acquire the majority behavior, such that copying did not extend to majorities that performed irrelevant actions. These results are consistent with a highly functional, adaptive integration of social and causal information, rather than explanations implying unselective copying or causal misunderstanding. This suggests that our species might be better characterized as broadly “optimal-” rather than “over-” imitators.

RESEARCH HIGHLIGHTS

- Children are frequently cast as “over-imitators”, yet previous studies have typically overlooked many real-world learning dynamics. Here we take a cultural evolutionary approach, focusing on a key learning strategy: majority-biased copying.
- We show that children flexibly and adaptively adopt a majority-biased learning strategy: Copying does not extend to majorities who perform irrelevant actions.
- Our results suggest that the presence of causally irrelevant actions might substantially alter the operation of adaptive learning biases.
- Our findings support a highly functional and selective integration of social and causal information in children, rather than accounts of “over-imitation” that imply unselective copying or causal misunderstanding.

1 | INTRODUCTION

Compared with other animals, humans show an exceptional ability to learn through the high-fidelity copying of others’ actions (Dean, Kendal, Schapiro, Thierry, & Laland, 2012). This propensity to engage in faithful copying is thought to play a crucial role in facilitating cumulative cultural improvement: a hallmark of human culture (Tomasello, 1999). However, human imitation has also been described as “surprisingly unselective” or “mindless” (Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009), and susceptible to behavioral “inefficiency” or “cost” (Lyons, Young, & Keil, 2007), following numerous reports that both children and adults often blanket copy even those parts of an action sequence that are manifestly causally irrelevant to obtaining the instrumental goal (e.g., Horner & Whiten, 2005; Kenward, Karlsson, & Persson, 2011; Lyons et al., 2007; McGuigan, Makinson, & Whiten,

2011; McGuigan, Whiten, Flynn, & Horner, 2007; Nielsen & Tomaselli, 2010). This phenomenon, dubbed “over-imitation” (Lyons et al., 2007), has received much attention in recent years, being replicated in several cultures (Nielsen, Mushin, Tomaselli, & Whiten, 2015; Nielsen & Tomaselli, 2010), and reported to increase with age into adulthood (McGuigan et al., 2011; Nielsen & Tomaselli, 2010) and to be impervious to cues of prestige or success (Chudek, Baron, & Birch, 2016).

The seemingly counterintuitive nature of “over-imitation”, which has not been observed in other species (Horner & Whiten, 2005), has led some to propose explanations grounded in causal cognition, suggesting that the demonstration leads individuals to imitate actions automatically, despite an understanding of the necessary causal mechanisms (Lyons, Damrosch, Lin, Macris, & Keil, 2011; Lyons et al., 2007). Such high-fidelity blanket copying, it is argued, might serve to promote facets of cultural learning that are causally opaque (Lyons et al., 2007, 2011), but may also occasionally malfunction, leading to irrelevant actions being copied blindly, and behavior that manifests as causal misunderstanding (Whiten et al., 2009).

Others have argued that the phenomenon results instead from more social processes (Kenward et al., 2011; Nielsen & Blank, 2011; Over & Carpenter, 2012). Indeed, the term “over-imitation” is misleading if copying of the causally irrelevant actions encompasses socially relevant pressures and functions. For example, individuals might copy causally irrelevant actions in order to be like, and share experiences with, the demonstrator, or to affiliate with and encourage the demonstrator to like them (Meltzoff, 2007; Nielsen & Blank, 2011; Over & Carpenter, 2013). Likewise, the unanimity and pedagogical context inherent in most experimental demonstrations of irrelevant actions might lead participants to believe that they are expected by the experimenter to perform the irrelevant action (Lyons et al., 2011), or that the demonstration is normative, and they ought to conform to its performance, despite its social or causal function being unclear (Kenward et al., 2011; Keupp, Behne, Zachow, Kasbohm, & Rakoczy, 2015).

The critiques levelled at hypotheses based solely on assumptions about causal understanding resonate with findings that imitation in both adults and children can be selective and strategic. Even young children are able to imitate rationally, adjusting imitative fidelity flexibly in response to a number of contextual factors, including demonstrator competency (Birch, Vauthier, & Bloom, 2008) and intentionality (Carpenter, Akhtar, & Tomasello, 1998), constraints upon demonstrators (Gergely, Bekkering, & Király, 2002), signs of pedagogical engagement (Csibra & Gergely, 2006), and the perceived task goal (Carpenter, Call, & Tomasello, 2005; Legare & Nielsen, 2015).

Here we take a cultural evolutionary approach to investigate whether children are better characterized as “over-” or broadly “optimal-” imitators. Cultural evolutionary theory predicts that social learning decisions should be strategic regarding whom and when individuals copy (Boyd & Richerson, 1985), and guided by adaptive learning biases that influence the emergence, stability and evolution of cultural traits (Boyd & Richerson, 1985; Laland, 2004). Evidence that learning biases are involved in guiding the use of social information has been provided using both theoretical (Boyd & Richerson, 1985; Kandler & Laland, 2013) and empirical approaches (Rendell et al., 2011; see

Wood, Kendal, & Flynn, 2013b, for a review in children). These biases should be especially tuned to decisions regarding the adoption of causally sub-optimal behavior, yet they have been little considered in investigations of “over-imitation” (see McGuigan, 2013; Wood, Kendal, & Flynn, 2012, for initial evidence).

Most previous “over-imitation” research has involved the demonstration of a single sequence of behavior (i.e., the target behavior is performed unanimously) to an observer (for exceptions see, e.g., Chudek et al., 2016; McGuigan & Robertson, 2015; Nielsen & Blank, 2011). However, real-world learning often involves observing multiple individuals behaving differently. Thus, comparing the operation of learning biases in situations that include, exclude, or vary the degree of irrelevant action performance, by multiple demonstrators, will be particularly informative regarding (i) the robustness of children’s propensity to “over-imitate” outside of unanimous conditions, and (ii) the evaluation of competing explanations of “over-imitation”.

Here we consider one type of learning bias that has been a major focus for cultural evolutionists and psychologists alike: majority-biased copying. The majority behavior represents the behavior that the greatest proportion of group members have converged upon, and there is empirical evidence that majority or consensus behavior informs copying in both children (Corriveau, Fusaro, & Harris, 2009; Haun, Rekers, & Tomasello, 2012; Morgan, Laland, & Harris, 2015) and adults (Coultas, 2004; Morgan, Rendell, Ehn, Hoppitt, & Laland, 2012). Majority behavior is expected to signal a relatively safe, reliable, and adaptive behavioral response (Boyd & Richerson, 1985; Wolf, Kurvers, Ward, Krause, & Krause, 2013), making it a particularly suitable transmission bias for testing hypotheses about the adoption of causally irrelevant information.

In the current study, we showed 4- to 6-year-old children a video demonstration in which we had all four demonstrators perform a causally relevant action, but systematically varied the number of demonstrators who additionally performed a causally irrelevant action while retrieving a reward from a puzzle box. Either all, the majority (3 of 4), the minority (1 of 4), or none of the demonstrators performed the causally irrelevant action.

In the first experimental condition, we examined whether children were more likely to adopt the majority over the minority solution when faced with alternative, but equivalent, *causally relevant* task solutions. In line with previous findings (Haun et al., 2012), we expected that children would demonstrate a bias towards copying the majority’s solution.

Importantly, we then investigated whether majority-biased copying in children extends to majorities who perform a causally irrelevant action. If children copy inflexibly—if “over-imitation” is robust outside of unanimous demonstrations—they might be expected to copy the solution used by the majority regardless of whether it omits or includes causally irrelevant actions. Instead, we predicted that when presented with a majority performing the irrelevant action and a minority omitting it, the instrumental framing of our task, coupled with children’s rational and selective imitation (Gergely et al., 2002; Want & Harris, 2001), would counter their tendency to copy the majority, and majority-biased copying would not be detected. In contrast,

in a condition in which the majority *omits* the irrelevant action and the minority performs it, we predicted majority-biased copying. We compared these results to those from a condition representing the paradigm typically used in “over-imitation” research: unanimous demonstration of the irrelevant action. Here we predicted that the unanimity of the demonstration would result in irrelevant action copying at similarly high levels as previously reported (e.g., Horner & Whiten, 2005; Lyons et al., 2007). A final condition, with no demonstration, provided the baseline level of irrelevant action production. Thus, when demonstration of the irrelevant action was unanimous, we expected it to be copied at high levels, but with anything less than unanimity we did not expect high levels of “over-imitation”.

Participants were provided with multiple (three) attempts at solving the puzzle box, permitting an evaluation of children’s initial tendency to copy and their tendency to “stick with” performing the demonstrated actions after their own initial experience with the task. We tested 4- to 6-year-olds, as children within this age range have developed sensitivity to demonstrator frequency in other learning contexts (Haun et al., 2012; Morgan et al., 2015; Wilks, Collier-Baker, & Nielsen, 2015), as well as an ability to engage in rational and selective imitation (Gergely et al., 2002; Want & Harris, 2001), and are considered prolific “over-imitators” (Kenward, 2012; Lyons et al., 2007; Nielsen & Tomaselli, 2010).

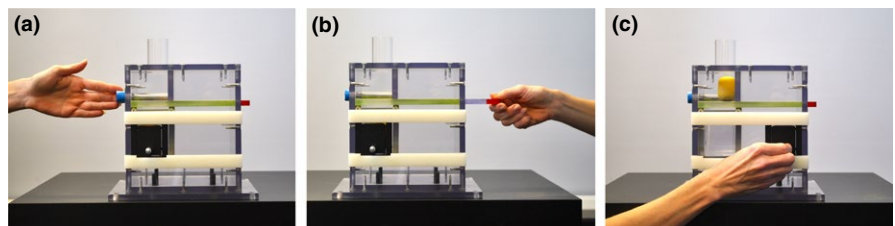
2 | METHOD

2.1 | Participants and materials

Two hundred and fifty-two 4- to 6-year-old children visiting UK science centers (128 males; 4-year-olds: $M = 4;5$, range = 4;0–4;11; 5-year-olds: $M = 5;6$, range = 5;0–5;11; 6-year-olds: $M = 6;5$, range = 6;0–6;11) were included in the final sample. Eight additional children were tested but excluded due to experimenter error (2), apparatus failure (3), parental interference (2), or refusal to interact with the apparatus (1).

The “Sweep-Drawer Box” (Wood, Kendal, & Flynn, 2013a; see Figure 1), a two-action transparent apparatus, was used with minor modifications. Retrieval of a capsule containing a sticker was dependent upon the capsule being moved to a sliding black opaque door by one of two spatially separated and functionally independent manipulanda: a silver sweeper with blue handle (Figure 1a), or a blue drawer with red handle (Figure 1b). In some demonstrations, a causally irrelevant action (see Figure 1c), involving the demonstrator twice sliding the black door open and closed, preceded use of the sweep/drawer manipulandum.

FIGURE 1 a–c The Sweep-Drawer Box. Demonstrator releasing the capsule by pushing the sweep manipulandum (a), or pulling the drawer manipulandum (b). Demonstrator performing the irrelevant action on the door prior to capsule release (c)



2.2 | Design and procedure

In a between-groups design, participants were randomly allocated to one of five conditions (C1–C5). There were no significant differences in the distribution of age ($F(4, 246) = 0.26$, $p = .91$) and approximately equal numbers of boys and girls in each condition. In four experimental conditions (C1–C4, $N = 201$), children watched a video showing four female demonstrators (distinguished by colored shirts) retrieving the sticker capsule from the apparatus in turn, before attempting capsule retrieval themselves three times. The fifth condition (C5, $N = 51$) served as a non-social baseline control in which participants received no video demonstration.

The first experimental condition (*relevant actions only*: C1) investigated whether children displayed majority-biased copying when choosing between two causally relevant actions: sweep versus drawer retrieval. Children in this condition saw the majority (three demonstrators) perform the alternative relevant action to the minority person. In the remaining three experimental conditions, each child saw all four demonstrators perform the *same* causally relevant action (i.e., sweep or drawer), but the number of demonstrators who additionally performed the irrelevant action varied between one (i.e., *minority irrelevant*: C2), three (i.e., *majority irrelevant*: C3), and four (i.e., *all irrelevant*: C4) across conditions (see Table 1 for an overview of the experimental conditions). The identity of the minority demonstrator, order in which the minority and majority performed, and use of sweep and drawer methods were counterbalanced within and between conditions. The majority demonstrators always appeared consecutively, with the minority individual demonstrating her method immediately before or after them. To control for demonstration frequency, the three majority demonstrators retrieved the capsule once each, while the minority individual demonstrated her method three times.

Children were tested individually in a screened-off area at the science center, with parents sitting at a distance. Each child chose a sticker, which the experimenter placed inside the reward capsule before dropping it into the puzzle box. The child was told that they had to get the capsule out of the box and then could keep the sticker. For the experimental conditions (C1–C4), the child was then shown a picture of the four demonstrators and asked to watch a video showing them retrieving the sticker (see supporting information S1 for a detailed procedural script).

Children were next told it was their turn to try to get the sticker out and were free to approach the apparatus and interact with it until (i) the capsule had been retrieved, (ii) 2 minutes had elapsed, or (iii) the child refused to continue. Participants who retrieved the sticker at T1 were offered two further attempts (T2 and T3); between trials the

TABLE 1 Overview of the demonstration and baseline conditions

Condition	Majority solution (3 demonstrators)	Minority solution (1 demonstrator)	N
(C1) Causal actions only	All retrieve using the same relevant action (sweep or drawer)	Retrieves using the alternative relevant action	51
(C2) Minority irrelevant	All retrieve using the same relevant action (sweep or drawer), without performing the irrelevant action	Performs irrelevant action then retrieves using the same relevant action as the majority	51
(C3) Majority irrelevant	All perform the irrelevant action before retrieval. All use the same relevant action (sweep or drawer)	Retrieves using the same relevant action as the majority, without performing the irrelevant action	49
(C4) All irrelevant	All demonstrators perform the irrelevant action before retrieval. All use the same relevant action (sweep or drawer)		50
(C5) Baseline	No demonstration		51

experimenter reset the apparatus out of sight while the child chose a new sticker.

Children assigned to the *baseline* condition (C5) received the same initial instructions and prompts as children in the experimental groups but watched no video. All children who participated in the study received a sticker reward.

2.3 | Coding and analysis

Each participant was scored for three measures on each response trial: (i) successful removal of the capsule, (ii) number of times they performed the irrelevant action (sliding the door open and closed prior to operating the manipulandi), and (iii) the manipulandum used during retrieval (sweep or drawer). The experimenter coded 100% of the sample from video records. An independent observer, blind to condition and hypotheses, coded a random sample of 25%. Inter-observer reliability was excellent: Chronbach's alpha = 0.99 for the number of irrelevant actions performed, and Cohen's kappa = 1.00 for the two other measures.

All analyses were carried out in R version 3.1.3. Significance testing of main effects in regression models was undertaken using Likelihood-ratio (χ^2) tests, and Tukey post-hoc comparisons were performed using the package *multcomp*. Conventional binomial tests were used to assess whether copying was biased towards the majority or minority behavior during a single response trial (i.e., differed from chance level at e.g., T1). To assess whether children demonstrated an overall copying bias across all response trials combined (i.e., data pooled across T1–T3), we adopted the option-bias method (Kendal, Kendal, Hoppitt, & Laland, 2009) to account for within-individual correlations in responses across trials (see supporting information S4). For analyses of persistence in copying across trials, we computed a binary (yes/no) measure of copying persistence to indicate whether children consistently reproduced the demonstrated action in every response trial (i.e., performed it in T1, T2, and T3). Two-tailed *p*-values are reported throughout.

3 | RESULTS

We present the results in three sections. First, we examine children's copying of unanimous demonstrators. We then investigate

the influence of the majority on children's tendency to copy. Finally, we additionally examine the effect of demonstrator unanimity on children's initial decisions to copy, and their tendency to persist with performing the demonstrated actions across all trials. A descriptive overview of irrelevant and relevant action copying for each trial in each condition can be found in the supporting information; see Table S1. Throughout, preliminary analyses were conducted to test for age, sex, and primacy effects (where applicable), and in most cases no significant effects were found; the few exceptions are reported below.

First, to confirm the utility of social information to naïve children attempting the task, we note that children who received a social demonstration (C1–C4) were significantly more successful at retrieving the reward at T1 (success rate = 100%) than those (C5) who did not (six participants failed in C5: success rate = 88.2%; Fisher's Exact Test: $p < .001$). All but three participants who retrieved the reward at T1 also did so at T2 and T3.

3.1 | Copying when the demonstrators were unanimous

3.1.1 | Causally relevant actions

We pooled data across the three conditions in which children saw all four demonstrators performing the same causally relevant action (i.e., sweep or drawer retrieval: C2–C4 combined, $N = 150$). Despite successful children in the *baseline* condition showing a bias towards retrieval using the sweep manipulandum (78% of all retrievals used sweep; Fisher's Exact Test: $p < .001$), children who saw a unanimous demonstration showed a strong tendency to copy the relevant action they had witnessed (92% copying across all trials combined [91% sweep, 93% drawer]; Fisher's Exact Test: $p < .001$). A logistic generalized linear mixed model (GLMM) revealed no significant effect of the method demonstrated (sweep vs. drawer), experimental condition (C2–C4), trial number, or whether the child copied the irrelevant action on whether the relevant action was copied (see supporting information, Table S2).

3.1.2 | Causally irrelevant action

Only 16% of children in the *baseline* condition performed the irrelevant action on their first retrieval attempt (T1). By contrast, when

irrelevant actions were demonstrated unanimously (*all irrelevant* condition: C4), a significantly larger percentage of children copied the irrelevant action at T1 (86%; $\chi^2(1) = 51.60, p < .001$), consistent with our predictions and the high levels of irrelevant action copying in previous studies (Horner & Whiten, 2005; Lyons et al., 2007). Similarly, across all trials (T1–T3) combined, the percentage of children's responses in the *all irrelevant* condition that included production of the irrelevant action (81%) was significantly greater than in the baseline (9%; $\chi^2(1) = 167.83, p < .001$).

3.2 | Majority-biased copying

3.2.1 | Causally relevant actions

Consistent with our predictions, Figure 2 demonstrates that at T1 children in the *relevant actions only* condition (C1) copied the majority significantly above chance when faced with demonstrations of two different, yet causally equivalent, relevant actions (76% copied the majority; binomial test: $\pm 95\%$ CI [62%–87%], $p < .001$). Likewise, children in this condition continued to demonstrate majority-biased copying when all responses across T1–T3 combined were considered (*option-bias test statistic* = 4.39, $p < .001$; majority: 73%).

3.2.2 | Causally irrelevant action

Participants were scored as demonstrating a majority bias if they copied the majority's behavior with regard to omitting (*minority irrelevant*: C2) or performing (*majority irrelevant*: C3) the irrelevant action. As expected, there was a strong preference for the efficient majority solution in the *minority irrelevant* condition at T1 (84% copied the majority; binomial test: 95% CI [71%, 93%], $p < .001$), that remained across T1–T3 combined (*option-bias test statistic* = 7.70, $p < .001$; majority: 85%, see Figure 2).

In contrast, but in line with predictions, majority-biased copying was not observed in the *majority irrelevant* condition at T1, where

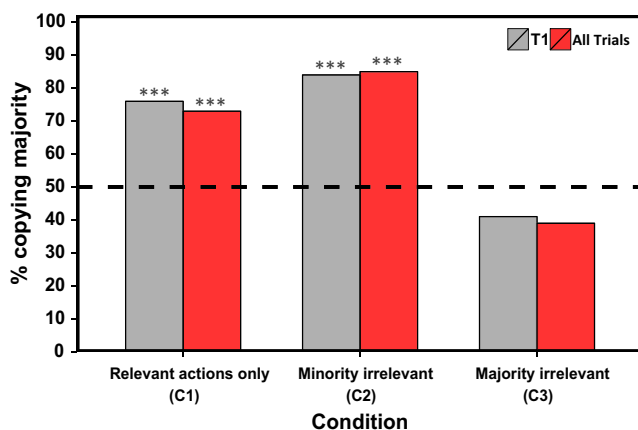


FIGURE 2 Percentage of participants copying the majority behavior (chance level copying indicated by dashed line) at T1 and across all three trials combined (collapsed across age groups, C1–C3). *** $p < .001$

most children copied the minority's omission of the irrelevant action (41% copied the majority; binomial test: 95% CI [27%–56%], $p = .25$). Majority-biased copying was also not observed across T1–T3 combined, where most children continued to copy the minority person's more efficient solution (*option-bias test statistic* = 1.82, $p < .08$; majority: 39.5%). Children in the *majority irrelevant* condition were influenced by the order in which the majority and minority performed: they more often copied the demonstration witnessed first (64% of all responses matched the solution demonstrated first; Fisher's Exact Test: $p < .001$).

3.3 | Demonstrator unanimity and copying persistence across trials

Previous research suggests that children persist with performing an irrelevant action at high levels after observing a single demonstrator, despite hands-on experience of task mechanics (Lyons et al., 2007; Wood et al., 2012). Children also typically persist in performing a demonstrated relevant solution, even when other equally efficacious solutions are discoverable (Wood et al., 2013a). Here we additionally examined the effects of demonstrator unanimity on both initial copying (in T1), and on children's persistence with the demonstrated method across all trials (T1–T3; i.e., children performed this action in each of the three response trials).

3.3.1 | Unanimous demonstrators

Within the *all irrelevant* condition (C4), where both causally relevant and irrelevant actions were demonstrated unanimously, the level of irrelevant action copying (86%) did not differ significantly from the high level of causally relevant action copying at T1 (96%; McNemar Test: $\chi^2(1) = 1.78, p = .18$). However, in contrast, children were less likely to persist with the irrelevant action in each of the three trials (T1–T3) (70%) than the relevant action (92%; McNemar Test: $\chi^2(1) = 5.88, p = .02$), suggesting that fidelity erodes more quickly for irrelevant actions.

3.3.2 | Causally relevant actions

We compared the behavior of children who witnessed a unanimous demonstration of the causally relevant action (i.e., sweep or drawer retrieval: C2–C4 combined, $N = 150$) with that of children who witnessed a less-than-unanimous majority (*causal actions only*: C1). Children were significantly more likely to adopt the relevant action at T1 when it was unanimously demonstrated than when it was demonstrated by a less-than-unanimous majority (Unanimous: 96%, Not Unanimous: 76%; $\chi^2(1) = 8.32, p < .004$), and were also more likely to persist with copying the unanimous demonstration across T1–T3 (Unanimous: 89%, Not Unanimous: 63%; $\chi^2(1) = 16.91, p < .001$). Thus, children were more likely to both adopt and persist with the majority action when the demonstration was unanimous compared to when it was not unanimous.

3.3.3 | Causally irrelevant actions

Logistic regression models, including participants' sex and age, were used to examine the effect of demonstrator unanimity on children's copying of the irrelevant action. The *baseline* condition was included for comparison in analyses of children's initial copying of irrelevant actions in T1 (C2–C5, $N = 201$), but dropped from analyses of their persistence in copying the irrelevant action across trials (T1–T3, C2–C4, $N = 150$) as it lacked the variation required to fit a logistic regression (i.e., no children in the *baseline* condition performed the irrelevant action in all trials).

The frequency of demonstrators performing the irrelevant action strongly influenced both children's initial copying of it in T1 (GLM: $\chi^2(3) = 81.20, p < .001$), and their persistence with it across T1–T3 (GLM: $\chi^2(2) = 51.19, p < .001$). Pairwise comparisons between conditions (see Figure 3 and Table 2) revealed that levels of initial and persistent irrelevant action copying decreased sharply from unanimous demonstration (*all irrelevant*: T1: 86%, T1–T3: 70%) to non-unanimous demonstration of the irrelevant action, including when the irrelevant action was demonstrated by the majority (*majority irrelevant*: T1: 41%, T1–T3: 21%). There was a further sharp reduction in children's initial (T1) copying of the irrelevant action when the number of demonstrators performing the irrelevant action dropped from three (*majority irrelevant*: 41%) to just one (*minority irrelevant*: 14%) out of four, although this initial difference did not remain significant when we considered children's persistence in performing the irrelevant action across T1–T3. Thus, when the demonstrators were not unanimous, children were influenced by the number of demonstrators who performed the irrelevant action at T1, but this did not translate into differences in persistence with the causally irrelevant behavior across trials. Comparisons of irrelevant action production with the *baseline* condition (16%) revealed that the percentage of children who performed the irrelevant action at T1 did not increase when it was demonstrated by the minority (*minority irrelevant*), but increased sharply when demonstrated by a non-unanimous (*majority irrelevant*) or unanimous majority (*all irrelevant*).

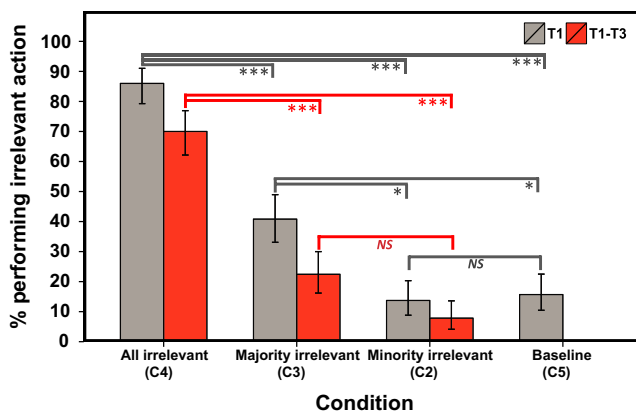


FIGURE 3 Percentage of participants performing the irrelevant action at T1 and persistently across T1–T3 (collapsed across age groups, C2–C5). *** $p < .001$; * $p < .05$; NS $p > .05$. Comparisons with baseline were made at T1 only. Binomial standard errors

Across conditions (C2–C5) children's age correlated negatively with irrelevant action performance at T1, such that older children produced fewer irrelevant actions (Table 2; supporting information Figure S1). However, the negative effect of age on irrelevant action copying (in conditions C2–C4) in T1 was confined to conditions in which the irrelevant action was not unanimously demonstrated (i.e., the *majority irrelevant* and *minority irrelevant* conditions), and was still significant following removal of the *all irrelevant* and *baseline* conditions from the analysis (C2–C3, $Z = -2.04$, Odds ratio = 0.95, $p = .041$, $N = 100$). By contrast, children's age had no significant effect on persistence in copying the irrelevant action across T1–T3, even when the analysis was confined to conditions with non-unanimous demonstration of the irrelevant action. Thus the initial (T1) tendency for increased copying of the efficient solution in older children was not maintained across repeated trials.

Although there was no effect of sex on children's initial performance of the irrelevant action (T1), boys were less likely to persist with the irrelevant action (T1–T3) than girls (Table 2). Follow-up analysis revealed no interaction effect between sex and age.

4 | DISCUSSION

The results presented here contribute an important new perspective to our understanding of human cultural transmission, and in particular to work on both "over-imitation" and majority-biased copying. The findings provide direct evidence that adaptive learning biases are implemented more flexibly than previously thought, and are substantially altered by both the social context (unanimity of demonstrators) and the type of actions demonstrated (causally relevant vs. irrelevant). As expected, we found that the previously reported pervasiveness of "over-imitation" (Chudek et al., 2016; Horner & Whiten, 2005; Lyons et al., 2007; McGuigan et al., 2011; Nielsen & Tomaselli, 2010) is substantially diminished in the more real-world situation of non-unanimous demonstrations, and that majority-biased copying did not extend to majorities who performed irrelevant actions, despite being detected in all instances where the majority performed a causally efficient task solution. Rather than representing a "puzzling" and "mindless" peculiarity of human imitation, or a "copy-all, correct-later" strategy (Chudek et al., 2016; Whiten et al., 2009), our data suggest that the occurrence of so-called "over-imitation" instead fits with the operation of a highly flexible, selective, and adaptive high-fidelity copying mechanism in our species.

4.1 | Irrelevant action copying

In line with previous research (Horner & Whiten, 2005; Lyons et al., 2007), children copied the irrelevant action at high levels when it was demonstrated unanimously, despite the instrumental framing of our task. Our experimental design offers some insight regarding the competing hypotheses proposed to explain why children and adults copy irrelevant information at such high levels in this context. For instance, it is unlikely that children in the *all irrelevant* condition blindly copied

TABLE 2 The effects of experimental condition and age on whether the irrelevant action was performed at T1 (C2–C5), and persistently across T1–T3 (C2–C4)

Model parameters	Pairwise comparisons	Estimate (SE)	Odds ratio
Model T1			
Intercept		0.66(1.21) ^{ns}	
Condition ^a	All (C4) – Majority (C3)	2.25(0.51) ^{***}	9.49
	All (C4) – Minority (C2)	3.81(0.60) ^{***}	45.15
	All (C4) – Baseline (C5)	3.81(0.60) ^{***}	45.15
	Baseline (C5) – Minority (C2)	–0.005(0.58) ^{ns}	1.00
	Majority (C3) – Minority (C2)	1.56(0.51) [*]	4.76
	Majority (C3) – Baseline (C5)	1.56(0.51) [*]	4.76
Participant's age ^b		–0.04(0.02) [*]	0.96
Participant's sex ^c		–0.33(0.37) ^{ns}	0.72
Total model:	$R^2 = 0.46$ (Nagelkerke), $\chi^2(5) = 84.41$, $p < .001$		
Model T1–T3			
Intercept		–0.71(1.48) ^{ns}	
Condition ^a	All (C4) – Minority (C2)	3.48(0.63) ^{***}	32.57
	All (C4) – Majority (C3)	2.18(0.48) ^{***}	8.87
	Majority (C3) – Minority (C2)	1.30(0.63) ^{ns}	3.67
Participant's age ^b		–0.02(0.02) ^{ns}	0.98
Participant's sex ^c		–1.01(0.44) [*]	0.37
Total model:	$R^2 = 0.43$ (Nagelkerke), $\chi^2(4) = 55.76$, $p < .001$		

^aCategorical variable (see Table 1); ^bNumeric variable (age in months); ^cDichotomous variable (0 = female, 1 = male); ^{ns} $p > .05$; ^{*} $p < .05$; ^{***} $p < .001$.

the irrelevant action as causally necessary (Lyons et al., 2007, 2011), as explanations based solely on assumptions about causal understanding imply that once the redundancy of the irrelevant action has been demonstrated (i.e., at least one demonstrator omits the irrelevant action), children should not show sensitivity to the relative frequency of demonstrators performing or omitting the irrelevant action. However, demonstrator frequency did influence children's irrelevant action copying in our study: children were more likely to perform the irrelevant action in the *majority irrelevant* than *minority irrelevant* condition. The low level of irrelevant action production in the *baseline* condition further implies that causal understanding of what was and was not required to extract the reward was not problematic for participants in any of the age groups. Considered together, these findings suggest that children's copying was influenced not by causal understanding but by demonstrator behavior.

Older children (age 6) were less likely to copy irrelevant actions at T1 than younger children (age 4), but only where irrelevant actions were not demonstrated unanimously. Previous studies in which the irrelevant action was demonstrated unanimously have found that irrelevant action copying increases with age (McGuigan et al., 2007, 2011; Nielsen & Tomaselli, 2010). A plausible explanation for these combined findings is that unanimous demonstrations generate normative pressures to copy behavior as the “way it is done”, despite the child's knowledge that it is causally unnecessary, which increases with age (Moraru, Gomez, & McGuigan, 2016). (Note that this amounts in effect to a sort of group-level rational imitation: If everyone does it this way, there must be a good reason for it.) However, when demonstrators

vary in their performance of the irrelevant action, as in our study, the pressure to conform is substantially reduced and becomes increasingly undermined by age-related increases in discarding the majority behavior for more accurate or reliable behavior (Einav, 2014; Seston & Kelemen, 2014).

4.2 | Majority-biased copying

These results provide strong evidence that while young children do use majority behavior as a heuristic to guide instrumental learning, they are able to do so flexibly, calibrating their decision-making according to additional cues, such as the majority's perceived efficiency. Wilks et al. (2015) found that children were more likely to copy a successful minority than an unsuccessful majority, despite being more likely to copy the majority when both the majority and minority solutions were equally successful. Here we extended Wilks and colleagues' investigation to superfluous behavior that did not result in goal failure, using a different measure of majority copying that allows us to make additional inferences about the cultural evolution of so-called “over-imitation”. Majority-biased copying (regarded as a key strategy for acquiring safe and effective behavior; Boyd & Richerson, 1985; Wolf et al., 2013) was strongest when the majority demonstrated the inefficiency of the minority's irrelevant action, and did not extend to a majority that performed irrelevant actions. Thus, children do not blindly follow the crowd.

While some evidence for majority-biased transmission has been observed in other species (notably nonhuman primates; Haun et al.,

2012), it remains untested whether nonhuman animals are able to calibrate majority-biased copying according to additional cues such as the efficiency of the majority's behavior. It is plausible that humans' ability to adjust adaptive learning heuristics flexibly and selectively—such as their tendency to follow the crowd—in concert with their remarkable ability to engage in high-fidelity copying, has played a major evolutionary role in the generation of our species' remarkable cultural prowess relative to nonhuman animals.

4.3 | Implications for cultural evolution

Cultural evolutionary theory states that a behavioral trait must be copied at levels proportional to the trait in the population if the trait is to be maintained at its current levels (Boyd & Richerson, 1985). Our data therefore suggest that majority-biased copying could potentially stabilize functionally relevant behaviors within a population over time, but not behaviors that contain functionally redundant information. That is, most participants who witnessed the majority perform an irrelevant action copied the minority's more efficient solution, both at T1 and across all three trials combined. In addition, participants who saw the majority performing the irrelevant action were not more likely to persist in performing it across trials than those who saw it performed by the minority. Moreover, there was a strong bias towards copying a majority who demonstrated greater behavioral efficiency over a minority, and children showed a greater tendency to reproduce the causally relevant than causally irrelevant action across trials following unanimous demonstration.

Taken together, our findings imply that without additional reinforcement of the irrelevant action (e.g., sanctions, punishments, explicit teaching, or other normative or social pressures), majority behavior containing functionally redundant information will rapidly evolve to a more efficient solution (i.e., irrelevant action omission), which would likely continue to increase towards fixation. However, by adding ritualistic or normative contextual cues (Clegg & Legare, 2016; Fusaro & Harris, 2008; Herrmann, Legare, Harris, & Whitehouse, 2013; Legare & Nielsen, 2015) or providing clear social functions (Nielsen & Blank, 2011; Over & Carpenter, 2012) to causally irrelevant actions in unanimous and non-unanimous demonstrations, a different pattern of results, and possibly majority-biased copying of irrelevant actions, might emerge, clarifying further what triggers causally irrelevant action copying.

We also anticipate that had the causally irrelevant action in our study encompassed more substantial efficiency costs, we would have observed lower rates of irrelevant action copying and faster rates of erosion over time; a suggestion consistent with the findings of Keupp, Bancken, Schillmöller, Rakoczy, and Behne (2016). Varying the ratio of majority versus minority demonstrators who performed the irrelevant action (for example 25:1 instead of 3:1), would also plausibly affect the rate of erosion, as would manipulating the relative age (Wood et al., 2012), group membership (Oostenbroek & Over, 2015), or status (McGuigan, 2013; although see Chudek et al., 2016) of the demonstrators. Examining the interaction of different types of learning biases in irrelevant action copying is an area ripe for future research.

4.4 | Conclusions

To our knowledge, we present the first evidence that young children flexibly and adaptively adopt a majority-biased learning strategy when faced with an instrumental learning goal and the opportunity to integrate social information from multiple individuals. Majority-biased copying did not extend to causally inefficient and irrelevant actions, despite these being copied at high levels when demonstrated unanimously. Akin to the findings of Asch (1956) with adults, when just one individual dissented from the majority, "over-imitation" plummeted. Thus, our data suggest that the presence of causally irrelevant actions might substantially alter the operation of adaptive learning biases. This finding has obvious implications for cultural evolutionary theory; namely that causally irrelevant, and potentially costly, actions are unlikely to be maintained in causal or instrumental real-world contexts where behavioral traits are often not exhibited unanimously. Rather, in many—perhaps most—circumstances, socially transmitted behavior is expected to evolve towards efficient solutions.

An easily envisaged exception to this expectation is when instances of copying causally irrelevant actions serve social, ritualistic or normative purposes. As children showed sensitivity to the degree of unanimity in demonstrator behavior, our findings provide support for the operation of socially driven motivations, and explanations, in causally irrelevant action copying. However, we suggest that the term "over-imitation" is inaccurate and misleading when copying of causally irrelevant actions encompasses socially functional properties, as their performance in this instance no longer represents puzzling or irrational behavior. On the contrary, our findings illustrate a flexible, and highly functional, integration of social learning strategies, through which individuals combine social and non-social sources of information to home in rapidly on the relevant actions in instrumental tasks, while remaining sensitive to the social functions of imitation. This suggests that our species might more accurately be cast as broadly "optimal" rather than "over"-imitators.

ETHICS STATEMENT

Full ethical approval for this study was provided by UTREC of the University of St Andrews, and informed consent was obtained for all participants.

AUTHOR CONTRIBUTIONS

CLE conceived and designed the study, carried out the data collection, analyses, and drafted the manuscript. RLK participated in the design of the study. RLK, KNL and MC helped interpret the data and revise the manuscript. All authors gave final approval for publication.

COMPETING INTERESTS

We declare no competing interests.

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ORCID

Cara L. Evans  <http://orcid.org/0000-0002-7116-3646>

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SUPPORTING INFORMATION

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