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PAPER

Exploring the evolutionary origins of overimitation: a comparison across domesticated and non-domesticated canids

Angie M. Johnston,* Paul C. Holden* and Laurie R. Santos

Department of Psychology, Yale University, USA

Abstract

*When learning from others, human children tend to faithfully copy – or 'overimitate' – the actions of a demonstrator, even when these actions are irrelevant for solving the task at hand. We investigate whether domesticated dogs (*Canis familiaris*) and dingoes (*Canis dingo*) share this tendency to overimitate in three experiments. In Experiment 1, dogs and dingoes had the opportunity to solve a puzzle after watching an ostensive demonstrator who used both a relevant action and an irrelevant action. We find clear evidence against overimitation in both species. In contrast to human children (Horner & Whiten, 2005), dogs and dingoes used the irrelevant action less often across trials, suggesting that both species were filtering out the irrelevant action as they gained experience with the puzzle (like chimpanzees; Horner & Whiten, 2005). Experiments 2 and 3 provide further evidence against overimitation, demonstrating that both species' behavior is better characterized by individual exploration than overimitation. Given that both species, particularly dogs, show human-like social learning in other contexts, these findings provide additional evidence that overimitation may be a unique aspect of human social learning. A video abstract of this article can be viewed at: https://youtu.be/g2mRniJZ7aU.*

Research highlights

- We investigate whether dogs (*Canis familiaris*) and dingoes (*Canis dingo*) overimitate.
- Across three experiments, we find clear evidence against overimitation.
- Both dogs and dingoes omit the irrelevant action as they gain experience with the puzzle.
- Canids' performance differs from that of children who overimitate after repeated trials.
- These results suggest that overimitation may be a unique aspect of human social learning.

Introduction

Humans have a vast storehouse of cultural knowledge that is unparalleled in any other species, even our closest primate relatives. Although some nonhuman primate species transmit specific behaviors that are shared across members of a group (e.g. Tennie, Call & Tomasello, 2009; van Schaik, Ancrenaz, Borgen, Galdikas, Knott *et al*., 2003; Whiten, Goodall, McGrew, Nishida, Reynolds *et al*., 1999), humans have an unusual ability to transfer entire domains of knowledge (e.g. fire-building, fishing, and theoretical physics) across individuals and generations.

Which aspects of human cognition have led to this uniquely efficient system of cultural transmission? Recent comparative research has revealed that the unusually faithful cultural transmission seen in humans may depend on unique human mechanisms for social learning (e.g. Csibra & Gergely, 2011; Tomasello, 2008). Evidence for this claim stems from studies demonstrating that non-human primates use information provided by other social agents in a very different way from human children (e.g. Hare & Tomasello, 2005; Horner & Whiten, 2005; Tomasello, 2008; Tomasello, Carpenter, Call, Behne & Moll, 2005). For instance, when trying to determine the location of a hidden object, young children use a wide variety of ostensive cues (e.g. gazing and pointing), including novel cues, in the absence of any training (e.g. a wooden marker; Tomasello, Call & Gluckman, 1997). In contrast, non-human primates

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Address for correspondence: Angie M. Johnston, 2 Hillhouse Ave., New Haven, CT 06511, USA; e-mail: angie.johnston@yale.edu

*The first two authors contributed equally to this work.

require dozens of trials to learn ostensive cues (e.g. Itakura, Agnetta, Hare & Tomasello, 1999) and fail to generalize to novel cues even with training (Povinelli, Reaux, Bierschwale, Allain & Simon, 1997; Tomasello *et al.*, 1997). Non-human primates' insensitivity to other agents' information is also observed in other social contexts. For instance, when learning how to open a puzzle box, children often reproduce a demonstrator's actions exactly, even when alternative solutions are available (e.g. Call, Carpenter & Tomasello, 2005; Horner & Whiten, 2005). In contrast, non-human primates only copy a demonstrator's actions if they are unable to see an alternative solution (e.g. Call *et al.*, 2005; Horner & Whiten, 2005). Thus, there seems to be a core difference in the way that human and non-human primates use information provided by other social agents.

Given that social learning in non-human primates differs in a number of important ways from that of humans, it is hard to pinpoint exactly which aspects of social learning are truly unique to our species. To gain greater insight into the specific social learning mechanisms that support human culture, it is necessary to examine species that show a more human-like tendency to attend to other social agents, such as the capacity to attend to and follow ostensive cues. By narrowing down the specific aspects of human social learning that are unique to our species, we can gain a better grasp on which traits likely support our unique system of cultural transmission.

One species that may prove particularly informative in the study of human unique social learning is the domesticated dog (*Canis familiaris*; e.g. Hare & Tomasello, 2005; Johnston, McAuliffe & Santos, 2015; Topál, Kis & Oláh, 2014). In contrast to non-human primates (e.g. Povinelli *et al.*, 1997; Tomasello *et al.*, 1997), dogs follow a wide range of human ostensive cues (e.g. Hare, Brown, Williamson & Tomasello, 2002; Miklósi, Polgárdi, Topál & Csányi, 1998) and do so from just 6 weeks of age (Riedel, Schumann, Kaminski, Call & Tomasello, 2008). In fact, dogs' sensitivity to ostensive cues parallels that of human children in many ways. For instance, dogs follow completely novel ostensive cues (e.g. provided via physical markers; Riedel, Buttelmann, Call & Tomasello, 2006), show perseverative search errors based on ostensive cues (e.g. Topál, Gergely, Erdőhegyi, Csibra & Miklósi, 2009), and only follow a human's gaze if it is preceded by ostensive cues (e.g. eye contact and dog-directed speech; Téglás, Gergely, Kupán, Miklósi & Topál, 2012; cf. Senju & Csibra, 2008). These parallels between social learning in dogs and human children suggest that dogs may be an ideal species for determining which features of human social learning are unique.

One particular feature of human social learning that has been posited to increase the efficiency of cultural transmission is children's tendency to prioritize ostensive information over other sources of evidence (e.g. Bonawitz, Shafto, Gweon, Goodman, Spelke *et al.*, 2011; Csibra & Gergely, 2011; Jaswal, Croft, Setia & Cole, 2010; Legare & Nielsen, 2015). For instance, when children learn how to solve a problem via ostensive instruction, they tend to copy the demonstrator's actions exactly, rather than taking time to explore alternative strategies or solutions (e.g. Bonawitz *et al.*, 2011; Király, Csibra & Gergely, 2013; Lyons, Damrosch, Lin, Macris & Keil, 2011; Nielsen & Tomaselli, 2010). Although researchers debate why children prioritize ostensive information (e.g. cultural normativity: Legare & Nielsen, 2015; automatic causal encoding: Lyons *et al.*, 2011; affiliation: Over & Carpenter, 2009), there is general agreement that this tendency to prioritize ostensive information likely serves as a crucial foundation for efficient social learning and transmission of knowledge (e.g. Bonawitz *et al.*, 2011; Csibra & Gergely, 2011; Legare & Nielsen, 2015; Lyons *et al.*, 2011). Specifically, by prioritizing ostensive information, children generally limit the amount of time they need to spend learning through repeated trial and error (e.g. Shafto, Goodman & Frank, 2012).

In the current set of studies, we examine whether this tendency to prioritize ostensive information is shared in dogs. To test this, we investigate whether dogs, like human children (e.g. Horner & Whiten, 2005; Lyons *et al.*, 2011; Nielsen & Tomaselli, 2010), *overimitate* the actions of a demonstrator. When human children are presented with ostensive demonstration that includes both relevant and irrelevant actions, they faithfully copy both the relevant and *irrelevant* actions (e.g. Lyons *et al.*, 2011; Nielsen & Tomaselli, 2010). This behavior has been termed 'overimitation' because it persists even when children have the opportunity to ignore the experimenter's demonstration and explore alternative solutions on their own. For instance, even when children (1) can see the inner workings of the puzzle and (2) have extended experience with that puzzle, they continue to copy the experimenter's irrelevant actions (while chimpanzees do not; Horner & Whiten, 2005).

If dogs overimitate in the same way as human children, this would suggest that the tendency to overimitate might depend on more basic features of human-like social learning (e.g. sensitivity to ostensive cues). In contrast, if dogs do not overimitate, this would provide stronger evidence that overimitation is a unique aspect of human social learning that may serve a crucial foundation for our unique system of cultural transmission. To differentiate between these possibilities, we presented dogs in Experiment 1 with a puzzle that had a very simple solution – open a lid to get a treat. However, before dogs were able to explore the puzzle, an experimenter ostensively demonstrated a solution that not only included the relevant action (opening the lid), but also an irrelevant action (moving a lever). We also varied whether the puzzle was opaque or transparent, which allowed us to investigate whether dogs would continue to use the irrelevant action even when the puzzle was causally transparent. Note that children continue to copy the experimenter's irrelevant actions even after they have had extended experience with a puzzle and can see its inner workings (i.e. when it is transparent, see Horner & Whiten, 2005). If dogs overimitate, then they should use the irrelevant action across *all* trials, regardless of whether they receive the opaque puzzle or transparent puzzle first. In contrast, if dogs do not overimitate, then – like chimpanzees (Horner and Whiten, 2005) – they should use the irrelevant action less often as they gain experience with the puzzle.

In addition, to isolate the role of domestication, we compared dogs' performance to that of their close but non-domesticated evolutionary relative, the Australian dingo (*Canis dingo*). Dingoes offer an ideal comparison species for this question since they lie somewhere between wolves and dogs in domestication (Smith, 2015). Moreover, although dingoes are sensitive to human ostensive cues, they are not as adept at using these cues as domesticated dogs (Smith & Litchfield, 2010a). If dingoes overimitate, this would suggest that only minimal features of human-like social learning are necessary to support overimitation.

Experiment 1

Method

Dog subjects

We tested 40 dogs (16 males; $M_{age} = 5.30$; $SD_{Age} = 3.34$) of varying breeds (see Supplementary Table 1). Nine additional dogs were tested but excluded due to lack of motivation (4), experimental error (3), or owner interference (2). All dogs were pets whose owners volunteered for participation by entering their dogs' information in an online database. Subjects were required to show no aggressive tendencies, be up to date on all their vaccinations, and be older than 6 months of age. Before participation, all dogs visited the center at least once before testing to become familiar with the center.

Dingo subjects

We tested 13 genetically pure dingoes (9 males; $M_{age} = 4.54$, $SD_{Age} = 3.38$; see Supplementary Table 1) at the Dingo Discovery Centre in Victoria, Australia (for a description of this population; see Smith & Litchfield, 2013). Two additional dingoes were tested but were excluded due to a lack of motivation. To participate, dingoes were required to leave their living quarters and walk on a leash to our testing area in a large outdoor area nearby. All dingoes spent 2 weeks prior to testing getting acclimated to the experimenter through proximity and feeding.

Apparatus and testing setup

We used a single (15.25 cm × 15.25 cm × 12.7 cm height) acrylic puzzle for both the opaque and transparent trials. (See Figure 1.) The puzzle was constructed with clear sides and a red translucent lid. The red lid extended 1.25 cm past the side of the puzzle and was designed so that it could flip up along acrylic hinges. We added a lever by inserting a round acrylic rod into an elliptical hole on the side of the puzzle. A plastic dog toy in the shape of a stick (diameter = 5 cm) surrounded the acrylic rod and extended 15.25 cm from the side of the puzzle. This lever could be moved forwards and backwards horizontally, but was not functionally relevant for solving the puzzle. We chose these features because previous studies have found that dogs can open lids (Marshall-Pescini, Passalacqua, Barnard & Valsecchi, 2009; Marshall-Pescini, Barnard, Branson & Valsecchi, 2013; Miklósi, Kubinyi, Topál, Gácsi, Virányi *et al.*, 2003) and move levers horizontally (Range, Heucke, Gruber, Konz, Huber *et al.*, 2009; Range & Virányi, 2014) to retrieve treats.

Subjects were tested in the presence of one experimenter (AJ or PH) and one handler (dogs: their owner, dingoes: a sanctuary staff caretaker). Dogs were tested in a large room (3.5 m × 3.15 m) at our center, and dingoes were tested in a large outdoor area at the sanctuary. Although the outdoor area used with dingoes was larger than the room used with dogs, a leash (approximately 2.5 m long) restricted subjects of both species to the same travelable area (see Figure 2). During testing, the handler sat in a chair and held the subject's leash until instructed to release the subject by the experimenter. For dogs, the leash was clipped to a built-in hook in the wall, and for dingoes the leash was held by the handler. In both testing locations, the puzzle was placed 1 m away from the subject, and oriented such that the lid and lever were equally accessible (see Figure 1). To ensure that the puzzle remained in the

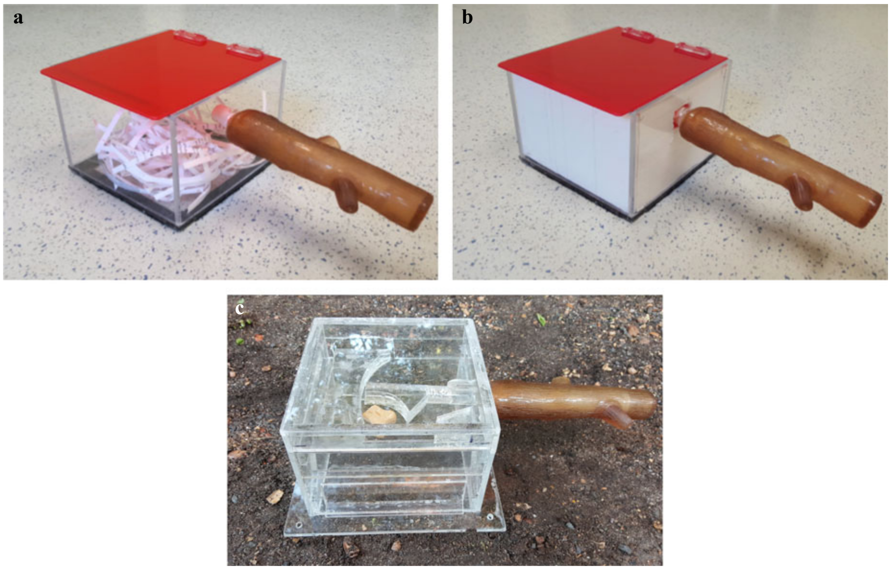

Figure 1 *Puzzles used in Experiments 1–3 (a: transparent puzzle used in Experiments 1 and 2; b: opaque puzzle used in Experiment 1; c: relevant lever puzzle used in Experiment 3). For puzzles a and b, the lever was functionally irrelevant, but for puzzle c, the lever was necessary for retrieving the treat.*

same orientation across trials and was not flipped over by subjects, we secured the puzzle to the ground, either using a rubber bathmat (for dogs tested indoors) or tent pegs (for dingoes tested outside).

On opaque puzzle trials, a white insert (foam core surrounded by white duct tape) was placed inside the puzzle. This insert covered all four sides of the puzzle, obscuring visual access to the inside of the puzzle. If subjects overimitate the experimenter, they should copy the irrelevant lever use regardless of whether the puzzle is transparent or opaque (see Horner & Whiten, 2005). In all test trials, the puzzle was filled with shredded paper to block visual access to the treat (in line with previous research, e.g. Horner & Whiten, 2005). Treats were either 1 cm^3 cubes of Natural Balance Beef sausage (for dogs) or 2 cm diameter discs of cooked chicken sausage (for dingoes). However, in cases in which subjects were not motivated by these treats (one dingo) or were allergic to the ingredients in the treats (seven dogs), we used alternative treats of the same size provided by their owners.

Design and procedure

All subjects participated in one warm-up phase, followed by two testing phases. In the *warm-up phase*, subjects retrieved treats from several easily accessible locations, including the inside of our puzzle. The goal of this warm-up phase was to ensure that subjects were motivated to retrieve treats and were unafraid of the puzzle. In each of the two *testing phases*, subjects received two ostensive demonstration trials in which they witnessed an experimenter ostensively demonstrate how to solve the puzzle using one irrelevant action and one relevant action. The transparent and opaque puzzle trials were grouped such that each phase consisted of either two transparent trials or two opaque trials. The order of these phases was counterbalanced such that half of subjects received the transparent phase first and half received the opaque phase first. If subjects overimitate the experimenter, then they should continue to copy the irrelevant lever use across *both* testing phases, regardless of whether they receive the transparent or opaque puzzle first (see Horner & Whiten, 2005). Regardless of order, each subject received a break (approximately 20 minutes) between the two testing phases. During this break subjects participated in unrelated studies, for which they received no more than four treats.

Warm-up trials. Subjects were warmed up across four trials in which the experimenter placed a treat (1) on a plate, (2) in an empty bucket, (3) in a bucket with paper shredding, and (4) inside the puzzle (which had already been opened out of the subject's view). Dingoes also participated in four additional warm-up trials prior to the experiment, which were necessary for experiments conducted during the break between testing phases. If the subject hesitated to retrieve the treat during any of these warm-up trials, both the handler and the experimenter encouraged the dog. If the dog still did not obtain

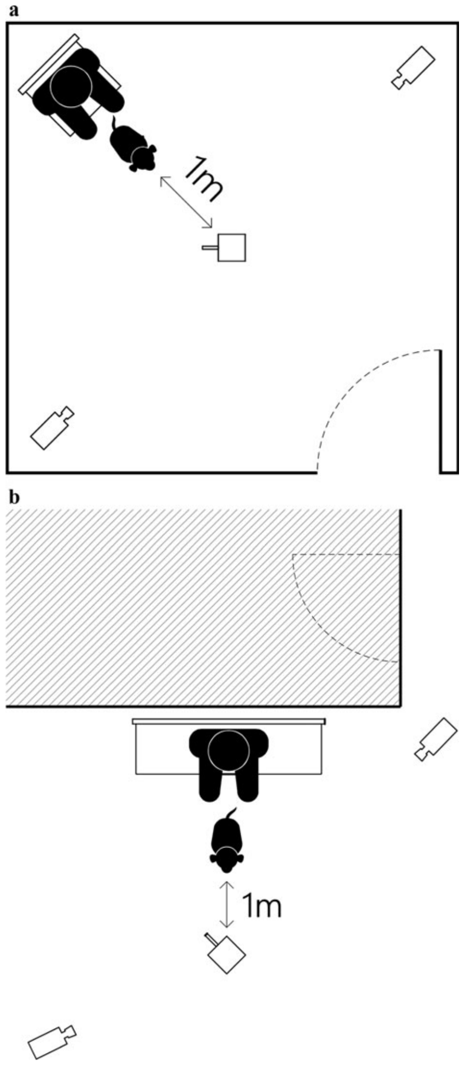

Figure 2 *Experimental setup for dogs in Experiments 1 and 2 (Figure a) and for dingoes in Experiments 1 and 3 (Figure b). For both populations, the puzzle was 1 meter away from the subject, and the study session was filmed from two different camera angles. The dogs (Figure a) were tested in a room with their owner, and the dingoes (Figure b) were tested outside. After the demonstration, the experimenter would leave the room in the case of dogs (Figure a) and go into a shed behind the testing area in the case of dingoes (Figure b).*

the treat, the experimenter repeated the trial. Four dogs and two dingoes that required more than two repetitions to obtain the treat were excluded.

Test trials. After completing the warm-up trials, the experimenter left the testing area and returned with paper shredding. This paper shredding was placed inside the puzzle, along with a treat, out of the subject's view. The experimenter then provided instructions to the handler. The handler was instructed to keep her eyes closed during the demonstration and to release the dog when she heard the door closing. In the case of dogs, the door closed when the experimenter left the room, and in the case of dingoes, the door closed when the experimenter went into a nearby storage area and closed the door. For both species, the handler was instructed to remain seated and encourage the subject to search for the treat if the subject lost interest. Subjects had 1 minute to solve the puzzle (i.e. lift the lid and get the treat), after which the trial was terminated. As in Horner and Whiten (2005), the trial was terminated if the subject solved the puzzle before the time limit.

After providing the handler with instructions, the experimenter first crouched near the puzzle, called the subject's name in a high-pitched, ostensive voice and established eye contact, saying, 'Look!' Then, the experimenter demonstrated how to open the puzzle (see Figure 3). Each demonstration had two parts: an *irrelevant action* (moving the lever) and a *relevant action* (opening the lid). After opening the lid, the experimenter removed the treat and showed it to the subject before returning it to the puzzle and closing the lid. Subjects who overimitate the actions of an experimenter should perform both the relevant *and* irrelevant actions before retrieving the treat. In contrast, subjects who do not overimitate should ignore the irrelevant action as they gain experience with the puzzle (see Horner & Whiten, 2005). In line with Horner and Whiten (2005), the experimenter provided the full demonstration sequence three times in the first trial of each phase, and only once in the second trial of each phase. After completing the demonstration phase, the experimenter asked the handler to open her eyes and left the testing area. Note that it was crucial that the experimenter was not present while the subject interacted with the puzzle because we wanted our experiment to be similar to tests with human children (e.g. Horner & Whiten, 2005), and we wanted to ensure that subjects did not simply follow the experimenter's demonstration as a command (e.g. Kupán, Miklósi, Gergely & Topál, 2011; Topál *et al*., 2009).

In between testing phases, the experimenter either removed the opaque siding of the puzzle or put the opaque siding inside, depending on the order in which the subject received the opaque phase and the transparent phase. Phase two began with one warm-up in which the subject retrieved the treat from the puzzle, which had already been opened by the experimenter out of sight. No subjects needed to be excluded on the basis of this warm-up.

It is worth noting that Horner and Whiten (2005) used a considerably more complex procedure in their studies with chimpanzees and children, including a five-element sequence that incorporated some two-action procedures

Figure 3 *The demonstration presented by the experimenter in Experiments 1 (top row) and 2 (bottom row). First, the experimenter ostensively cued the subject (1), then moved the lever (2) and lifted the lid (3) to show the subject the treat (4).*

(i.e. actions that can be performed in two different ways, such as pulling a bolt versus pushing a bolt). However, Horner and Whiten (2005) only coded one relevant action (i.e. inserting a tool in the front of the box) and one irrelevant action (i.e. inserting a tool in the top of the box) in their analyses on overimitation, and these actions were performed in the same way by the demonstrator for all subjects. Given that dogs have considerably less dexterity than chimpanzees and children, their range of actions is more limited. Thus, in order to keep our puzzle with dogs as simple as possible, we included only the actions we would need to analyze for overimitation (i.e. one relevant action and one irrelevant action). That said, some of the additional actions included in Horner and Whiten (2005), particularly the two-action procedures, are useful for establishing whether subjects are imitating the actions of an experimenter per se, or acquiring the behaviors due to other social/non-social learning processes (e.g. individual learning, stimulus enhancement, etc.; Dawson & Foss, 1965; Galef, 1988; Whiten & Ham, 1992). Rather than address this issue by making a more complex sequence of actions with two-action procedures, we conduct a no demonstration control with a new set of dogs in Experiment 2.

Coding and analyses

Solve outcome, latency to solve, and lever use were each fully coded both by the second author (PH) and an additional coder (RK) who was blind to hypothesis. Solve outcome was defined as whether the subject lifted the puzzle's lid high enough to obtain the treat, solve latency was defined as the amount of time it took the subject to solve the puzzle after the moment of release, and lever use was defined as whether the subject moved the lever via direct contact at any point before solving the puzzle. All trials were analyzed for lever use regardless of whether the subject solved the puzzle or not. Thus, it was possible for subjects to (1) use the lever without solving the puzzle, (2) use the lever *and* solve the puzzle, or (3) solve the puzzle without using the lever. To see how these patterns were distributed across species and trial, see Supplemental Figure 1. However, it is important to note that since the trial was terminated after the subject solved the puzzle (as in Horner & Whiten, 2005), subjects could only use the lever if they did so before solving the puzzle.

One trial was excluded from analysis for puzzle error (the dog flipped the entire puzzle over) and three for experimenter error (the experimenter inadvertently stopped these trials several seconds early). Reliability was high for each of the outcome variables (r = 98% for solve outcome, r = 98% for latency to solve, r = 90% for lever use). For trials in which there was a discrepancy between the coders (solve outcome: n = 2 trials; lever use: n = 10 trials), a third coder (AR) who was blind to hypothesis recoded the discrepant trials. In these rare cases of discrepancy, we replaced PH's codes with AR's codes. Latency to solve was only included for trials on which the subject solved the puzzle.

Statistical analyses were conducted using R statistical software (version 3.2.1, R Foundation for Statistical Computing, Vienna, Austria). Both solve outcome and lever use were analyzed using generalized linear mixed models (GLMMs) with a binary response term (for solve outcome: solved = 1 and did not solve = 0; for lever use: used lever = 1 and did not use lever = 0). Solve latency was log transformed and analyzed using linear mixed models (LMMs) as the transformed response variable had a normal error distribution. Predictors of interest were species (dog or dingo), puzzle type (transparent or opaque), and trial number. To control for repeated measures, subject identity was included as a random effect. All mixed models were run using R package 'lme4' (Bates, Maechler & Bolker, 2012).

In mixed model analyses, we first examined a null model, which included only subject identity. We then compared the null models with full models that included all predictor variables and their interactions. Model comparisons were conducted with likelihood ratio tests.

Results

Our model for irrelevant lever use revealed that subjects' lever use was predicted by trial (LRT: $\chi^2 = 10.35$, $p = .001$) and marginally predicted species (LRT: $\chi^2 = 3.08$, $p = .079$; see Supplementary Table 2 for all model output). No other factors or interactions were significant predictors (LRT: *ps* > .28). As shown in Figure 4 (see also Supplementary Figure 1), subjects in both species used the lever less frequently across trials, suggesting that they learned that the lever was irrelevant across trials. However, the dingoes used the lever less frequently than dogs did overall (42% of trials, $SE = 7\%$, compared to 59%, $SE = 4\%$; see also Supplementary Figure 2), suggesting that dingoes were more likely to ignore the irrelevant lever.

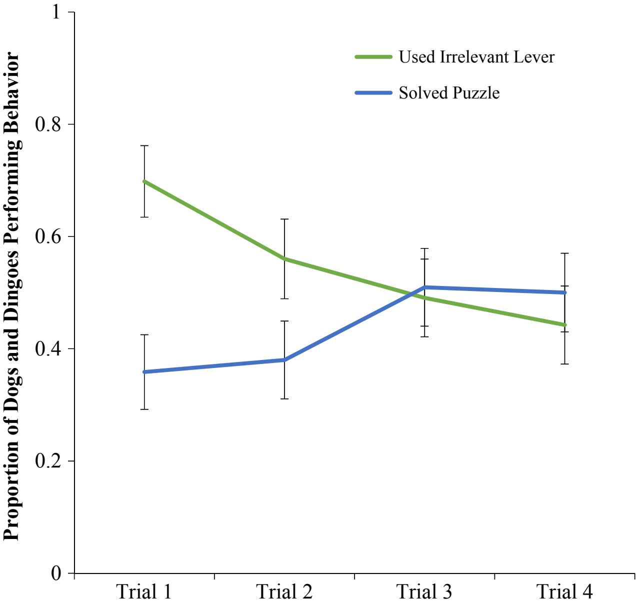

Figure 4 *Proportion of dogs and dingoes (combined) that used the irrelevant lever and solved the puzzle (i.e. lifted the lid) across trials in Experiment 1. Error bars indicate standard error.*

Our model for solve outcome revealed that subjects' tendency to solve the puzzle was predicted by trial (LRT: $\chi^2 = 9.44$, $p = .002$) and marginally predicted by an interaction between species and puzzle type (LRT: $\chi^2 = 3.29$, $p = .070$). No other factors or interactions were significant predictors (LRT: *ps* > .52). As shown in Supplementary Figure 4, subjects from both species solved the puzzle more frequently across trials. When considered in conjunction with subjects' decreased lever use (also shown in Figure 4), these results suggest that subjects learned which actions were relevant for solving the puzzle as they gained experience across trials. Importantly, this provides evidence *against* overimitation, as overimitating subjects should continue to perform irrelevant actions even as they learn how to solve the puzzle (see Horner & Whiten, 2005). The interaction between species and transparency for solve outcome is a bit more unexpected (see Supplementary Figure 3). Although dogs were uninfluenced by the transparency of the puzzle, dingoes solved the puzzle less often when it was transparent than when it was opaque. Though somewhat surprising, these results line up with prior research comparing wolves and dogs on a task designed to measure inhibitory control (i.e. the 'cylinder task'; Marshall-Pescini, Virányi & Range, 2015). In this task, animals are presented with a cylindrical tube that had a treat hidden inside. On some trials, animals were given a transparent tube – allowing subjects direct visual access to the treat – but on others, they were given an opaque tube – obscuring subjects' visual access to the treat. As in our task, dogs performed equally well on both types of tubes, but wolves performed worse when the tube is transparent (Marshall-Pescini *et al.*, 2015). Although it is not fully clear what is driving these findings, our results with dogs and dingoes are strikingly similar to those of dogs and wolves.

Our model for solve latency revealed that subjects' latency to solve the puzzle was predicted by trial (LRT: $\chi^2 = 11.84$, $p < .001$) and species (LRT: $\chi^2 = 5.78$, $P = .009$). No other factors or interactions were significant predictors (LRT: *ps* > .20). Subjects from both species solved the puzzle more quickly across trials. This further suggests that dogs and dingoes were learning how to solve the puzzle across trials, rather than overimitating the experimenter's actions. As for the main effect of species, dogs solved the puzzle more quickly overall than dingoes. (See Supplementary Figure 4.) Given that species did not interact with any other factors for solve latency, this effect of species likely reflects general differences in subject motivation or willingness to approach the puzzle across the two species.

Discussion

Both dogs and dingoes not only solved the puzzle more quickly and more frequently across trials in Experiment 1, but also used the lever less frequently across trials. These results suggest that subjects were learning both which action was necessary for solving the puzzle (i.e. lifting the lid) and which action was irrelevant (i.e. moving the lever). Importantly, however, this pattern of performance also suggests that neither dogs nor dingoes were overimitating. Unlike children in Horner and Whiten (2005), who continued to copy the irrelevant action across repeated trials, dogs and dingoes in our study used the irrelevant action less often as they gained experience with the puzzle. These findings suggest that both species were learning how to solve the puzzle through individual experience, rather than overimitating the actions of the demonstrator.

This pattern of results suggests that overimitation may be a unique feature of human social learning. Although dogs' sensitivity to human ostensive cues parallels that of human children in many ways (e.g. Hare & Tomasello, 2005; Miklósi *et al*., 1998; Téglás *et al*., 2012), we find that they do not overimitate the actions of an ostensive demonstrator in the same way as human children (e.g. Horner & Whiten, 2005; Lyons *et al*., 2011; Nielsen & Tomaselli, 2010). In addition, even though dogs show more human-like sensitivity to ostensive cues than dingoes, we failed to find any species differences in the rate of overimitation; indeed, neither species showed a tendency to continue copying the irrelevant action over trials.

In addition to finding evidence against overimitation in both species, we also saw several cross-species differences between dogs and dingoes: (1) dogs used the irrelevant lever more often than dingoes overall; (2) dogs solved the transparent and opaque puzzles at equal rates, but dingoes solved the opaque puzzle more often than the transparent puzzle; and (3) on trials in which subjects solved the puzzle, dogs solved the puzzle more quickly than dingoes. Although some of these cross-species differences were likely due to differences in subjects' motivation to complete the task (as reflected in solve latency times) or inhibitory control (as reflected in the puzzle type by species interaction for solve outcome), there is one species difference that warrants further investigation: dogs used the irrelevant lever marginally more often than dingoes overall. This overall difference in irrelevant lever use may indicate that dogs' initial lever use was influenced by ostensive demonstration, even though they learned to filter out the irrelevant lever across trials. Indeed, an inspection of Supplementary Figures 1 and 2 reveals that approximately 75% of dogs used the lever on trial 1, compared to 54% of dingoes.

Although it is clear that dogs were learning to filter out the irrelevant lever across trials, rather than overimitating the actions of the experimenter, it is unclear whether their initial lever use was a product of individual exploration or social learning (e.g. imitation, stimulus enhancement, etc.). To begin to disambiguate these possibilities, we conducted a no demonstration control with a new set of dogs in Experiment 2. If dogs' initial lever use in Experiment 1 was driven by social learning factors, then dogs in Experiment 2 should use the lever less often in the absence of experimenter demonstration. In contrast, if dogs' initial lever use in Experiment 1 was driven by individual exploration, then dogs in Experiment 2 should use the lever at equal rates, even in the absence of experimenter demonstration.

Experiment 2

Experiment 2 examines the possibility that dogs in Experiment 1 used the irrelevant lever more often than dingoes because they were – at least initially – more prone to copying the experimenter's actions (due to imitation, stimulus enhancement, etc.). Previous work has shown that dogs are more sensitive than dingoes to human ostensive cues in other contexts (Smith & Litchfield, 2010a), and thus it seems possible that this tendency to focus on human cues may have caused dogs to copy the experimenter's actions more often in Experiment 1 than dingoes did. Although both species used the irrelevant lever less frequently in Experiment 1 across trials, dogs' initial attempts on the puzzle may have been anchored by the experimenter's ostensive demonstration, leading them to have a higher baseline lever use. This increased baseline would not provide evidence for overimitation (since overimitating subjects would continue to use the irrelevant lever even after experience with the puzzle), but it would suggest that the difference in irrelevant lever use between the two species was driven by dogs' enhanced sensitivity to the ostensive demonstration. We tested this possibility in Experiment 2 by blocking dogs' visual access to the experimenter's demonstration. If dogs in Experiment 1 used the irrelevant lever more often than dingoes because they were generally more likely to copy the experimenter's actions, then we should expect dogs to use the irrelevant lever less often when they cannot witness the demonstration.

Method

Subjects

We tested a new group of 20 dogs (8 males; M_{age} = 4.80; SD_{Age} = 2.12; see Supplementary Table 1) that had never seen the puzzle before. Two additional dogs were tested but excluded due to owner interference (1) or experimental error (1). All dogs were recruited from the same database described in Experiment 1; however, none of the dogs tested in Experiment 1 were tested in Experiment 2. As in Experiment 1, we used 1 cm^3 cubes of Natural Balance beef sausage for all but two dogs that received alternative treats of the same size because they were allergic to the sausage.

Design and procedure

The method of Experiment 2 was identical to that of Experiment 1 with two exceptions. First, and most importantly, dogs never witnessed the experimenter demonstrate how to solve the puzzle. The experimenter performed the same actions as in Experiment 1, but performed them behind an opaque screen so that subjects could not see which actions the experimenter was performing (see Figure 3). However, to keep the visual access to treats consistent across studies, the experimenter raised the treat above the screen after retrieving the treat from the puzzle. This close matching between Experiments 1 and 2 allowed us to control for any differences in motivation that might occur across studies due to social factors (e.g. eye contact, ostensive speech, etc.) or other motivating factors (e.g. noises coming from the puzzle, seeing treats associated with the puzzle, etc.).

Second, dogs were only presented with the transparent puzzle. Our goal in using only the transparent puzzle was to allow dogs visual access to all of the relevant features of the puzzle to ensure that they had the best chance of discovering how to solve the puzzle on their own. Thus, dogs in Experiment 2 only participated in one phase of testing, which consisted of two consecutive transparent puzzle trials.

Coding and analyses

As in Experiment 1, solve outcome, latency to solve, and lever use were each fully coded by the second author (PH) and an additional coder (RK) who was blind to hypothesis. The same coding criteria used in Experiment 1 were used in Experiment 2. Reliability was high for each of the outcome variables (r = 100% for solve outcome, r = 99% for latency to solve, r = 100% for lever use). In all analyses, PH's codes were used. Latency to solve was only included for trials on which the subject solved the puzzle.

Statistical analyses were conducted in the same way as in Experiment 1. Solve latency was log transformed and analyzed using linear mixed models (LMMs), as the transformed response variable had a normal error distribution. In these analyses, we included the full data set from Experiment 2, and the transparent puzzle trials from Experiment 1 (only for those dogs who received the transparent trials first). This allowed us to directly compare demonstration trials (from Experiment 1) to no demonstration trials (in Experiment 2) in order to determine whether dogs who witnessed the demonstration (in Experiment 1) approached the task differently from dogs who did not witness the demonstration (in Experiment 2). The between-subjects predictor of interest was experiment (Experiment 1: demonstration or Experiment 2: no demonstration) and the within-subjects predictor of interest was trial number (trial 1 or 2). To control for repeated measures, subject identity was included as a random effect.

Results

Our full models for irrelevant lever use and solve outcome were no better at predicting lever use or solve outcome than our null models (*p*s > .26). Thus, we did not find any evidence to suggest that dogs used the irrelevant lever or solved the puzzle more often when receiving demonstration (in Experiment 1) than when exploring the puzzle on their own (in Experiment 2). Our model for solve latency revealed that trial was a significant predictor of dogs' latency to solve the puzzle (LRT: χ^2 = 14.68, p < .001; see Supplementary Table 2 for all model output), indicating that dogs solved the puzzle more quickly across trials (trial 1: M = 24.84s, SE = 3.45 s; trial 2: M = 10.57 s, SE = 2.14 s). No other factors or interactions were significant predictors for latency to solve the puzzle (LRT: *ps* > .23).

Discussion

The results of Experiment 2 rule out one potential explanation for the species difference in lever use observed in Experiment 1. Specifically, the results of Experiment 2 suggest that dogs did not initially use the irrelevant lever more often than dingoes because they were more prone to copy the experimenter's actions. Given that dogs were equally likely to use the irrelevant lever, regardless of whether they witnessed a demonstration (in Experiment 1) or not (in Experiment 2), social learning differences alone cannot explain why dogs used the lever more often than dingoes in Experiment 1.

Experiment 3

Although the results of Experiments 1 and 2 provide consistent evidence that dogs fail to overimitate, the question of why dingoes used the lever less often than dogs in Experiment 1 is still open. Experiment 3 examines two alternative explanations for this species difference in lever use. One possibility is that dingoes used the irrelevant lever less often than dogs in Experiment 1 because they were better at filtering out the irrelevant action when exploring the puzzle. In line with this possibility, previous work has suggested that dingoes are better independent problem solvers than dogs. Not only are dingoes more likely to employ independent problem-solving strategies than dogs (e.g. persisting on a task, rather than seeking help from a human; Smith & Litchfield, 2013; cf. Miklósi *et al.*, 2003), but they are also able to solve challenging problems more quickly (e.g. in a detour task in which they must travel around a V-shaped fence to get a treat; Smith & Litchfield, 2010b; cf. Pongrácz, Miklósi, Vida & Csányi, 2005). More generally, several studies comparing dogs and wolves suggest that dogs may have become *worse* at independently solving problems across domestication (Frank, 1980, 2011; Frank & Frank 1982, 1985; Hiestand, 2011; Marshall-Pescini *et al.*, 2015; for a review, see Bensky, Gosling & Sinn, 2013). Thus, it is possible that dingoes in Experiment 1 used the lever less often than dogs because they were better at filtering out the irrelevant action when exploring the puzzle. Having the ability to determine which action was relevant would allow dingoes to go straight to the most direct solution. However, it is also possible that dingoes used the lever less often than dogs in Experiment 1 because they were unwilling or afraid to manipulate the lever at a more general level. No work to date has shown that dingoes can manipulate levers, so it may be that dingoes avoided the lever in Experiment 1 because they are generally averse to levers.

To distinguish between these two alternatives, we tested dingoes on a similar puzzle in Experiment 3, but this time the lever was *relevant*. If dingoes were sensitive to whether the lever was relevant or not in Experiment 1, then they should use the lever more often when it is relevant in Experiment 3. This pattern of results would provide (1) some initial evidence that dingoes used the lever less often than dogs in Experiment 1 because they were better at filtering out the irrelevant action when exploring the puzzle, and (2) further evidence against overimitation in dingoes. If dingoes can use the lever when it is relevant in Experiment 3, then this would demonstrate that dingoes theoretically had the ability to overimitate the experimenter's irrelevant lever use in Experiment 1 if they had been inclined to do so. In contrast, if dingoes in Experiment 1 used the lever less than dogs because they were simply averse to the lever, then they should also fail to use the lever in Experiment 3.

Method

Subjects

We tested 14 dingoes (9 males; $M_{age} = 3.79$; $SD_{Age} = 2.46$; see Supplementary Table 1) from the same population as in Experiment 1.

Apparatus and testing setup

In Experiment 3, we tested dingoes on a new puzzle for which the lever was relevant for opening the puzzle. In this new puzzle, the treat rested on a ledge in the top portion of the puzzle, and the lid was sealed to prevent dingoes from getting the treat out from the top. Instead, dingoes had to move the lever to push the treat off the ledge and through a slot on the front of the puzzle. To ensure that dingoes could see that the lever was relevant, we used an entirely transparent puzzle (see Figure 1c). Moreover, to ensure that the treat did not get stuck in the apparatus, we used a hard dog biscuit cut into square pieces (2.5 cm long and 1.25 cm thick). Given that these biscuits are more filling and take longer to eat, we continued to use chicken sausage in the warm-up trials to ensure that dingoes did not get satiated.

Dingoes were tested by the same female experimenter (AJ) as in Experiment 1, but a different sanctuary staff member acted as the handler. Dingoes were tested in the same location and setup as in Experiment 1 (see Figure 2), but the puzzle was oriented so that the treat slot was directly facing the subject to ensure that they saw the treat come out of the puzzle during the demonstrations (see Figure 1c).

Design and procedure

As in Experiment 1, dingoes participated in one warm-up phase, followed by two testing phases. In one of the testing phases, the experimenter ostensively demonstrated how to solve the puzzle, and in the other, she blocked her demonstration from the dingo’s view. The goal of these two phases was to explore whether dingoes’ performance on the puzzle was influenced by experimenter demonstration. The order of the two testing phases was counterbalanced such that half of subjects received the demonstration trial first and half received the no demonstration trials first. Regardless of order, each subject received a break (approximately 10 minutes) between the two testing phases. During this break subjects participated in other, unrelated studies, for which they received no more than four treats.

Warm-up trials. The warm-up trials were the same as in Experiment 1.

Test phases. At the beginning of each test phase, the experimenter placed a treat on the ground where it would land when pushed out of the puzzle. This was done in line with Experiments 1 and 2 to ensure that dingoes were willing to approach the puzzle and were aware that there was a treat. After this warm-up, the experimenter baited the puzzle out of the dingo’s view and began the demonstration phase. At the beginning of each demonstration, the experimenter ostensively called the dingo’s name and established eye contact in the same way as Experiment 1. Then, the experimenter moved the lever such that it pushed the treat out of the puzzle and showed the dingo the treat. In one testing phase the entire demonstration was done in full view, and in the other testing phase the portion of the demonstration where the experimenter moved the lever was done out of the dingo’s view. To block the lever movement from the dingo’s view, the experimenter turned her back to the dingo and used her body to block the dingo’s visual access to the lever movement (see Figure 5). For each test trial this demonstration was repeated twice. The experimenter left the area while the dingo interacted with the puzzle.

Coding and analyses

As in Experiments 1 and 2, solve outcome, latency to solve, and lever use were each fully coded by the second author (PH) and an additional coder (RK) who was blind to hypothesis. Solve outcome was defined as whether the treat fell out of the puzzle and onto the ground, solve latency was defined as the amount of time between the moment of release and the moment the treat hit the ground, and lever use was defined as whether the subject moved the lever via direct contact at any point before solving the puzzle. Reliability was high for each of these outcome variables (r = 92% for solve outcome, r = 98% for latency to solve, r = 90% for lever use). For trials in which there was a discrepancy between the coders (solve outcome: n = 1 trial; lever use: n = 1 trial), a third coder (AR) who was blind to hypothesis recoded the discrepant trials. In these rare cases of discrepancy, we replaced PH’s codes with AR’s codes. Latency to solve was only included in our analyses for trials on which the subject solved the puzzle.

Statistical analyses were conducted in the same way as Experiments 1 and 2. Solve latency was log transformed and analyzed using linear mixed models (LMMs), as the transformed response variable had a normal error

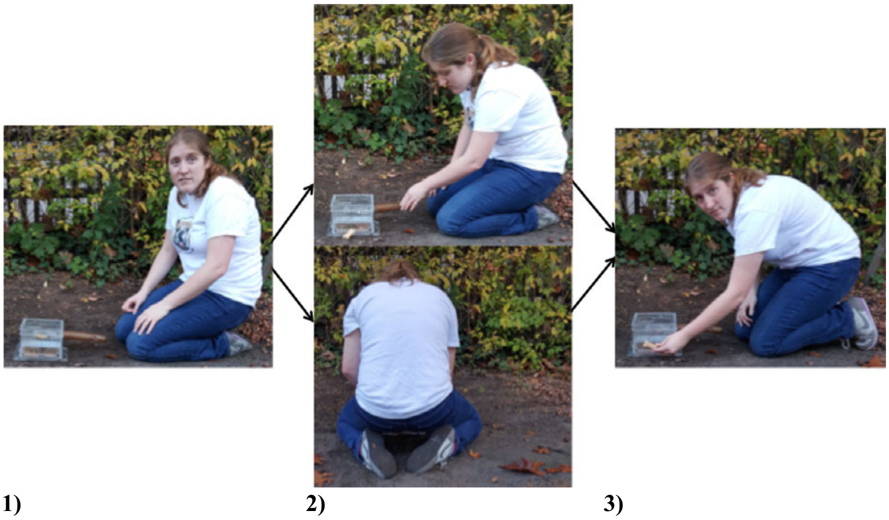

Figure 5 *The demonstration presented by the experimenter in Experiment 3 for the demonstration (top row) and no demonstration trials (bottom row). First, the experimenter ostensively cued the subject (1), then she moved the lever, either in view of the subject or out of view of the subject (2), and showed the treat (3).*

distribution. In these analyses, we included the full data set from Experiment 3, and the transparent puzzle trials with dingoes from Experiment 1. This allowed us to directly compare trials in which the lever was relevant (in Experiment 3) to those in which the lever was irrelevant (from Experiment 1) in order to see whether dingoes used the lever more often when it was relevant. Predictors of interest were experiment (lever relevant: Experiment 3 and lever irrelevant: Experiment 1) and trial number (trial 1 or 2).

Results

Preliminary results revealed that condition (i.e. demonstration or no demonstration) made no difference in Experiment 3 (ps > .17), so the results were collapsed across condition for the remainder of analyses. In addition, since our full model for solve latency was no better at predicting solve latency than our null model (LRT: $\chi^2 = 2.63$, $p = .451$), we did not pursue further analyses with this predictor variable.

Our model for irrelevant lever use revealed that experiment was a significant predictor of dingoes' lever use (LRT: $\chi^2 = 5.03$, $p = .025$; see Supplementary Table 2 for all model output). No other factors or interactions were significant predictors (LRT: ps > .41). Dingoes used the lever more often in Experiment 3 when it was relevant than in Experiment 1 when it was irrelevant (79% of trials, $SE = 8\%$, compared to 46%, $SE = 10\%$). These results suggest that dingoes did not ignore the lever more often than dogs in Experiment 1 because they were afraid of it. Instead, these results suggest that dingoes were attuned to whether the lever was relevant or not, using the lever more frequently when it was relevant.

Our model for solve outcome revealed that the interaction between experiment and trial number was a significant predictor of dingoes' solve outcome (LRT: $\chi^2 = 17.46$, $p < .001$). When the lever was relevant for solving the transparent puzzle (i.e. in Experiment 3), dingoes solved the puzzle more often on trial 2 than trial 1. In contrast, when the lid was relevant for solving the transparent puzzle (i.e. in Experiment 1), dingoes solved the puzzle less often in trial 2 than trial 1 (see Supplementary Figure 5). These results suggest that dingoes may have found it easier or more intuitive to solve the transparent puzzle using the lever than using the lid.

Discussion

Dingoes used the lever significantly more often in Experiment 3 when it was relevant (79% of trials) than in Experiment 1 when it was irrelevant (46% of trials). This provides clear evidence that dingoes in Experiment 1 did not use the lever less often than dogs because they were simply averse to it. This finding not only sheds light on the species difference in lever use we saw in Experiment 1, but it also provides more conclusive evidence against overimitation in dingoes. Given that dingoes demonstrated their ability to move the lever when it was relevant in Experiment 3, it seems that they simply were not inclined to overimitate the experimenter's irrelevant lever use in Experiment 1.

These results also provide some initial evidence that dingoes may be better than dogs at determining which aspects of a puzzle are relevant. When the lever was irrelevant in Experiment 1, dingoes only used it around half the time, but when the lever was relevant in Experiment 3, they used the lever at high rates, similar to dogs. These results build on previous work showing that dingoes tend to approach problems more independently (Smith & Litchfield, 2013) and efficiently (Smith & Litchfield, 2010b) than dogs. However, future work should investigate this question further. For instance, on a transparent puzzle with multiple levers, some relevant and some irrelevant, would dingoes be able to determine *which* levers were relevant? Future work investigating this question, among others, has the potential to shed light on the hypothesis that domestication not only improved the social problem-solving abilities of dogs, but also impaired their individual problem-solving abilities (Bensky *et al.*, 2013; Frank 1980, 2011; Frank & Frank 1982, 1985; Hiestand, 2011; Marshall-Pescini *et al.*, 2015).

General discussion

Across three experiments, our findings provide clear evidence against overimitation in both dogs and dingoes. Both dogs and dingoes reduced their irrelevant lever use across trials in Experiment 1, suggesting that both species were filtering out the irrelevant action as they gained experience with the puzzle (like chimpanzees in Horner & Whiten, 2005). This finding is in stark contrast to the performance of human children who continue to overimitate the experimenter's irrelevant actions even after repeated trials (e.g. Horner & Whiten, 2005).

Follow-up studies provide further evidence against overimitation in both species and also shed light on the species difference we observed in Experiment 1. Although both species in Experiment 1 showed a decrease in lever use across trials, dogs showed high rates of lever use on initial trials, especially in comparison to dingoes (75% of dogs used the lever on trial 1, compared to 54% of dingoes). One possible reason for this initially high lever use was that dogs were generally more likely than dingoes to copy the experimenter's actions. However, Experiment 2 showed that this was not the case, as dogs used the irrelevant lever equally often, regardless of whether they witnessed the experimenter's actions or not. Yet another possible reason that dogs used the irrelevant lever more often than dingoes in Experiment 1 was that dingoes were simply unwilling to move the lever. However, Experiment 3 showed that this was not the case either, since dingoes used the lever more often when it was relevant than when it was irrelevant. Together, these findings demonstrate that both species' behavior was characterized by individual exploration rather than overimitation.

The absence of overimitation in dogs, in particular, provides additional evidence that overimitation may be a unique aspect of human social learning. Even though dogs demonstrate striking similarities to human children in other domains of social learning (e.g. Hare & Tomasello, 2005; Miklósi *et al.*, 1998; Téglás *et al.*, 2012), we found that this species fails to faithfully copy the irrelevant actions of a human demonstrator. In this way, our results show that merely possessing more basic features of human social learning – such as an attention to social agents and ostensive cues – is not sufficient to support overimitation. Accordingly, our results go beyond prior work in primates (Horner & Whiten, 2005) to suggest that the human-like tendency to prioritize ostensive information over individual exploration may be unique to our species.

One perhaps surprising aspect of our findings stems from the fact that dogs showed similar performance in Experiments 1 and 2, even though they were unable to see any of the demonstrator's actions in Experiment 2. One possible reason for these results is the fact that the experimenter provided ostensive cues in both Experiments 1 and 2. It is possible, then, that the presence of these ostensive cues served to enhance dogs' motivation to explore the puzzle. However, it's still worth noting that dogs did not do better when they were able to see the experimenter's complete actions than when they merely received ostensive cues alone. This raises the surprising possibility that – at least when ostensive cues are present – dogs fail to learn anything about how to solve the puzzle from the actions of the human demonstrator. While this interpretation does not affect our main conclusion – that dogs fail to show evidence of *overimitation* – it raises the possibility that dogs' ability to learn causal structure from human actions may be limited. In fact, the evidence for dogs' ability to learn through direct imitation is mixed; while there is ample evidence that dogs imitate the actions of human experimenters in behavioral copying tasks (e.g. Fugazza & Miklósi, 2014; Fugazza, Pogány & Miklósi, 2016), there is less clear evidence that dogs directly imitate human actions in instrumental learning tasks (e.g. Kubinyi, Topál, Miklósi & Csányi, 2003; Mersmann, Tomasello, Call, Kaminski & Taborsky, 2011; Miller, Rayburn-Reeves & Zentall, 2009; Pongrácz, Bánhegyi & Miklósi, 2012). Future studies could therefore profit from further examining how and when dogs learn from human actions in problem solving contexts.

Taken together, the current studies reveal that overimitation may be a unique aspect of human social learning. Even domesticated dogs – a species that demonstrates striking similarities to human children in other domains of social learning (e.g. Hare & Tomasello, 2005) – do not overimitate the actions of an ostensive demonstrator. Rather than faithfully copying the irrelevant actions of an experimenter trial after trial (as human children do; Horner & Whiten, 2005), dogs learn to filter out irrelevant actions. Although this filtering process makes dogs' performance relatively more efficient in our task, it also prevents the faithful transmission of information. Our findings suggest that overimitation, and perhaps other learning mechanisms that promote the faithful transmission of information (e.g. Bonawitz *et al.*, 2011; Király *et al.*, 2013), may be a crucial mechanism supporting human-unique cultural transmission of knowledge.

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Figure S1. Proportion of dogs (Figure a) and dingoes (Figure b) using the lever without solving the puzzle (leftmost bar), using the lever and solving the puzzle (middle bar), solving the puzzle without using the lever (rightmost bar) on each trial.

Figure S2. Proportion of dogs and dingoes that used the irrelevant lever across trials in Experiment 1. Error bars indicate standard error.

Figure S3. Proportion of dogs and dingoes solving the puzzle on opaque and transparent puzzle trials in Experiment 1. Error bars indicate standard error.

Figure S4. Latency to solve the puzzle (in seconds) for dogs and dingoes across trials in Experiment 1. Error bars indicate standard error.

Figure S5. Proportion of dingoes solving the puzzle across trials 1 and 2 in Experiments 1 and 3. Error bars indicate standard error.

Table S1. List of animals, indicating species, owner-reported breed, sex (Male/Female), age (in years), and the experiment(s) in which each subject's data was included. Dogs listed as "Experiments 1 & 2" only participated in Experiment 1, but their data was used as a comparison for dogs that participated in Experiment 2. Dingoes listed as "Experiments 1 & 3" participated in both experiments, with an 8-month break in between experiments.

Table S2. Estimate (±SE) of fixed effects in generalized linear and linear mixed models predicting subjects' lever use, solve outcome, and solve latency in Experiments 1-3. Baselines were set as follows: species = dingo; experiment = Experiment 1; box style = opaque. Table also shows goodness-of-fit statistics.