Learning & Behavior (2023) 51:127–130
https://doi.org/10.3758/s13420-022-00544-2

COMMENTARY

Rearing condition and willingness to approach a stranger explain differences in point following performance in wolves and dogs

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Accepted: 9 September 2022 / Published online: 12 October 2022

Abstract

The relative importance of adaptation and individual ontogenetic experience in dogs' high levels of behavioral compatibility with humans has been a topic of intense scientific attention over the past two decades. Salomons et al. *Current Biology, 31,* 3137–3144, (2021) recently presented a particularly rich data set of observations on both wolf and dog puppies that has the potential to contribute substantially to this debate. In their study subjecting wolf and dog puppies to batteries of tests, including the ability to follow human pointing gestures, Salomons et al. (2021) reported that dogs, but not wolves, have a specialized innate capacity for cooperation with humans. However, upon reanalyzing this data set, we reach a different conclusion—namely, that when controlling adequately for various environmental factors, wolves and dogs perform similarly in their cooperation with humans.

The claim that dogs may have unique abilities to recognize the implications of human intentional gestures is not new. In 2002, Hare et al. proposed the domestication hypothesis, which stated that "dog's social-communicative skills with humans were acquired during the process of domestication" (p. 1636). This hypothesis was largely based on findings suggesting that dogs outperform wolves in following human pointing gestures and that dogs' performance in following pointing did not vary with age. In 2008, Riedel et al. added to the domestication hypothesis by reporting that dog puppies as young as six weeks would follow human pointing gestures, thereby supporting the narrative that, as a result of domestication, dogs possess a unique, innate capability to interpret human social-communicative cues.

However, several findings call into question the robustness of the claim that dogs have unique abilities in interpreting human gestures as a consequence of domestication. First, methodological concerns have been raised in relation to both studies cited above. Udell et al. (2008) identified that the wolves in Hare et al. (2002) were tested under different conditions from the dogs. Further, Udell et al. (2008; see also reanalysis of original results in Udell & Wynne, 2010) demonstrated that, when tested under identical conditions, wolves may even outperform dogs in following human pointing gestures. Second, when testing puppies ranging from nine to 21 weeks of age, Dorey et al. (2010) found a significant developmental trajectory in the ability to interpret human pointing gestures. Third, various studies have demonstrated that, if socialized to humans at an early age, a wide range of nondomesticated and domesticated species—including wolves (*Canis lupus*; Udell et al., 2008), megachiropteran bats (*Pteropus*; Hall et al., 2011), African elephants (*Loxodonta africana*; Smet & Byrne 2013), pigs (*Sus scrofa*; Nawroth et al., 2014), and goats (*Capra hircus*; Nawroth et al., 2020)—can follow human social-communicative cues as given in pointing tests. It has even recently been revealed that hand-raised wolf puppies as young as eight weeks, without any prior training, will spontaneously engage in cooperation with a stranger based on human intentional gestures (Hansen Wheat & Temrin, 2020), thereby indicating that such capabilities were present in the ancestral populations to domestic dogs. Together, these studies make a strong case that phylogeny alone is not enough to account for any animal's ability to follow human social cues. Rather, only when phylogeny is considered in conjunction with ontogeny can an individual's success or failure in following human pointing gestures be properly interpreted (Udell et al., 2010).

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Salomons et al. (2021) have now reinvigorated this debate by testing 44 dog and 37 wolf puppies on a variety of tasks relating to their comprehension of communicative gestures. They concluded that their data offered "support [for] the predictions of the domestication hypothesis [that d]og but not wolf puppies are attracted to humans and show early emerging skills for reading human gestures, even though the wolf puppies received more intense human socialization" (p. 3141). They further concluded that "dog puppies are specialized for cooperative communication with humans" (p. 3142).

Salomons et al. (2021) exposed their dog and wolf puppies once each to a battery of tests. The most relevant tests for this commentary are the ability to follow a human pointing gesture and the willingness to approach an unfamiliar human (classified by the authors as temperament). Point-following addresses a central issue in the ongoing debate over the relative importance of phylogeny and ontogeny in dogs' adaptation to human-dominated environments. Willingness to approach an unfamiliar human enables a test of the proposition that any advantage dogs might show in point following could be due to a hypersocial phenotype (vonHoldt et al., 2017)—in other words, it could be due to a social rather than a cognitive advantage over wolves.

Clearly, in order to rigorously test for the impact of domestication on any behavioral differences between dogs and wolves, it is essential to adequately control for environmental effects. Because the availability of hand-reared wolves is a limiting factor, studies of this kind are inherently characterized by small sample sizes, and eliminating environmental bias therefore becomes even more important. In Salomons et al. (2021), wolf and dog puppies received varying degrees of socialization and environmental conditions prior to testing, and, importantly, conditions for the two subspecies were not matched. Specifically, wolf puppies were hand-raised, but received varying levels of socialization, with 24% of the puppies being in contact with their human caregivers to a far lesser extent: "Wolf puppies remained with littermates but received 12 h (24%) or 24 h (76%) human care from 10 to 11 days after birth" (p. 3138). In contrast, "all dog puppies remained with their mothers until weaning, around 6 weeks of age, and with their littermates until ~8 weeks of age. During this time, they mainly socialized with humans during short routine caretaking tasks. Around 8 weeks of age, puppies were then sent to live with human families" (p. 3138). That is, dogs, but not wolves, were moved to human homes. Importantly, 18 out of 31 of the dog puppies were tested in the pointing test at >9 weeks of age after they had been sent to live with human families. This environmental change strongly altered their exposure to people and was not matched in the wolf puppies. Furthermore, in the pointing test dogs were tested up to 17 weeks of age, whereas none of the wolves were older than 13 weeks when tested. Because age and degree of human exposure is inherently confounded in the dog population in the data set provided in Salomons et al. (2021), but the human exposure is not controlled for in the original analyses, we consequently reanalyzed Salomons et al.'s data separating the dogs tested after they had moved to human homes from the wolves and younger dogs tested while they lived with their mothers. We find that dog puppies only significantly outperformed wolf puppies after they have been moved to human households (Fig. 1a). Furthermore, the apparently superior performance of dogs compared to wolves may be a consequence of their heightened tendency to approach strange humans.

Since testing of the dog puppies' willingness to approach people and follow their pointing gestures was conducted for some dogs before, and for some after, they were moved to human homes, the possible effect of this environmental change on point following needs to be controlled for. Thus, to test whether rearing conditions or species identity better accounts for the differences in human-gesture-following performance between wolf and dog puppies, we re-ran the comparison of performance on the gesture-following task, dividing the dogs into two groups: those still living with their litter and thus had less human contact when tested (i.e., those dogs ≤9 weeks old), and those placed with human families (>9 weeks old). Since only five wolves were tested before the age of 10 weeks, we grouped all wolves together for our analyses. This reanalysis (binomial generalized linear mixed model [GLMM]) showed that the wolves differed from older ($b_{\text{older dogs - wolves}} = 1.05$, $SE = 0.334$, $p = .0046$), but not younger dogs ($b_{\text{young dogs - wolves}} = 0.42$, $SE = 0.338$, $p = .42$), thus contradicting Salomons et al.'s (2021) claim that dogs outperform extensively socialized wolves in a cooperative communication task with humans "despite having far less human exposure than the wolf puppies" (p. 3141; Fig. 1a).

Salomons et al. (2021) also reported that dog puppies were around 30-fold more willing to approach a strange human than wolf puppies of comparable ages. Since gesture-following in an experimental context necessarily also involves approaching a stranger, this large difference in willingness to approach could account for the difference in gesture following between the two species. However, Salomons et al. (2021) stated that after the effect of species was entered in the statistical model to account for gesture following, approach performance was not a significant covariate (we note that species is also not significant in this model). We redid this analysis, using a corrected dataset provided by the authors. We found that the single best model (binomial GLMM, AIC: 404.25) to explain the gesture following data has only one fixed effect, the willingness to approach a stranger (Fig. 1b). This is indistinguishable from a model that only has species as a fixed effect (AIC: 404.75), and a model that has both willingness to approach a stranger and species as fixed effects (AIC: 405.55). Thus, previously

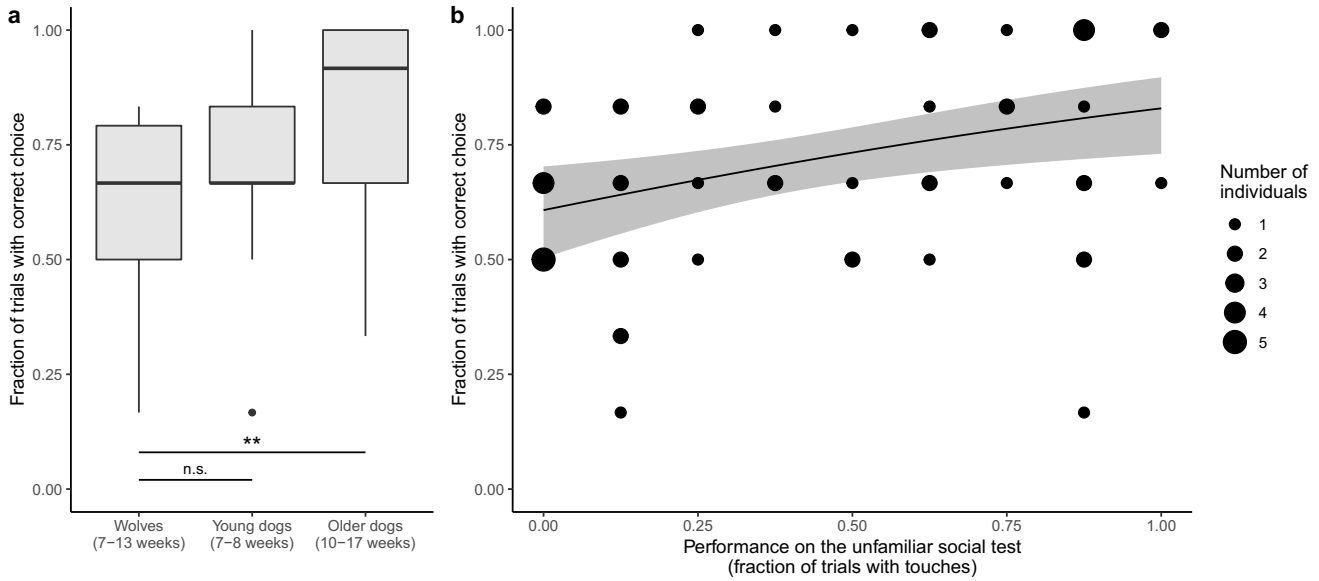

Fig. 1 **a** Proportion of trials in which an animal followed a human pointing gesture, comparing wolves with young dogs (7–8 weeks, living with their mother and littermates) and older dogs (10–17 weeks, living with human families). Only the difference: wolves—older dogs (10–17 weeks) is significant. **b** Proportion of trials in which an animal followed a human pointing gesture is related to the willingness to approach an unfamiliar human. The line represents the model fit from a generalized linear mixed model, with the grey area showing the 95% confidence interval ($b_{slope} = 1.14$, $SE = 0.42$, $p = 0.006$)

established differences in willingness to approach a stranger (termed temperament in Salomons et al., 2021) are sufficient to explain differences in test performance, and there is no need to attribute superior communicative skills to dogs.

It is well-established that hand-raised wolves, even when extensively socialized, do not generalize this socialization to strangers and remain fearful of unfamiliar humans (Hansen Wheat et al., 2022; Klinghammer & Goodman, 1987; Zimen, 1987). Indeed, Salomons et al. (2021) report that "we attempted to test a total of 49 wolf puppies and were able to collect data from 37. We were unable to collect any data with the other 12 wolf puppies because they were too nervous around unfamiliar humans (i.e., experimenters), even though they had been heavily exposed to humans" (p. e3). Even when successfully tested, hand-raised and socialized wolves that have been exposed to strangers under controlled conditions during their upbringing still express significantly elevated stress and fear responses towards strangers in test situations (Hansen Wheat et al., 2022). On the other hand, prior studies have demonstrated that dogs have a greatly enhanced propensity to approach and interact with people (Udell, 2015; vonHoldt et al., 2017) and express little, or no stress or fear behaviors around strangers in test situations (Hansen Wheat et al., 2022). The use of unfamiliar humans as experimenters in the pointing tests in Salomons et al. (2021) thus highlights a potential bias favoring the dogs' performance. The emotional engagement towards people and lack of fear around strangers is likely a key factor in dogs' success in human-dominated environments (Wynne, 2021), and is sufficient to explain the differences between species reported in Salomons et al. (2021) without the need to evoke specialized cognitive adaptations.

In sum, Salomons et al. (2021) make an appreciable contribution to the literature by offering a substantial data set which can be used to test various behaviors in wolves and dogs. While we agree that wolves and dogs differ behaviorally in important ways, we do not believe that these data demonstrate that dogs have an evolved capacity to follow human gestures at an earlier age than wolves. Rather, when rearing contexts and willingness to approach strange humans are taken into account, dog and wolf puppies perform very similarly. We further disagree that rearing condition and willingness to approach a stranger can be ruled out as significant determinants of cognitive performance in these subspecies. We therefore emphasize the importance of designing studies in which wolves and dogs are reared and tested under identical conditions, in order to adequately disentangle domestication effects on behavior.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.3758/s13420-022-00544-2.

Acknowledgments We thank Salomons et al. (2021) for providing us with a corrected data set for this reanalysis and for being very

forthcoming in answering our questions. We also thank the editor and three anonymous reviewers for helpful comments on an earlier draft.

Open practices statement All data and material are available in the original paper by Salomons et al. (2021). The R script used for reanalysis for this paper is provided as supplemental material.

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