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repertoire was also preserved during the early stages of antigen-induced proliferation (2, 15). Notably, one of these studies showed that, whereas early during the response TCR diversity was still highly reflective of the naïve repertoire, at the peak of the immune response TCR diversity was skewed toward higher-affinity clones (15). In line with this, recent data have shown that lower-affinity interactions do result in T cell activation *in vivo*, but these responses undergo premature contraction (16). Together with our data, these studies support a model in which the immune system maximizes its potential to react toward invading pathogens by allowing a near-complete recruitment of high-affinity T cells, independent of the conditions of infection (fig. S8). Although this may lead to concomitant activation of lower-affinity cells, the abortive expansion of these clones

forms a filter against their further participation (15, 16).

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Materials and Methods

Figs. S1 to S8

Table S1

References

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Differential Sensitivity to Human Communication in Dogs, Wolves, and Human Infants

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Ten-month-old infants persistently search for a hidden object at its initial hiding place even after observing it being hidden at another location. Recent evidence suggests that communicative cues from the experimenter contribute to the emergence of this perseverative search error. We replicated these results with dogs (*Canis familiaris*), who also commit more search errors in ostensive-communicative (in 75% of the total trials) than in noncommunicative (39%) or nonsocial (17%) hiding contexts. However, comparative investigations suggest that communicative signals serve different functions for dogs and infants, whereas human-reared wolves (*Canis lupus*) do not show doglike context-dependent differences of search errors. We propose that shared sensitivity to human communicative signals stems from convergent social evolution of the *Homo* and the *Canis* genera.

Convergent findings indicate that human infants pay special attention to various nonverbal communicative signals directed at them [such as eye contact, gaze-shifts, and pointing (1–5)]. This skill may provide the basis for preverbal infants' early emerging competence to engage in triadic communicative interactions with others (6–8). Recent evidence suggests that signals conveying manifestation of intention to communicate induce a learning attitude in infants, which enables them to acquire knowledge from observation of adults' demonstrations (9). In brief, infants are biased to assume that the information manifested by the adult can be generalized to other situations. We have shown (10) that this bias can account for young infants' perseverative search error (11) in the A-not-B object search task. In our study with 10-month-olds (10),

participants observed a human demonstrator repeatedly hiding (and then allowing the infant to retrieve) an object at one of two potential hiding locations: four times at location A and then 3 times at location B, either in a communicative context or without any social cues. In the communicative context, we replicated the standard finding of a strong tendency to search (erroneously) for the object at its previous hiding location (A) during the B trials. This perseverative bias has been substantially reduced, however, when no communicative cues accompanied the object-hiding actions. The robust association between the ostensive-communicative context of the hiding actions and the perseverative search error supports the "natural pedagogy" hypothesis (9), according to which the perseverative error is in large part due to a pragmatic misinterpretation of the experimenter's hiding actions as constituting a communicative teaching demonstration rather than being just a hide-and-search interactive game.

Humans are not the only species that show special sensitivity to human ostensive-referential signals. Recent results indicate a functionally sim-

ilar sensitivity and preference in dogs for certain nonverbal cues of human ostensive and referential communication (12). Unlike great apes (13), dogs exhibit some understanding of human referential intentions expressed in communicative gestures, such as pointing, as shown by their success in solving the so-called object choice tasks (14, 15).

To investigate the functional nature of dogs' sensitivity to ostensive-referential cues in a comparative manner, we used the A-not-B object search paradigm that had been used to demonstrate the influence of communicative cues on human infants' perseverative search errors (10). In the first experiment, we tested whether communicative signals would have a notable effect on dogs' tendency to perseverate in a search task. Three groups of adult dogs (12 in each) participated in a task involving searching for an object that they saw being hidden behind one of two identical screens. In the first phase, the dog was allowed to fetch a toy repeatedly from behind the screen where it was hidden (four A trials). In the test phase, the experimenter repeatedly hid the toy object behind the alternative B screen (three B trials). Each dog participated in one of the following three conditions:

In the social-communicative (SocCom) condition, the hider attracted the dog's attention by ostensive addressing signals ("[dog's name] + Watch!"). Then she picked a rubber ball from the floor while establishing eye contact and addressing the dog ("Watch!") and walked to screen A with the toy in her hand being constantly visible to the dog. As she placed the ball behind screen A, she displayed gaze shifts looking back and forth between the hiding location and the dog (A trials). During the B trials, she passed behind screen A with the ball visibly held in her hand and moved on to screen B, placing the object behind it. After showing her empty hands to the dog, the subject was allowed to choose which screen to go behind to retrieve the toy.

In the noncommunicative (NonCom) condition, the experimenter performed the same object-hiding manipulations as in the SocCom condition with her back turned toward the dog. Thus, neither

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eye contact nor facial cues were displayed while the experimenter held the object in her hand clearly visible to the subject. In addition, she did not talk to the dog but attracted the dogs' attention by clapping her hands and making a conspicuous noise with the toy.

In the nonsocial (NonSoc) condition, the experimenter remained still next to the dog while another experimenter, who was invisible to the dog, made the ball move behind the screens by pulling a transparent string (invisible to the dog) to which it was attached. No communicative signals were displayed toward the dogs.

Dogs' search responses were categorized as correct (selecting the baited location scored 1), ambiguous (score of 0.5) or incorrect (selecting the nonbaited location scored 0) (16). Dogs fetched the object reliably during the A trials in all three conditions (mean percentage of correct choices were 94% in SocCom and 98% in NonCom and NonSoc groups). However, during the B trials we found striking context-dependent differences in the number of dogs committing the A-not-B error (table S1), and a one-way analysis of variance (ANOVA) on the response scores also showed highly significant differences ($F_{2,33} = 10.436$, $P < 0.001$). Post-hoc pairwise comparisons (Tukey–Kramer test) revealed that dogs in the SocCom condition searched at the baited screen (B) less often than those in the NonCom condition ($P < 0.05$) or in the NonSoc condition ($P < 0.001$). In addition, dogs in the SocCom condition displayed a search bias toward the empty (A) screen because they performed well below the success rate expected by random search ($t_{11} = 3.576$, $P = 0.004$). In contrast, dogs in the NonSoc condition were significantly more successful than chance during the B trials ($t_{11} = 3.867$, $P = 0.003$) (Fig. 1).

These results clearly indicate that, similarly to human infants (10), the communicative context induced in dogs a tendency to perseveratively (and erroneously) search for a hidden object at a previously repeatedly baited location (A) even when they observed the object being hidden at a different location (B). This error, however, has been eliminated when the hiding events were not accompanied by communicative signals. Thus, contrary to previous accounts (17, 18), the perseverative search tendency found in both species cannot be explained as stemming from an inability to locate hidden objects or to inhibit a search response at a previously rewarded location (A). Moreover, if the social-communicative signals simply had a distracting effect, one would expect random search and not an explicit bias to the empty location (A), which we found in the SocCom condition. Therefore, we propose that search error in dogs and infants may be indicative of their shared social competence that involves preparedness for learning from humans through communication.

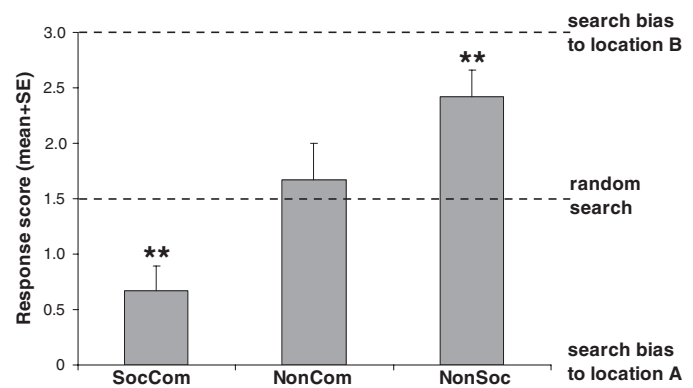
One intriguing question is whether dogs' sensitivity to human communicative signals is the evolutionary consequence of domestication. It is

increasingly assumed that, during their evolution in an anthropogenic environment (and paralleled by the divergence from the wolf), dogs have become selected to display increased sociality (19, 20), cooperability (21), and communicability (22, 23). This preparedness enables the dog to become sensitized to human communicative cues (12) if the individual is properly socialized to humans (24).

This account predicts that only dogs but not human-reared wolves would respond differentially to communicative versus nonsocial hiding contexts in a search task. We tested this prediction in experiment 2, in which we compared the performance of a different group of naive pet dogs ($n = 12$) to that of 10 extensively socialized, hand-reared wolves [for more details on socialization of wolves, see (19–21)] in the SocCom and NonSoc conditions. The procedure was similar to that which was used in experiment 1 except that the bait was a piece of food in a small plastic cup, and dogs and wolves participated in both the communicative and the nonsocial hiding conditions (within-subject design) (16).

Dogs and wolves selected the baited location reliably during the A trials in both conditions (mean percentage of correct choices were 95% and 88% for wolves and 94% and 92% for dogs in the SocCom and NonSoc conditions, respectively). However, the performance during the B trials differed markedly between species and contexts (Fig. 2 and table S2). A two-way ANOVA on the response scores for hiding context and species as factors revealed more correct responses in the NonSoc than in the SocCom condition ($F_{1,20} = 15.003$, $P = 0.001$), more correct responses by the wolves than by the dogs ($F_{1,20} = 4.675$, $P = 0.043$), and a significant interaction between these factors ($F_{1,20} = 13.027$, $P = 0.002$). This interaction was due to the fact that, similar to experiment 1, dogs selected the baited location on B trials less frequently in the SocCom condition ($t_{11} = 5.043$, $P < 0.001$), whereas no such effect was found in wolves ($t_9 = 0.208$, $P = 0.840$).

Fig. 1. Scores of correct responses (mean + SE) in the B trials as a function of the hiding context. The dogs ($n = 12$ for each condition) received four A trials followed by three B trials. The SocCom condition was that the human experimenter repeatedly hid a toy object behind screen A and then behind screen B using ostensive-communicative signals. The NonCom condition was that the experimenter performed the same object-hiding manipulations as in the SocCom but without ostensive-communicative signals. The NonSoc condition was that the experimenter remained still next to the dog while the object moved behind the screens without any perceivable human manipulation. $**P < 0.01$, one-sample t test, in comparison with the success rate expected by random search (0.5 times three B trials).



The robust A-not-B error in the communicative hiding context in dogs, which was absent in extensively socialized wolves, represents a striking interspecies difference, which could be best explained by assuming that selective processes in the course of domestication of dogs led to sensitivity to human ostensive and referential signals (21, 25). However, the fact that dogs, like human infants, commit the perseverative search error when (and only when) the repeated hiding events are presented in a communicative context does not necessarily imply that this effect is mediated by the activation of the same type of interpretive bias that the ostensive cues were hypothesized to trigger in human infants (9, 10). Evidence suggests that dogs' response to human communication is primarily driven by a motivation to satisfy ostensibly cued human imperatives even when the human's action demonstration conveys an inefficient or mistaken solution to goal approach (26), food choice (27), or object choice (28). These findings, along with the results presented in experiments 1 and 2, raise the question of whether human ostensive and referential signals serve the same communicative functions in dogs that they do in human infants. If human communication is functionally interpreted as imperatives by dogs, it might be tied to the situational context, whereas infants, whose primary motivation is to learn from ostensive demonstrations, would attempt to generalize the communicative content to new situations.

Because one of the crucial components of the A-not-B task is the identity of the person they interact with, in experiment 3 we investigated how dogs and 10-month-old human infants react if, after the A trials, the identity of the hiding person is changed and a new experimenter continues the hiding during the B trials in the SocCom condition. If the ostensive hiding action is interpreted as an imperative order associated with a specific "instructor," we could expect the perseverative search bias to diminish during the B trials, which would represent a different imperative to act on because it is given by a different

person. In contrast, if the ostensive hiding action is interpreted (or misinterpreted) as conveying some generalizable information about the type of object hidden or the function of the hiding location (9) that is not related to the identity of the particular demonstrator, switching the experimenter should not reduce the tendency to commit A-not-B error.

For naïve infants ($n = 12$), we applied the same procedure used by Topál *et al.* (10) in the ostensive-communicative hiding context, and the procedure for a group of naïve dogs ($n = 12$) was similar to that which was used in the SocCom condition of experiment 1. However, after the experimenter had repeatedly hidden the toy in the A trials, she left and another familiar person continued to demonstrate the hiding actions during the B trials (16). During the A trials, dogs fetched the object reliably from behind screen A (mean percentage of correct choices was 98%), showing a performance similar to that found in the SocCom condition of experiment 1 (94%). Infants also searched for the toy correctly in the majority of A trials (82%), replicating the success rate (88%) reported by Topál *et al.* (10) in the same ostensive-communicative hiding context. However, infants and dogs responded to the new experimenter in the B trials differentially (Fig. 3 and table S3). Infants displayed a perseverative search bias to reach toward location A, and their success rate was significantly below chance level ($t_{11} = 2.932, P = 0.014$). In contrast, dogs did not show a significant search bias toward the empty A location ($t_{11} = 0.103, P = 0.920$), suggesting

that they did not generalize to the new situation in the B trials what they had learned during the A trials.

These results show the differential influence of changing a basic stimulus parameter (the identity of experimenter) on dogs' and human infants' tendency to commit the perseverative search error. The finding that, as compared with the SocCom condition in Experiment 1, dogs did not perseverate after switching the experimenter is consistent with the hypothesis that dogs anchor communication to the specific situation and especially to the specific communicator who is ostensively addressing it to them. At the same time, and unlike in the NonSoc condition of Experiment 1, dogs were not always successful in finding the object hidden by the new experimenter. Their random search pattern indicates that the unchanged aspects of the situation (such as same object, same room, and same screen) carried sufficient cues of the previous context to confuse them and suggests that it is the overall similarity of the test situation to the training situation that determines whether dogs extend the scope of the learned imperative to the new context. Crucially, the human who ostensively communicates toward the dog forms an indispensable element of the context. For infants, however, it does not seem to matter who performs the ostensive hiding demonstration, and they readily generalize their erroneously learned object-finding action to the new-person context. This result provides further validation for the natural pedagogy hypothesis (9) as an explanatory

framework of the Piagetian A-not-B error in infants (10).

In summary, these results show an apparent behavioral analogy between human infants and dogs. In both species, one of the most important causal factors leading to perseverative search errors is the communicative ostensive-referential context. The seemingly mistaken response, called A-not-B error, is not (or at least not only) due to insufficient attentional and motor functioning but paradoxically may be indicative of sophisticated social competence in both dogs and human children. However, the precise function of the cognitive-interpretive mechanisms elicited by communication differs between dogs and humans. For infants, ostensive and referential communicative signals serve a primarily epistemic function by indicating an opportunity to acquire culturally shared knowledge about referent kinds (9). Dogs' sensitivity to these signals is parasitic on human communication by exploiting them for a different function: to give orders to perform some specific action at a referentially indicated particular location in the presence of (and for) a specific person presenting the imperative.

The lack of a similar sensitivity to human ostensive-communicative signals in extensively socialized wolves supports the view that this is an evolutionary novel skill in the *Canis* genus, providing a typical case for convergent social evolution (as the consequence of domestication) between man and dog. In addition to human-ape comparisons, the study of the behavioral convergence between dogs and humans (29) offers a comprehensive framework for understanding the evolutionary emergence of human social behavior.

Fig. 2. Comparison of dogs and wolves in the A-not-B task. Scores of correct responses (mean + SE) in the B trials as a function of the hiding context. ### indicates $P < 0.0001$ in a paired t test.

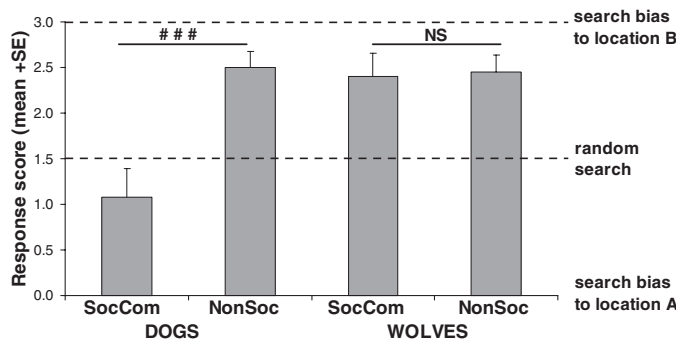
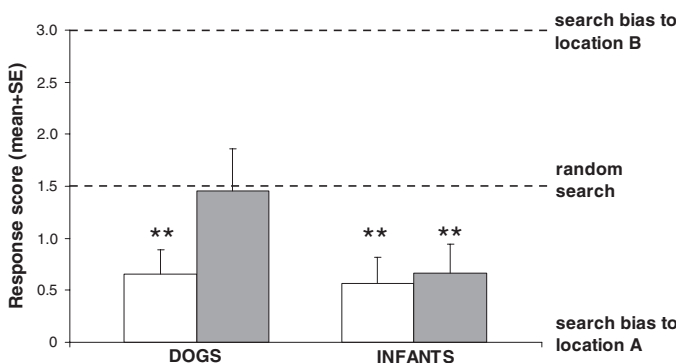


Fig. 3. Dogs and 10-month-old infants respond differentially to the switch of the experimenter in the ostensive communicative hiding context. Left (white) columns indicate correct responses (mean + SE) with the same experimenter [data from experiment 1 (dogs) and from Topál *et al.* 2008 (infants)] in B tests. Right (gray) columns indicate the performance during the B trials in the experimenter-switch condition (experiment 3). ** $P < 0.02$, one-sample t test, in comparison with the success rate expected by random search (0.5 times three B trials).



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Positive Interactions Promote Public Cooperation

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The public goods game is the classic laboratory paradigm for studying collective action problems. Each participant chooses how much to contribute to a common pool that returns benefits to all participants equally. The ideal outcome occurs if everybody contributes the maximum amount, but the self-interested strategy is not to contribute anything. Most previous studies have found punishment to be more effective than reward for maintaining cooperation in public goods games. The typical design of these studies, however, represses future consequences for today's actions. In an experimental setting, we compare public goods games followed by punishment, reward, or both in the setting of truly repeated games, in which player identities persist from round to round. We show that reward is as effective as punishment for maintaining public cooperation and leads to higher total earnings. Moreover, when both options are available, reward leads to increased contributions and payoff, whereas punishment has no effect on contributions and leads to lower payoff. We conclude that reward outperforms punishment in repeated public goods games and that human cooperation in such repeated settings is best supported by positive interactions with others.

The prisoners' dilemma illustrates the tension between private and common interest. Two people can choose between cooperation and defection. If both cooperate, they get more than if both defect, but if one person defects while the other cooperates, the defector gets the highest payoff and the cooperator gets the lowest. In a one-time prisoners' dilemma game, it is therefore in each person's interest to defect. However, if pairs of people play the game repeatedly, it is no longer obvious that defection promotes the defector's private interest, because today's defection may lead the opponent to defect in the future. Under suitable conditions, such direct reciprocity can support cooperation (1–6). Even if people play different opponents in every round, my opponent tomorrow may condition her choice on my play today. Such indirect reciprocity can also sustain cooperation (7, 8). Direct and indirect reciprocity represent fundamental aspects of human interaction, both in evolutionary history and in

modern life: Repetition is often possible, and reputation is usually at stake.

The public goods game is a prisoners' dilemma with more than two people (9). Typically, there is a choice of how much to contribute to a common pool, which then benefits all participants equally. The maximum payoff for the group is achieved if everyone contributes the full amount, but free riders increase their own payoff by withholding their contribution and still benefiting from the public pool. All of us are engaged in many public goods games, on both large and small scales. For example, reducing CO₂ emissions by driving fuel-efficient cars and minimizing waste is a global public goods game. On a more local level, public goods games include volunteering on school boards or town councils and helping to maintain the roads and fire department in your city, as well as cleaning your dishes at home and doing your share of work at the office.

It has been suggested that costly punishment can uphold cooperation in public goods games (10–12). People are willing to pay a cost for others to incur a cost. Typically, such punishment is directed toward free riders and therefore could be a deterrent for defection (13–15). One problem with punishment is that it generates a social loss by reducing both players' payoffs. This effect, however, could be small if sanctions are used rarely, such that in the long run punishment increases net payoffs by discouraging free riding (16), or if punishments are merely symbolic (17–21). Another

problem is that punishment is sometimes used by free riders against cooperators, either randomly or as an act of revenge (22–25). Moreover, the extent to which punishment is perceived as justified can greatly affect the response of those who have been punished (26). These observations question the proposal that costly punishment is an ideal force for promoting cooperation (12). More generally, the substantial literature emphasizing the beneficial effects of material and symbolic rewards and the negative effects of sanctions on interpersonal relationships (27–31) casts doubt on whether the threat of costly punishment provides the most appropriate incentive for cooperation.

In this study, we demonstrate that it is not costly punishment that is essential for maintaining cooperation in the repeated public goods game but instead the possibility of targeted interactions more generally. In the normal repeated public goods game, if one person lowers his contribution, then I cannot directly reciprocate against this person. I could also lower my contribution, but this action harms everyone in the group. Ultimately, this leads to a decline in cooperation. Therefore, we consider public goods games in which after each round there is also the possibility of targeted interactions with other individuals in the group. One such interaction is costly punishment, but another is costly rewarding, as captured by the standard prisoners' dilemma game. In this scenario, I can reward people who have contributed in the public goods game with cooperation but punish free riders with defection.

In the course of daily life, people are always involved in both public and private interactions. Opportunities exist for mutually beneficial trade, as well as harmful punishment. My behavior toward others is affected by their previous decisions, both in the private and public domain. If I resent my neighbor's gas-guzzling SUV, I could exercise costly punishment by slashing his tires. Conversely, I could be extra helpful to my other neighbor who just bought a low-emission vehicle. Punishment is destructive and carries the risk of retaliation by those who have been punished. This is particularly true in situations where, unlike in most laboratory studies, interactions are not anonymous. Without the cover of anonymity, it seems probable that people would be less inclined to punish and more likely to reward. Here, we ask whether rewards can lead to cooperation in the repeated public goods game.

A total of 192 subjects participated in our study at the Harvard Business School Computer Lab for Experimental Research (32). Subjects

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