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Dogs rapidly develop socially competent behaviour while interacting with a contingently responding self-propelled object

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The relative contribution of evolutionary and ontogenetic mechanisms to the emergence of communicative signals in social interactions is one of the central questions in social cognition. Most previously used methods utilized the presentation of a novel signal or a novel context to test effects of predisposition and/or experience. However, all share the common problem that the familiar social partners used in the test context as actors carry over a variety of contextual information from previous interactions with the subjects. In the present study we utilized a novel method for separating the familiar actor from the action. We tested whether dogs behave in a socially competent way towards an unidentified moving object (UMO) in a communicative situation after interacting with it in a different context. We found that dogs were able to find hidden food based on the approach behaviour of the UMO only if they obtained previous experience with it in a different context. In contrast no such prior experience was needed in the case of an unfamiliar human partner. These results suggest that dogs' social behaviour is flexible enough to generalize from previous communicative interactions with humans to a novel unfamiliar partner, and this inference may be based on the dogs' well-developed social competence. The rapid adjustment to the new context and continued high performance suggest that evolutionary ritualization also facilitates the recognition of potentially communicative actions.

The key question in sociocommunicative interactions is how communicative signals achieve their function, i.e. how the action of the sender becomes a signal for the receiver. It is widely accepted that two mechanisms may play a fundamental role in the emergence of communicative interactions. (1) The process of evolutionary ritualization assumes (Hinde & Tinbergen, 1958) that during evolution an executive behaviour is transformed into a communicative behaviour with signal properties if it has the potential to predictably modify the behaviour of the partner. During this process the behaviour pattern is subjected to changes making it repetitive, exaggerated and stereotyped. (2) Ontogenetic ritualization takes place if the individuals mutually shape their behaviour during repeated instances of social interactions; that is, regularly occurring behavioural actions gain communicative function (Hinde, 1970). In this case one individual performs behaviour X to which its partner reacts consistently with behaviour Y. As a consequence of many dyadic interactions the first individual comes to anticipate the other's action. Importantly, action X is not a communicative signal at the start of the process but develops into one as a result of mutual interaction and learning (Tomasello, 1996).

Several studies have focused on the relative contribution of evolutionary versus ontogenetic mechanisms controlling certain communicative signals and their species- or context-specific aspects. For example, Halina, Rossano, and Tomasello (2013) examined gestural communication of captive bonobos, *Pan paniscus*. Based on the flexibility and variability of these signals they suggested that ontogenetic ritualization is the primary underlying mechanism for the emergence of diverse signalling behaviour. In contrast, Hobaiter and Byrne (2011) argued that ape gestures are rather innate and are acquired through evolutionary ritualization even if they are often used intentionally and flexibly.

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A similar argument has emerged in relation to the comprehension of human pointing gestures in dogs, *Canis familiaris* (for reviews see Miklósi & Soproni, 2006; Udell, Dorey, & Wynne, 2009). One assumption is that dogs must learn to use human communicative signals during early ontogeny (ontogenetic ritualization); thus this ability emerges as a consequence of habitual interaction between dog and owner (Bentosela, Barrera, Jakovcevic, Elgier, & Mustaca, 2008; Udell & Wynne, 2010). The alternative but nonexclusive explanation is that during the process of domestication dogs have been selected by humans to be sensitive to specific human behavioural cues (e.g. pointing: Riedel, Buttelmann, Call, & Tomasello, 2006; gazing: Soproni, Miklósi, Topál, & Csányi, 2001; human voice: Rossano, Nitzschner, & Tomasello, 2014). The superior performance with the human pointing gesture in young dog puppies over socialized wolf puppies provides support for this latter argument (e.g. Gácsi et al., 2009).

Recent discussion has converged to the idea that both mechanisms might play a role in the emergence of such interspecific signalling (Miklósi & Topál, 2013; Udell, Ewald, Dorey, & Wynne, 2014); however, it is still an open question how the relative contribution of evolutionary and ontogenetic ritualization could be determined. Methodologically, three different approaches have been used so far: (1) deprivation of social experience (e.g. shelter dogs: Hare et al., 2010; Udell, Dorey, & Wynne, 2010); (2) demonstration of the effect of learning on the performance in a communicative interaction between dogs and humans (Elgier, Jakovcevic, Mustaca, & Bentosela, 2009; Udell, Dorey, & Wynne, 2008); (3) testing the effectiveness of (relatively) novel communicative human signals in typical dog populations (Lakatos, Soproni, Dóka, & Miklósi, 2009).

Tomasello, Call, and Gluckman (1997) proposed that observing infants' and apes' reaction to novel signals would be a feasible method to examine their understanding of communicative signals. They also argued that any genetic predisposition would lead to lesser need for learning (or experience) or rapid learning. The method of triangulation (e.g. Heyes, 1997) is useful for such investigations: (1) first, the naïve individual is exposed to a specific experience (or has to learn to discriminate) in Context 1 then (2) the individual is exposed to a novel context (Context 2) which overlaps only in specific ways with Context 1 by sharing only a small set of specific features. This method, however, is not really informative when investigating communication skills because the social partner carries over a considerable part of the contextual information from Context 1 to Context 2. For example, dogs experience human pointing gestures in everyday life (Context 1), and this experience with humans, including a possible genetic predisposition, does not allow researchers to set up an experiment (Context 2) that overlaps only specifically with Context 1 because the human is present in both contexts. Thus it is difficult to judge the relative role of evolutionary/developmental processes. The introduction of an unfamiliar communicative partner might be a solution to this problem because it has the potential to reveal subjects' ability to recognize the communicative aspects of the partner's behaviour.

In this paper we propose a new method which is based on the idea of introducing an unidentified moving object (UMO) to the experimental setting. Accordingly, (1) the subject is exposed to a particular type of social interaction in Context 1 and to a different kind in Context 2; (2) in order to reduce the potential effects of previous experience, the social agent (UMO) shares no physical attributes with either the subject (dog) or other potential social partner (human); (3) social interactions share specific features with the natural social interactions among conspecifics and/or heterospecific familiar social agents (A).

The underlying assumptions are that (1) the subject has earlier experience with A and knows that A is able to perform actions X and Y, (2) it recognizes that the UMO is performing action X in Context 1, (3) and it infers that the UMO can also perform action Y in Context 2.

In the present study dogs were presented with two different partners (Human and UMO) in four different conditions in a between-subjects design. The Interactive UMO and the Noninteractive UMO were remote-controlled cars. In the Interactive Human and Noninteractive Human conditions the partner was an unfamiliar female human (see Gergely, Petró, Topál, & Miklósi, 2013). During the familiarization phase, dogs in the Interactive UMO and Human conditions were presented with a problem situation (Context 1) in which the UMO or a human helped the dog to get an unreachable food reward (see Gergely et al., 2013; Miklósi, Polgárdi, Topál, & Csányi, 2000). In contrast, no such interaction took place in the Noninteractive conditions. Then in the test phase (Context 2) all dogs had the opportunity to find the hidden food based on the indicating ('signalling') behaviour (directional movement towards one of the two potential hiding places) of the UMO or the human partner. The differences in the familiarization phase tested for the effect of previous social experience with the Human or UMO partner on dogs' choice behaviour when observing the partner's indicating behaviour (Context 2).

METHODS

Ethical Note

Our experiment is based on noninvasive procedures for assessing dogs' behaviour. Noninvasive studies on dogs are currently allowed to be done without any special permission in Hungary by the University Institutional Animal Care and Use Committee (UIACUC, Eötvös Loránd University, Hungary) as under current law ('1998. évi XXVIII. Törvény', the Animal Protection Act) they are not considered as an animal experiment. The owners responding to our advertisement at the department's homepage (http://kutyaetologia.elte.hu) volunteered to participate.

Subjects

We recruited 82 adult pet dogs (36 females, 46 males, mean age ± SD 4.1 ± 2.4 years, from 23 different breeds and 25 mongrels) from the Family Dog database of the Department of Ethology, Eötvös Loránd University, Hungary. Dogs were randomly divided into four conditions (groups): Noninteractive Human, Noninteractive UMO, Interactive Human and Interactive UMO. We only tested dogs that could be motivated by food. Fourteen dogs lost interest (i.e. they did not make their choice in 60 s in the test trial). We also excluded eight dogs because they showed strong side bias (they always approached the same pot either on the left or on the right in all 16 trials: two dogs in the Noninteractive Human condition; two dogs in the Noninteractive UMO condition; three dogs in the Interactive Human condition; one dog in the Interactive UMO condition). However, including these dogs in the analyses does not change our conclusions (for the analysis see Appendix). After these exclusions we had 60 dogs in the four conditions: 15 in the Noninteractive Human (six males, nine females, mean age ± SD 4.70 ± 2.48 years), 15 in the Noninteractive UMO (seven males, eight females, mean age ± SD 3.57 ± 1.69 years), 15 in the Interactive Human (10 males, five females, mean age ± SD 4.20 ± 2.46 years) and 15 in the Interactive UMO condition (six males, nine females, mean age ± SD 17 ± 2.05 years). Dogs' age did not differ significantly between conditions (ANOVA: $F_{3,56} = 1.42$, $P = 0.25$). Each subject participated only in one condition.

Apparatus

Dogs were tested at the Department of Ethology, Eötvös Loránd University in a 4.5 m × 3.5 m test room. Each trial was recorded by four cameras from different angles.

During the familiarization phase in the Interactive Human and Interactive UMO conditions we used a metal wire-mesh box (61 × 46 cm and 54 cm high) with a magnet fixed inside. In these conditions we also used a plastic plate (10 cm × 10 cm) with two metal sheets on its sides. A piece of food (dry dog food) was placed on the plate during the familiarization phase in the Interactive conditions, and the plate was placed in the wire-mesh box so that the dog could get the food only with the partners' help. We covered the dogs' eyes with an occluder (102 cm × 76 cm) between test trials.

Test Partners

In the Noninteractive UMO and Interactive UMO conditions we used a remote-controlled (RC) car (32710 RTR SWITCH, 28 cm × 16 cm × 13 cm) which was equipped with a magnet on its front and a small loudspeaker under the cover. As an attention-getting cue we used a high-pitched beeping sound (3200 Hz) emitted from the loudspeaker. In the Noninteractive Human and Interactive Human conditions an unfamiliar woman played the role of the partner. In the Noninteractive Human condition she wore sunglasses and did not use any verbal or nonverbal cues during the test. She used the small loudspeaker in order to emit the same beeping sound (salient attention-getter) as the UMO. In the Interactive Human condition the human partner used verbal as well as nonverbal cues. She said 'Hi (dog's name), look!' to attract the dog's attention. The test partner's starting point was at a predetermined location (see Fig. 1).

Procedure

Pretraining phase

In the pretraining phase the dogs were made aware that the pot may contain food. The owner and the dog entered the test room and the dog was allowed to explore the room, while the experimenters provided information for the owner about the test. After this the owner sat in the chair and held the dog in front of him/herself (Fig. 1). Experimenter 1 (E1) came in with a pot and put it down. She attracted the dog's attention with a piece of food in her hand (she said: 'Hi (dog's name), look!'). She put one piece of food into the pot and the owner was told to release the dog. If the dog ate the food, the owner called the dog back. We repeated this procedure four times, then E1 left the room with the pot. The pretraining phase was exactly the same in every condition.

Familiarization phase

Noninteractive human. The unfamiliar woman entered the room and walked around for 2 min and 30 s while the owner made the dog stand facing her. Then the partner stopped at the starting point (Fig. 1).

Noninteractive UMO. E2 brought the UMO to the room, placed it at the starting point and then stood in the corner on the right side of the dog (Fig. 1). Then the UMO started to move around the room for 2 min and 30 s. During this time the owner held the dog in front of him/herself. Then the partner stopped at the starting point.

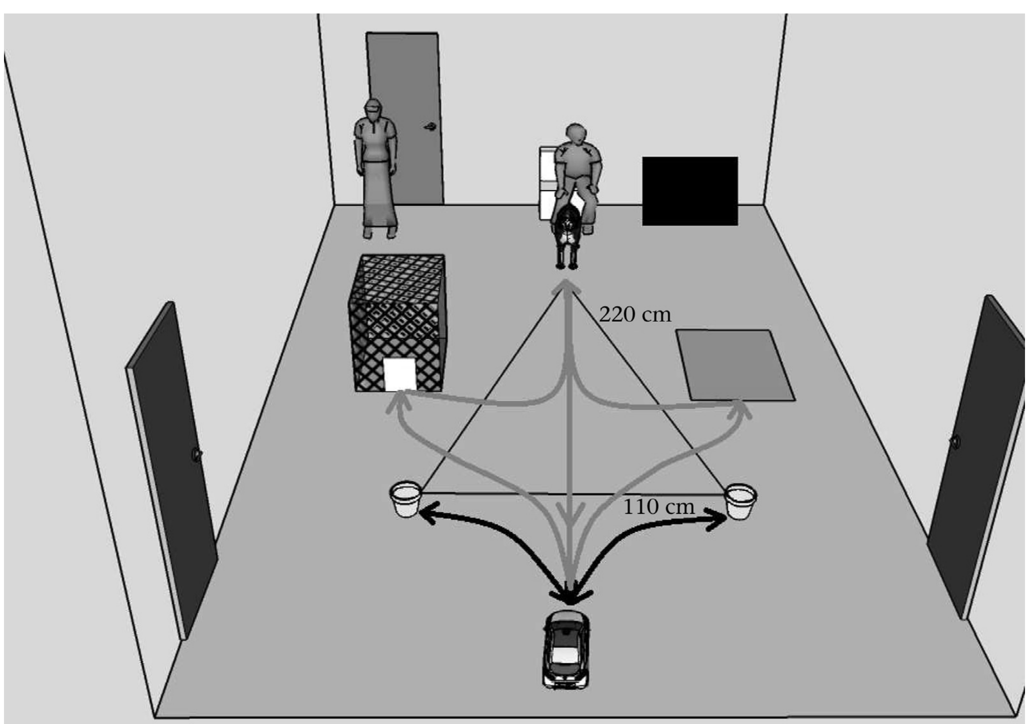

Figure 1. Experimental layout for the familiarization phase (Interactive conditions) and test phase (all conditions). The UMO's location represents the partner's (UMO or Human) starting point. For the familiarization phase the grey rectangle indicates the altered position of the box and grey lines show the paths of the partners (UMO or Human) to the box (location of the food), to the dog and back to the start point. For the test phase the triangle indicates the distances between the dog and the two pots. Black lines show the paths of the partner to the pots (location of the food) and back to the start point. The black rectangle at the back wall represents the position of the occluder (used for covering the dog's eyes).

Interactive human. E1 brought the box into the room and placed it halfway between the dog and the partner on the left (L) or right (R) side of the room. During this the human partner entered and took up her initial standing position at the predetermined point. Next E1 left the room and then re-entered with a piece of food and a plastic plate in her hand. She attracted the dog's attention ('Hi (dog's name), look!') and put the food on the plate. She attached the plate to the magnet inside the box. After E1 left the room the dog was allowed to explore the room and search for the food for 15 s. When the time elapsed, the owner called the dog back. Then the partner addressed the dog ('Hi (dog's name), look!') and brought out the plate with the food from the box to the dog. The dog ate the piece of food and the partner returned to her starting position. Then E1 entered the room and placed the box on the other side of the room (Fig. 1). The procedure was repeated as described above except that from the second trial during the 15 s exploration phase, at the moment when the dog looked at the partner, the partner started to move and brought the plate out. If, however, the dog did not look at the partner during the 15 s, the owner called the dog back. The trial was repeated six times in LRLRLR order (L = the box was placed to the left; R = the box was placed to the right).

Interactive UMO. The familiarization phase was the same as in the Interactive Human condition, except that the human partner was replaced by the UMO and the Interactive UMO attracted the dog's attention by emitting a beep-beep sound, and the UMO brought out the plate with the help of the magnet attached to its front.

Test phase

The partner stood at the starting point, facing the dog. E1 entered the room with two identical pots and placed them on each side of the partner (see Fig. 1) and attracted the dog's attention with a piece of food in her hand ('Hi (dog's name), look!'). Then the dog's eyes were covered by an occluder, E1 put one piece of food into one of the pots and left the room. The occluder was removed and the partner called the dog's attention (according to the condition) from the start point and approached the baited pot, touched it with her leg (in Noninteractive and Interactive Human conditions) or its front (in Noninteractive and Interactive UMO conditions) and returned to its/her starting position. The owner released the dog, and it was allowed to select one of the pots. If the dog chose the baited container, it could eat the food, but if it approached the nonbaited one, the owner showed the piece of food in the baited one, but the dog was not allowed to eat it. Dogs were presented with 16 test trials during which the baiting followed RLRLLRLRRLLRLRRL order.

Behavioural Variables and Data Analysis

All trials were videotaped and the dogs' behaviour during the familiarization (in the Interactive UMO and Interactive Human conditions) and the test phase (all four conditions) was analysed with Solomon Coder 090913 (A. Péter, http://solomoncoder.com).

For the trials we obtained the following response variables. Looking at the partner (binary variable) during the familiarization phase (Interactive UMO and Interactive Human conditions): we scored each familiarization trial as 1 if the dog looked at the partner (UMO or human; i.e. when the subject's head was oriented towards the partner) within the 15 s or as 0 if the dog did not look at the partner (UMO or human) within the 15 s. Choice (binary variable): we scored each test trial as 1 (if the dog approached the baited pot within 10 cm) or 0 (if the dog approached the nonbaited pot within 10 cm). Looking at the approaching partner (%) during test trials: relative duration of time spent with the head oriented towards the partner during the indication (from the emission of the attention sound until the partner returned to its/her starting position).

Interobserver agreements (between two coders) for 'Looking at the partner' and 'Choice' were assessed by means of parallel coding of a randomly selected 25% of the subjects (Cohen's Kappa values: 0.94 for Looking at the partner and 0.99 for dogs' Choice).

To control for the nonindependence of our data (a dog participated in several trials) we applied random intercept generalized linear mixed-effect models (GLMMs) using the lme4 package (version 1.1.7) in the R statistical environment (version 3.1.2, The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). In all models Dog ID (dog's name) was included as a random grouping factor. Looking at the partner during familiarization (binary) and Choice (binary) were analysed by GLMMs with binomial error distribution, whereas Looking at the approaching partner (%) was analysed by GLMM with Gaussian error distribution after arcsine square-root transformation of the response. The significance of explanatory variables was investigated using likelihood ratio tests (LRTs). For Looking at the approaching partner (%; Gaussian error distribution) we used maximum likelihood fitting for the LRTs. Post hoc analyses were conducted using the lsmeans package (version 2.12) in R applying the Tukey method to adjust P values for multiple comparisons. The binary models were not overdispersed and assumptions of models were checked graphically. For extracting predictions from models for the figures only fixed effects were taken into account and for the arcsine square-root transformation, predictions were back transformed to the original scale.

First we tested whether condition influenced Choice during the test trials in a model including condition (factor with four levels) and trial (factor with 16 levels) as fixed explanatory variables. The nonsignificant interaction term (LRT: $\chi^2_{45} = 48.74$, $P = 0.325$) was removed from the model. Second, we examined within-task learning in dogs in a model including condition and trial phase (factor with four levels) as fixed explanatory variables. For trial phase the 16 test trials were divided into four phases (for details see Results). The interaction term was not significant ($\chi^2_9 = 4.26$, $P = 0.893$) and was removed from the model. Third, we tested whether Looking at the partner during familiarization differed in the two Interactive conditions in a model including condition (factor with two levels) and familiarization trial (factor with six levels) in the model. The nonsignificant interaction term ($\chi^2_5 = 3.39$, $P = 0.639$) was removed from the model. Fourth, Looking at the approaching partner (%) was analysed to investigate whether looking time differed between the conditions in a model including only the condition with four levels.

RESULTS

First we investigated the effect of condition and repeated test trials on dogs' performance and it was also compared to chance level (0.5) in each condition. Our results showed that dogs' performance during the test trials was influenced by both condition and trials (binomial GLMM, LRTs: condition: $\chi^2_3 = 11.02$, $P = 0.012$; trials: $\chi^2_{15} = 76.24$, $P < 0.001$). During the test phase dogs chose the approached/baited (correct) container above chance level in all except the Noninteractive UMO condition. At the same time dogs' performance was significantly higher in the two Interactive conditions than in the Noninteractive UMO condition while we found no significant difference between the Noninteractive Human condition and the Interactive Human, Interactive UMO and Noninteractive UMO conditions (see Fig. 2).

Then the 16 test trials were divided into four phases to examine within-task learning in dogs (first phase: trials 1–4; second phase: trials 5–8; third phase: trials 9–12; fourth phase: trials 13–16;

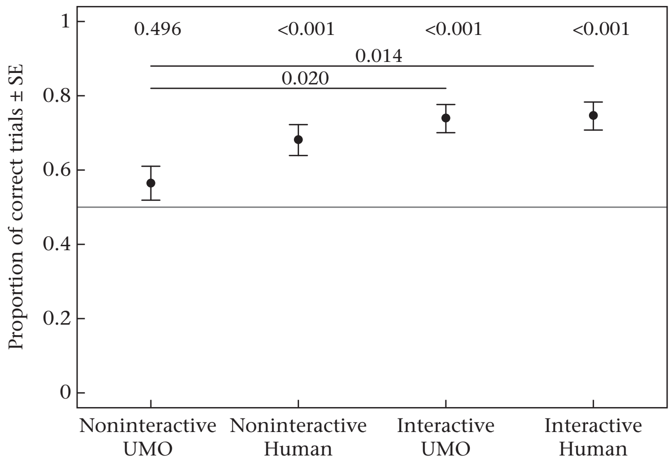

Figure 2. Proportion of trials in which the dogs chose correctly during the tests in the four conditions. Estimated means ± SE from a binomial GLMM including condition and trial as fixed effects are given. Values above each error bar give the *P* value of the comparison to the 0.5 chance level (horizontal grey line). Horizontal black lines show significant pairwise comparisons with the corresponding *P* value above the line.

every phase included two left and two right trials). Analysis of trial phases showed that dogs' performance was influenced by both condition and trial phase (binomial GLMM, LRTs: condition: $\chi^2_3 = 11.04$, $P = 0.012$; trial phase: $\chi^2_3 = 21.82$, $P < 0.001$). However, per condition analyses revealed that the effect of trial phase was only significant in the Interactive UMO condition ($\chi^2_3 = 9.74$, $P = 0.021$) and pairwise comparisons revealed that the first trial phase differed from the third (Fig. 3). Furthermore, the performance of the dogs did not differ between conditions in the first trial phase ($\chi^2_3 = 5.32$, $P = 0.150$).

Next we examined whether repeated encounters with the UMO had an effect on dogs' looking behaviour (i.e. Looking at the UMO/Human partner) during familiarization trials in the Interactive

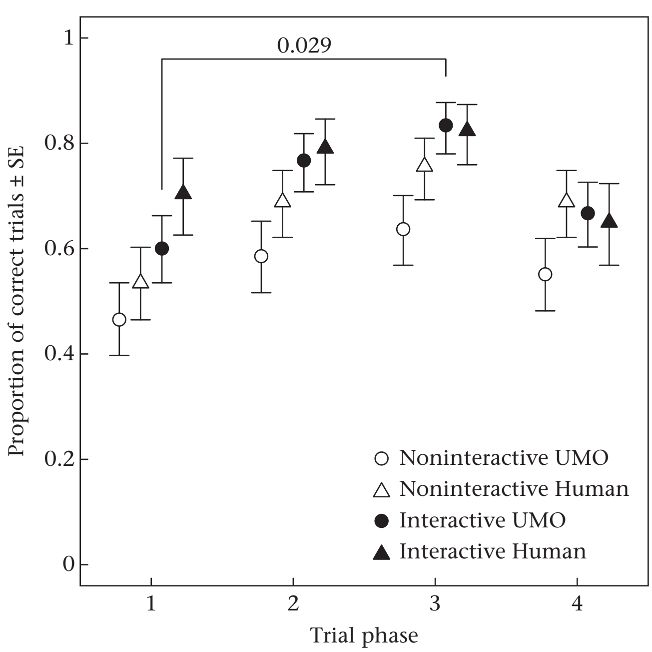

Figure 3. Proportion of trials in which the dogs chose correctly during the four trial phases in the four conditions. Estimated means ± SE from separate binomial GLMMs for each condition including trial phase as fixed effect are given. The black line shows the only significant pairwise comparison and the corresponding *P* value.

conditions. We found that dogs' looking behaviour during the familiarization trials was not different between the Interactive UMO and Interactive Human conditions (binomial GLMM, LRT: $\chi^2_1 = 1.27$, $P = 0.260$); however, it differed between the familiarization trials (LRT: $\chi^2_5 = 22.64$, $P < 0.001$). Pairwise comparisons showed that the first trial was different from all other trials (all pairwise $P < 0.05$), but the other trials were not different from each other (all pairwise $P \geq 0.736$).

Finally, we investigated dogs' looking behaviour (i.e. Looking at the UMO/Human partner) during the approach of the partner during the test trials to exclude the possibility that dogs in the Noninteractive UMO condition performed poorly because they did not watch the partner's action. We found that condition had a highly significant effect on Looking at the approaching partner (Gaussian GLMM, LRT: $\chi^2_3 = 34.61$, $P < 0.001$); however, there was no difference between the Interactive and Noninteractive UMO (pairwise $P = 0.611$) or between the Noninteractive and Interactive Human conditions (pairwise $P = 0.907$; Fig. 4).

DISCUSSION

The present study demonstrates that dogs are able to use directional movement (approach) of a nonliving interactive partner (UMO) as effectively as a similar human signal to locate the hidden food. The finding that dogs performed at chance with the Noninteractive UMO supports the notion that previous social interaction with the UMO is indispensable when interpreting a partner's movement as cues for food location. It seems that the ‘turn-taking’ behaviour of the UMO during familiarization could promote learning about the informing aspects of the agent's directional behaviour. At the same time dogs utilized human directional behaviour efficiently from the beginning and irrespective of prior experience in the familiarization phase.

Dogs in the present study had no previous experience with the UMO. They perceived its skills for the first time in the familiarization phase (Context 1) when the UMO obtained the food for the dogs that they could not get from the box. We assume that based on this short social interaction dogs had formed some expectations about the behaviour of the UMO which facilitated the recognition of the goal directedness of its directional action in the novel situation (Context 2).

The changes in dogs' performance during the test phase also provide interesting insights. In line with our predictions we found

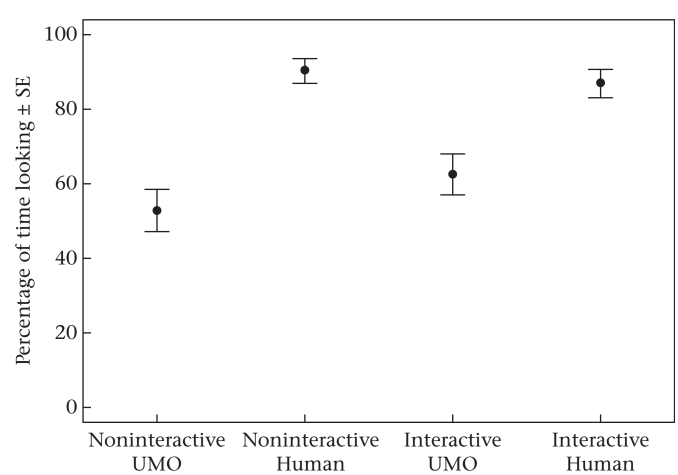

Figure 4. Percentage of time the dog was looking at the partner during the test trials. Estimated means ± SE from a Gaussian GLMM including condition as fixed effect are given.

no evidence of within-task learning with the Interactive Human and Noninteractive Human partner, which suggests that the ‘quality’ of previous social experience with the unfamiliar human (in the familiarization phase) had no effect on the way dogs interpreted her directional signal. Similarly, there was no learning during repeated trials in the Noninteractive UMO condition. In contrast, rapid learning occurred in the Interactive UMO condition. This rapid learning about a novel action of the Interactive UMO suggests that dogs may have generalized from past experience with humans but a facilitating effect of some genetic predisposition cannot be excluded.

Thus dogs may recognize that the partner is attempting to communicate with them via some signal (Tomasello et al., 1997). Dogs may have endowed the Interactive UMO with some agency cues following the familiarization phase, and consequently they tended to relate to the UMO socially in the novel test context. This is also in agreement with findings that dogs failed to use a physical marker by itself as a simple spatial index but consider it as a communicatively significant cue if they can associate the placing of a marker with a human (Agnetta, Hare, & Tomasello, 2000; Riedel et al., 2006). Apparently, dogs considered the action of the Noninteractive UMO merely as a physical marker, and in the absence of specific experience they did not associate its movements and the place of food during 16 trials.

Our findings are open to post hoc interpretations of an associative nature (Byrne & Bates, 2007); however, a close investigation shows that this interpretation may actually be more complex. Taken at face value one may argue that dogs associated the actions of the Interactive UMO with getting a food reward. However, dogs in the familiarization phase (Context 1) observed the following sequence of events (E_{fam}): UMO produced attention-getting sound ($E_{fam}1$); it approached the food plate in the cage (food visible) ($E_{fam}2$); UMO approached the dog ($E_{fam}3$). In contrast, in the test phase (Context 2), the dogs observed the following sequence of events (E_{test}): UMO produced attention-getting sound ($E_{test}1$); it approached the bowl ($E_{test}2$); UMO left the bowl ($E_{test}3$). Apart from many physical differences between Contexts 1 and 2 (location of food, food bowls, etc.), only $E_{fam}1$ and $E_{test}1$ were the same; the following events were different ($E_{fam}2 \neq E_{test}2$ and $E_{fam}3 \neq E_{test}3$). Note that in $E_{fam}3$ and $E_{test}3$ the UMO moved in different directions (approach versus departure). Based on learning theory, dogs should have associated the last action with the reward during the familiarization phase and learnt the whole sequence of events backwards (Pearce & Bouton, 2001). In addition, it is common to find that family dogs' performance in executing a newly learnt action drops significantly in a novel context (Braem & Mills, 2010), and usually more trials (experience) are needed to establish an association between an arbitrary action of the partner and the presence of food (Elgier et al., 2009; Udell et al., 2008). Lakatos et al. (2013) have recently reported an experiment in which dogs had an opportunity to observe their owners interacting with a human-like robot (PeopleBot). At the end of this interaction the robot attracted the dog's attention by emitting a ‘beep—beep’ sound and dropped a piece of food to the dog from its hand. This was repeated three times. This interaction was followed by a pointing session (similar procedure which was applied in our test phase) in which the robot indicated the location of the hidden food by pointing with its arm. Despite the robot providing food three times, the dogs' performance was at chance level. Thus the food reward provided by a robot was insufficient to initiate learning in dogs about the informative aspect of its pointing movement.

Although we cannot exclude that some underlying associative mechanisms play a role here, in our view the interpretation of the dog's behaviour and performance as being based on more general inference from previous social experience is a viable alternative explanation.

We emphasize that the utilization of a UMO has the potential to investigate the relative role of evolutionary/developmental processes behind dogs' social skills. The hypothesis of genetic predisposition predicts that dogs in the present experiment should rely on a human partner's directional (‘indicative’) behaviour efficiently from the very beginning of the test phase regardless of prior social interaction in the familiarization phase. Furthermore, dogs from both the interactive and noninteractive familiarization conditions with the UMO showed rapid learning about the informative aspects of the UMO's directional behaviour (but they probably learnt more quickly after interactive familiarization).

The ontogenetic hypothesis also predicts that dogs efficiently use the human partner's directional movements as signals regardless of prior social interaction in the familiarization phase because they have extensive experience of interacting with people. In contrast, dogs would not be able to find the hidden food based on the directional movements of the UMO after a short prior social experience in the familiarization phase because they lack the necessary ontogenetic experience to rely on the UMO's directional movements. In line with the previous assumptions (e.g. Gácsi et al., 2009; Miklósi & Topál, 2013; Rossano et al., 2014) we assume that the two hypotheses are not mutually exclusive but complementary. During domestication, dogs evolved an inherent sensitivity to those human communicative signals that have directional components. We suggest that this skill is flexible enough to allow the dog to learn in a wide range of situations and generalize to a UMO's directional movement. In summary, we propose that the observed flexibility of dogs' social behaviour is due to sharing an environment with humans (heterospecific agents); thus they are probably able to generalize their wide range of social experience with humans to another type of agent as well. These results support the findings that dogs are able to attend to some social aspect of the behaviour of a UMO which resembles neither conspecifics nor humans (Gergely et al., 2013). The relatively little experience with the UMO suggests that it is unlikely that the present results can be explained solely on the basis of ontogenetic processes. Our results suggest that a genetic predisposition is also involved which facilitates the socially competent reaction to actions performed by a UMO if it shows behavioural signs characteristic of a social partner (Miklósi & Topál, 2013).

Acknowledgments

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Appendix

Here we report the analyses of the full data ($N = 68$) including the eight dogs showing strong side bias (they always approached the same pot either on the left or on right in all 16 trials).

Effect of Condition and Repeated Test Trials on Dogs' Performance

A binomial generalized linear mixed-effect model (GLMM) was fitted with Dog ID (dog's name) as random grouping factor. The significance of explanatory variables was investigated using likelihood ratio tests (LRTs). The nonsignificant interaction ($\chi^2_{45} = 42.28$, $P = 0.588$) was removed from the model. Results showed that dogs' performance during the test trials was influenced by both condition ($\chi^2_3 = 9.75$, $P = 0.021$) and trials ($\chi^2_{15} = 108.20$, $P < 0.001$; see Fig. A1).

Effect of Condition and Trial Phases on Dogs' Performance

The nonsignificant interaction ($\chi^2_9 = 3.92$, $P = 0.917$) was removed from the binomial GLMM. Analysis of trial phases showed that dogs' performance was influenced by both condition and trial phase (binomial GLMM, LRTs: condition: $\chi^2_3 = 9.78$, $P = 0.021$; trial phases: $\chi^2_3 = 18.64$, $P < 0.001$). Per condition analyses revealed that the effect of trial phase was only significant in the Interactive UMO condition ($\chi^2_3 = 8.92$, $P = 0.030$). Furthermore, the performance of the dogs did not differ between conditions in the first trial phase ($\chi^2_3 = 4.86$, $P = 0.182$) and pairwise comparisons revealed that the first trial phase was different from the third (see Fig. A2).

Dogs' Looking Behaviour During Familiarization Trials

The nonsignificant interaction ($\chi^2_5 = 4.56$, $P = 0.472$) was removed from the binomial GLMM. Our results showed that dogs' looking behaviour during the familiarization trials did not differ between the Interactive UMO and Interactive Human conditions (binomial GLMM, LRT: $\chi^2_1 = 1.56$, $P = 0.212$) but differed between familiarization trials (LRT: $\chi^2_5 = 26.26$, $P < 0.001$). Pairwise comparisons using the Tukey method revealed that the first trial was different from all other trials (all $P < 0.021$), whereas other trials were not different from each other (all $P \geq 0.795$).

Dogs' Looking Behaviour During the Test Trials

A GLMM with Gaussian error distribution after arcsine square-root transformation of the response showed that condition had a highly significant effect on Looking at the approaching partner (LRT: $\chi^2_3 = 39.04$, $P < 0.001$). At the same time, there was no difference between the Interactive and Noninteractive UMO (pairwise $P = 0.850$, using Tukey adjustment), or between Noninteractive and Interactive Human conditions (pairwise $P = 0.978$, using Tukey adjustment; see Fig. A3).

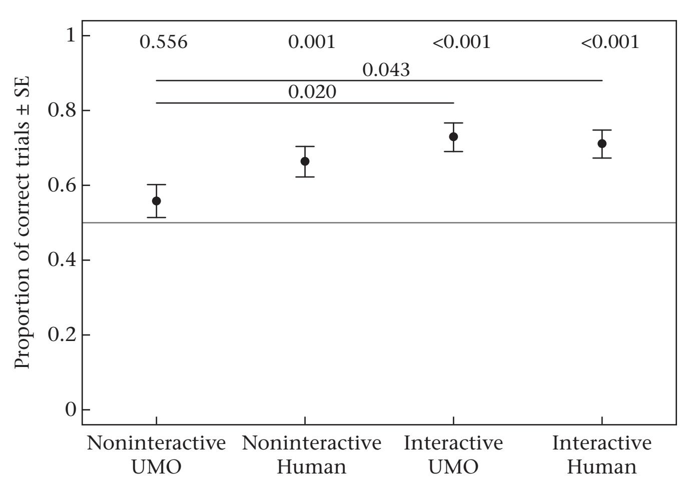

Figure A1. Proportion of trials in which the dogs chose correctly during the tests in the four conditions. Estimated means ± SE from a binomial GLMM including condition and trial as fixed effects are given. Values above each error bar give the *P* value of the comparison to the 0.5 chance level (horizontal grey line). Horizontal black lines show significant pairwise comparisons with the corresponding *P* value above the line (*P* values were adjusted by the Tukey method).

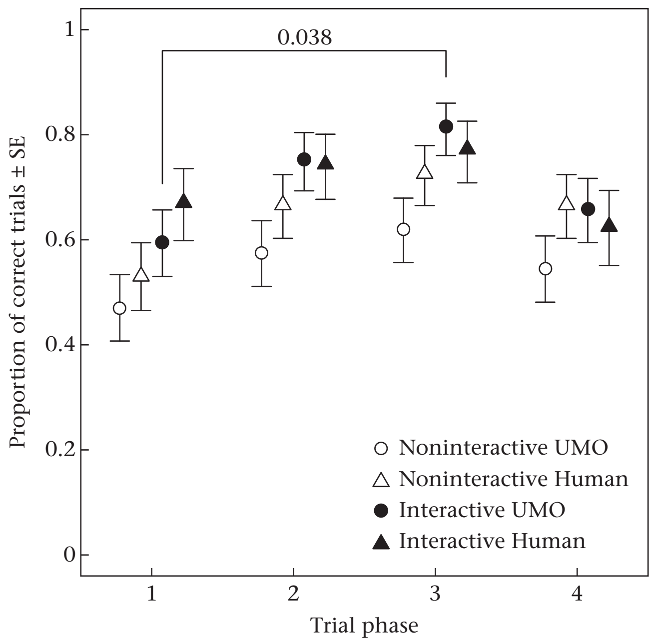

Figure A2. Proportion of trials in which the dogs chose correctly during the four trial phases in the four conditions. Estimated means ± SE from separate binomial GLMMs for each condition including trial phase as fixed effect are given. The black line shows the only significant pairwise comparison and the corresponding *P* value after Tukey adjustment.

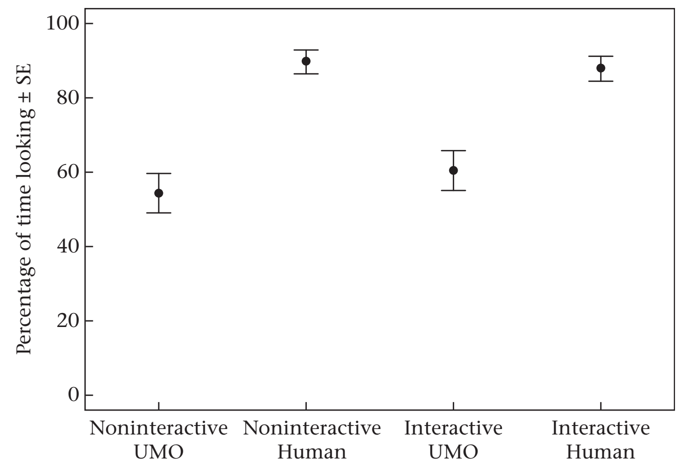

Figure A3. Percentage of time the dog was looking at the partner during the test trials. Estimated means ± SE from a Gaussian GLMM including condition as fixed effect are given.