



Dogs re-engage human partners when joint social play is interrupted: a behavioural signature of shared intentionality?

Daniel J. Horschler^{a, *}, Emily E. Bray^{b, c}, Gitanjali E. Gnanadesikan^{b, d}, Molly Byrne^e, Kerinne M. Levy^c, Brenda S. Kennedy^c, Evan L. MacLean^{b, d, f, g}

^a Department of Psychology, Yale University, New Haven, CT, U.S.A

^b School of Anthropology, University of Arizona, Tucson, AZ, U.S.A

^c Canine Companions for Independence, National Headquarters, Santa Rosa, CA, U.S.A

^d Cognitive Science Program, University of Arizona, Tucson, AZ, U.S.A

^e Department of Psychology, Boston College, Chestnut Hill, MA, U.S.A

^f Department of Psychology, University of Arizona, Tucson, AZ, U.S.A

^g College of Veterinary Medicine, University of Arizona, Tucson, AZ, U.S.A

ARTICLE INFO

Article history:

Received 22 March 2021

Initial acceptance 16 July 2021

Final acceptance 6 September 2021

MS. number: A21-00189R

Keywords:

cooperation

dog cognition

joint action

joint commitment

shared intentionality

social play

Hypotheses regarding the evolution of uniquely human social cognition often emphasize not only mental state representation, but also mental state sharing. Mental state sharing is evident in instances of joint intentionality – mutual understanding between individuals of each other's simultaneous and interdependent commitment to a shared activity or goal. Comparative studies supporting the human uniqueness of joint intentionality show that, as compared to human children, chimpanzees, *Pan troglodytes*, who engage with humans as cooperative partners do not altruistically help others achieve their goals across the same range of contexts, do not attempt to re-engage cooperative partners in problem-solving or social games at the same rate and do not show spontaneous role reversal. Although recent work supports the possibility that bonobos, *Pan paniscus*, may re-engage conspecific partners after interrupted social grooming, the extent to which other animals show similar behaviour across more diverse contexts remains largely unexplored. Domestic dogs', *Canis familiaris*, propensity to interact with humans in cooperative contexts makes them a potentially promising comparative model of prosocial mental state sharing. Here, we investigated a behavioural signature of joint intentionality during social play between humans and dogs ($N = 82$). Our results present the first experimental evidence of re-engagement behaviour in dogs, as dogs preferentially attempted to reinitiate an interrupted social game with their previous partner relative to a passive bystander. These findings suggest that dogs exhibit a key marker of joint intentionality and open the door for future research on the cognitive mechanisms supporting this behaviour.

© 2021 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Cooperation, broadly defined as behaviour that confers some benefit to either an actor and a recipient or the recipient alone (Melis & Semmann, 2010; Stevens et al., 2005), is commonly observed across species (Brown, 1983). This is especially the case among many primates, whose rich social lives and cooperative interactions have been a productive subject of research for decades (e.g. Boesch, 1994; Clutton-Brock & Parker, 1995; Trivers, 1971; West-Eberhard, 1975). Even among highly social primates, however, human cooperation has been proposed as unique (Burkart et al., 2009, 2014; Melis & Semmann, 2010; Stevens et al., 2005),

with some scholars arguing that the extent and scale of cooperation in human society makes it a 'spectacular outlier' in the animal kingdom (Fehr & Fischbacher, 2004).

Hypotheses proposing to explain the cognitive mechanisms underpinning human 'ultrasociality' and large-scale cooperation have centred principally on mental state representation and mental state sharing (Bettle & Rosati, 2020; Herrmann et al., 2007). A large body of research has focused on mental state representation, especially whether other animals have the ability to represent others' knowledge (e.g. Hare et al., 2001; Horschler et al., 2021; Kaminski et al., 2008; Martcorena et al., 2011; Martin & Santos, 2014), ignorance (e.g. Horschler, Santos et al., 2019; Kaminski et al., 2008) and beliefs (for reviews see Horschler et al., 2020a, 2020b; Kano et al., 2020; Krupenye & Call, 2019; Lewis & Krupenye,

* Corresponding author.

E-mail address: daniel.horschler@yale.edu (D. J. Horschler).

2021). However, comparatively little research has focused on mental state sharing, including whether other animals exhibit joint intentionality (Tomasello & Carpenter, 2007; Tomasello, Carpenter, Call et al., 2005, Tomasello & Moll, 2010) – mutual understanding between individuals of each other's simultaneous and interdependent commitment to participating in shared activities or attaining shared goals (Gilbert, 1990). Moll and Tomasello (2007) argued that joint intentionality requires cooperative partners to adopt a 'bird's eye view' of joint activities in which each partner understands their own and their partner's role in triadic interactions (e.g. between two agents directed towards an external goal, activity or object). Joint intentionality holds particular promise in helping to explain human ultrasociality because of its hypothesized role in evolutionarily scaffolding the group level collective intentionality evident in human societies and institutions (Tomasello, 2016) and developmentally scaffolding the perspectival cognitive representations requisite of representing others' false beliefs (Tomasello, 2018).

While of growing interest to comparative psychologists (Tomasello & Carpenter, 2007; Tomasello, Carpenter, Call et al., 2005; Tomasello & Moll, 2010), the concept of joint intentionality originated in the philosophy of mind literature (Gilbert, 1990; Searle, 1979; Tuomela, 2002; Tuomela & Miller, 1988). Searle (1979) described how the representational content of intentional mental states contains 'propositional attitudes', such as knowledge or beliefs about some referent. Applying this idea to social cognition, Tuomela and Miller (1988) defined 'we-intentions' as intentional states that relate to forms of joint social action – cases where agents do something together, occasionally to attain a goal that both agents share. Gilbert (1990) elegantly illustrated the concept of we-intentions by exploring the simple act of two people taking a walk together. She argued that taking a walk with someone cannot be fairly characterized by simply the physical act of walking side by side, but rather that it requires a richer conception of togetherness on the part of both parties. This togetherness may be illustrated by, for example, one person asking the other to slow down if they start to walk too far ahead, along with the other feeling some obligation to do so in order to continue to fulfil both parties' commitment to walking together (Gilbert, 1990). In this way, we-intentions are contingent on interdependent as well as simultaneous commitment to the activity. The degree to which this commitment must be explicitly understood by each party is subject to debate (Bratman, 1992; Butterfill, 2012), and some scholars have argued for a minimal framework of commitment that need not require common knowledge (Michael et al., 2016a, 2016b). Regardless, most of our communicative acts as humans, including those using language, can be characterized as these sorts of joint or collective actions (Tuomela, 2002) in which multiple parties are interdependently and simultaneously committed to a shared activity.

Joint intentionality is therefore a multifaceted cognitive ability with the potential to help explain several features of human ultrasociality. To empirically study joint intentionality, it is helpful to propose and examine more narrowly defined processes that may support mental state sharing. One key behavioural marker proposed to indicate the presence of joint intentionality is attempted re-engagement of recalcitrant partners upon interruption of a joint activity (Tomasello & Carpenter, 2007; Tomasello, Carpenter, Call et al., 2005; Tomasello & Moll, 2010). If both cooperative partners understand each other's commitment to the activity, when one partner breaks their commitment, the other should attempt to reinstate the activity with them. For example, if two people are jointly committed to playing a game of chess and one person walks away from the chess board without explanation, the other is likely to make some attempt to re-engage them in the game (e.g. asking why they left or whether they intend to finish the game).

From early in development, human children appear to readily form joint intentions with others as evidenced in part by re-engagement behaviour (Gräfenhain et al., 2013; Kachel & Tomasello, 2019; Warneken et al., 2006, 2012). Ross and Lollis (1987) first showed that 9- to 18-month-old children vocalized in response to unwanted interruptions in coordinated problem-solving activities with adults. Demonstrating that these behaviours were unlikely the result of general frustration about the interruption, Warneken and colleagues (Warneken et al., 2006) found that 18- and 24-month-olds made communicative re-engagement attempts via gesturing and vocalizing directed at recalcitrant partners after the interruption of both joint social games (e.g. one person rolling an object down a ramp for the other to catch in a tin cup) and joint problem-solving tasks (e.g. retrieving a toy enclosed in a tube that required each partner to simultaneously pull opposite ends of the tube). Furthermore, similarly aged children were more likely to make re-engagement attempts when partners were unable rather than unwilling to continue joint activities, demonstrating that children are likely sensitive to their partner's mental state rather than simply using them as 'social tools' to attain individual goals (Warneken et al., 2012). Three-year-old children are even sensitive to whether interruptions stem from their partner's intention to defect or lack of knowledge about how to participate (Kachel et al., 2018) and to whether partners ask for permission to dissolve a joint commitment before doing so (Kachel et al., 2019).

Comparative psychologists have begun to probe whether joint intentionality is unique to humans mostly by conducting studies of nonhuman apes (Heesen et al., 2020, 2021; MacLean & Hare, 2013; Warneken et al., 2006). In their study of 18- and 24-month-old human children, Warneken et al. (2006) also tested how chimpanzees, *Pan troglodytes*, responded to interruptions of similar cooperative activities with human partners. While chimpanzees never made attempts to re-engage recalcitrant partners in joint social games, the authors noted that chimpanzees' initial interest in engaging in these games was low. However, chimpanzees also did not re-engage human partners after interruptions of joint problem-solving tasks where initial coordination was higher and motivation to achieve a shared goal was induced via a food reward. Additionally, chimpanzees do not altruistically help others achieve their goals across the same range of contexts (Warneken & Tomasello, 2006) or show the same type of spontaneous role reversal in cooperative activities (Tomasello, Carpenter, & Hobson, 2005) as human children do. In contrast to the studies by Warneken et al., MacLean and Hare (2013) found that chimpanzees and bonobos, *Pan paniscus*, did readily engage in some simple triadic activities with a human partner. In these studies, although nonhuman apes sometimes touched a human partner in response to interruptions of joint social games, similar behaviour was observed in a control condition lacking triadic engagement, suggesting that this behaviour likely did not indicate attempted re-engagement of a previous joint activity.

While these experimental studies support the idea that joint intentionality may be unique to humans, some observational accounts have noted apparent re-engagement behaviour in nonhuman apes. Pika and Zuberbühler (2008) reported that bonobos seemed to re-engage human partners in a variety of interrupted joint social games via human-directed communicative behaviours (e.g. physical contact or offering objects involved in play). Tanner and Byrne (2010) presented narrative descriptions of gorillas, *Gorilla gorilla*, who appeared to re-engage conspecific partners in interrupted social play via gesturing, gazing and object offering. Additionally, Gómez (2010) offered an account of similar behaviours exhibited by a hand-reared infant gorilla during triadic cooperative interactions with humans.

Recently, Heesen et al. (2020) reported new experimental evidence of re-engagement behaviour in bonobos by comparing subjects' propensities to resume interrupted activities including joint social grooming, solitary grooming and solitary play. In this study, interruptions to each activity were either targeted to a specific individual (i.e. by calling a subject's name for a food reward) or were untargeted and thus likely to disrupt the entire group (i.e. by opening and closing a sliding door in the enclosure). Heesen and colleagues found that bonobos were less likely to resume solitary grooming or solitary play as compared to social grooming, suggesting that bonobos exhibited a sense of commitment to their social partners rather than a general desire to resume unfinished activities. Bonobos also communicated with their partners more during the resumption of social grooming when they themselves were responsible for suspending the activity (after targeted interruptions) as opposed to when both individuals were equally responsible (after untargeted interruptions). These findings suggest that bonobos may show a similar propensity as human children to resume interrupted joint activities, at least in the context of social grooming.

While nonhuman apes may exhibit re-engagement behaviour in some contexts, it remains unclear whether any other nonhuman animals show these same potential signatures of joint intentionality. Additionally, beyond observational reports in nonhuman apes (Gómez, 2010; Pika & Zuberbühler, 2008; Tanner & Byrne, 2010), there remains no conclusive empirical evidence that any nonhuman animals exhibit re-engagement behaviour in the context of interrupted social play as human children do.

Domestic dogs', *Canis familiaris*, propensity to interact with humans in cooperative contexts makes them an especially promising comparative model for these questions. Dogs correctly interpret communicative human social cues even from 8 weeks of age (Bray, Gnanadesikan et al., 2021; Bray et al., 2020; Bray, Gruen et al., 2021; Hare et al., 2002), do so at a higher level than similarly reared wolf, *Canis lupus*, puppies (Salomons et al., 2021) and show a similar oxytocin feedback loop from eye contact with humans as is present in human mother–child bonding (MacLean & Hare, 2015; Nagasawa et al., 2009, 2015). Additionally, unlike nonhuman apes, human children and dogs share analogous patterns of individual differences in cooperative communication, suggesting a similar psychological structure for these processes (MacLean et al., 2017). Finally, scholars have argued for the utility of social play as an avenue for exploring questions about joint intentionality in nonhuman animals (Arre & Horschler, 2021; Heesen et al., 2017) and that humans and dogs likely exhibit 'shared reality' in their dyadic interactions (Johnston et al., 2017). Therefore, dog–human interaction presents a potentially powerful context for comparative studies of joint intentionality.

Although dogs effectively engage with humans as cooperative partners in a variety of contexts, researchers have proposed alternative explanations regarding the phylogenetic origins and potential adaptive significance of these abilities (Gácsi et al., 2009; Hare & Tomasello, 2005a, 2005b; Range & Virányi, 2015; Wynne, 2021). Whereas some researchers argue that inherited social skills from a common ancestor with wolves can account for dogs' interspecific cooperative communicative skill (Lampe et al., 2017; Range et al., 2019; Udell et al., 2012; Virányi et al., 2008), others hypothesize that domestication altered dog social cognition to enable new forms of cooperation and communication with humans (Bray, Gnanadesikan et al., 2021; Hare et al., 2002; Hare & Tomasello, 2005a, 2005b; Salomons et al., 2021). Under the latter account, selection against fear and aggression towards humans was a key initial stage of dog domestication (Hare, 2017; Hare & Woods, 2020), opening a niche in which sensitivity to human communication and motivation to cooperate with humans may have become

adaptive (possibly involving selection for interest in humans as social partners). Interestingly, like dogs, both humans (Hare & Woods, 2020) and bonobos (but not chimpanzees) (Hare et al., 2012) show morphological, behavioural and cognitive traits consistent with selection against aggression, spurring recent hypotheses about potential self-domestication in these species (see Hare, 2016 for a review). Given robust evidence for the early emergence of joint intentionality in humans (Gräfenhain et al., 2013; Kachel et al., 2018, 2019; Kachel & Tomasello, 2019; Warneken et al., 2006, 2012) and recent evidence of re-engagement behaviour in bonobos (Heesen et al., 2020), if dogs do show similar behavioural signatures of joint intentionality, it is possible that these characteristics reflect convergent evolution among these taxa, stemming from similar selection pressures on socioemotional processes.

In the present study, we tested whether dogs attempt to re-engage human partners after interruptions to joint social play. Here, we define attempted re-engagement as a behavioural indication of dogs' potential desire to continue a previously established activity with a social partner upon that partner's abnegation to participate. Dogs first engaged with a human partner in a social game designed to elicit coordinated joint activity. After disruption of this joint activity, we assessed the extent to which dogs preferentially recruited the original social partner compared to a second individual who had not participated in the game. As no previous study to our knowledge has attempted to measure re-engagement in dogs, we coded a range of behaviours (e.g. physical contact, eye contact, toy offering) based on the developmental and comparative studies reviewed above, as well as other communicative behaviours that dogs typically exhibit (e.g. pawing, vocalizing). If dogs form joint experiences linked to a specific partner, we expected that they would preferentially attempt to reinitiate the game with their former partner as opposed to the person who was not previously involved. By contrast, if dogs are simply motivated to continue the activity, but without a commitment to a particular individual, we expected that they would choose indiscriminately between the two humans. A demonstration of preferential re-engagement of their former partner would indicate that dogs exhibit a behavioural marker of joint intentionality and would help guide future work examining whether mental state sharing underlies this behaviour.

METHODS

Ethical Note

All testing procedures were reviewed and adhered to regulations set forth by the Institutional Animal Care and Use Committee at the University of Arizona (IACUC No. 16-175). Behavioural testing was designed to be nondisruptive, lasting a maximum of 10 min and consisting of dogs' natural play behaviour (i.e. dogs were free to engage with human experimenters however they preferred for the entire duration of the study). No food was withheld for the purpose of this study. We adhered to strict abort criteria specifying that testing would be immediately terminated if dogs showed any signs of distress.

Subjects

We tested 82 adult dogs from March to July of 2019 at Canine Companions for Independence (CCI), a national nonprofit organization that breeds, raises and trains assistance dogs for people with disabilities. Our sample had a mean age and standard deviation of 2.10 ± 0.21 years, contained 47 females and included 23 Labrador retrievers, 1 golden retriever and 58 Labrador \times golden retriever crosses. Subjects were tested at CCI regional training centres (Santa

Rosa, CA, U.S.A., $N = 55$; Oceanside, CA, U.S.A., $N = 27$) after being raised in private homes by volunteer puppy raisers throughout the western United States. Subjects tested at the Oceanside campus completed this task immediately following participation in the Dog Cognitive Development Battery (DCDB; described in [Bray et al., 2020](#)); subjects tested at the Santa Rosa campus completed only this task at the time of testing. Subjects who completed the DCDB immediately prior to this task were tested by the same individuals who administered the DCDB, and the roles of experimenter versus handler in the DCDB were balanced across the roles of player versus bystander (described below) in this task. All other subjects were naïve to both the player and bystander prior to completing this task.

Procedure

Each trial consisted of a play period followed by an interruption period. To begin each play period, one experimenter (the player) started a 45 s countdown timer and called the dog's name while squeaking and waving two identical dog toys (KONG Wubba™) to engage the dog in play. After the player started the timer, they were free to move around the $\sim 3 \times 4.3$ m testing space to play with the dog however the dog preferred, including throwing one or both toys for the dog to fetch or playing tug with one of the toys ([Fig. 1a](#)). Throughout the play period, the player continuously encouraged the dog using dog-directed speech ([Ben-Aderet et al., 2017](#); [Gergely et al., 2017](#)) and attempted to engage the dog in play regardless of the dog's interest or participation in the activity. During this time, a second experimenter (the bystander) remained seated and silent at one end of the testing space, not interacting with the dog in any capacity.

After the 45 s play period ended, the player called 'time' and retrieved both toys. The player then walked back to their starting position (~ 1.5 m adjacent to the seated bystander, with side of room balanced between subjects) to sit down, stopping to hand one of the toys to the bystander along the way. When the player was seated, both the player and bystander held their respective toys up, said '(dog's name), look!' in unison, squeaked their toys twice and threw their toys towards the centre of the back wall of the testing

space, equidistant from the two experimenters ([Fig. 1b, c](#)). The bystander then started a 30 s countdown timer signalling the beginning of the interruption period. During the interruption period, the player and bystander remained seated and silent while attempting to make eye contact with the dog, but they did not engage the dog in any other capacity, even if the dog attempted to engage them ([Fig. 1d](#)). After the 30 s ended, the bystander called 'time' and the next play period began. We conducted four trials per subject, all in the same session.

Measures

All trials were recorded by two high-definition video cameras, and all measures were subsequently coded from video. To assess the extent to which dogs engaged with the toys during the play period, we first coded an ordinal 'playfulness score' of 1 (the subject never touched either toy even if offered by the player), 2 (the subject touched a toy at least once, but never took possession of the toy even if offered by the player) or 3 (the subject took possession of the toy at least once either by retrieving it from the ground or accepting it from the player's hand). For this measure, taking possession of the toy was defined as the subject holding the toy in their mouth without human assistance for at least 1 s.

We next coded several measures aimed at capturing possible re-engagement behaviour during the interruption period, taking inspiration from re-engagement measures previously reported in the developmental and comparative literatures (e.g. [MacLean & Hare, 2013](#); [Tomasello, Carpenter, & Hobson, 2005](#); [Tomasello & Moll, 2010](#); [Warneken et al., 2006](#)): (1) proximity – time in seconds the dog spent near each experimenter, defined as having both front paws within a $\sim 3 \times 1.8$ m rectangle taped on the floor that each experimenter sat in; (2) physical contact – time in seconds the dog spent with any part of their body touching any part of each experimenter's body; (3) eye contact – time in seconds the dog spent with their snout/eyes directed towards each experimenter's head or shoulders; (4) toy offering – count measure of each time the dog dropped a toy within one arm's length of each experimenter; (5) directed licking – binary measure of whether the dog licked each experimenter at least once during a given trial; (6)



Figure 1. A depiction of the experimental set-up and procedure. In all panels, the bystander appears on the left and the player appears on the right. Both experimenter role (player versus bystander) and the side of the room each experimenter sat on were balanced between subjects. (a) During the 45 s play period at the beginning of each trial, one experimenter (the player) engaged the subject in a social game designed to elicit coordinated joint activity while a second experimenter (the bystander) remained seated and ignored the subject. (b) At the conclusion of the play period, both the player and bystander simultaneously called the subject's attention and threw identical toys to the opposite end of the testing space. (c) During the 30 s interruption period that followed, both experimenters remained seated while attempting to make eye contact with the subject. (d) Here, the subject offered a toy to the player while standing in their lap during the interruption period.

directed vocalizing – binary measure of whether the dog vocalized at least once while oriented (i.e. with snout/eyes directed) towards each experimenter during a given trial; (7) directed pawing – count measure of each time the dog pawed at each experimenter.

Reliability

To assess reliability, each measure was independently coded by two individuals who were naïve to the hypotheses of the study on a randomly selected subset of 20% of the trials. As zero instances of directed pawing were observed after coding 20% of the trials, this measure was dropped from subsequent coding. Reliability was excellent for the playfulness score (Pearson's $r = 0.97$), proximity ($r = 0.97$), physical contact ($r = 0.89$), eye contact ($r = 0.89$), toy offering ($r = 0.91$) and directed licking (Cohen's $\kappa = 0.94$). Reliability for directed vocalizing ($\kappa = 0.66$) was considerably lower due to its rarity despite only one case of disagreement between coders: as this behaviour occurred on less than 5% of trials, it was excluded from further analysis.

Statistical Analyses

Analyses were conducted in the R environment (v.4.0.0; R Core Team, 2020). Our main hypothesis concerned an effect of experimenter role (player versus bystander) on the five behaviours coded during the interruption period. To assess this effect, we fitted linear mixed models predicting each behavioural measure as a function of experimenter role with a random intercept for subject. However, we also assessed whether this effect was moderated by either (1) playfulness during the play periods prior to the interruption periods, or (2) whether subjects had participated in the DCDB immediately prior to this task. As re-engagement is based on resumption of a previously established engagement, we expected that this effect would be strongest during trials in which dogs actively engaged in the joint activity prior to the interruption period. To assess this moderation effect, we fitted mixed models including an interaction between experimenter role and participation during the play period. For these models, participation during the play period was indexed by the playfulness score; this ordinal measure was collapsed to a binary variable where scores of 1 or 2 indicated no toy possession (54 total trials) and scores of 3 indicated toy possession (274 total trials). We collapsed the playfulness score measures in this way because of the relatively low number of trials scored as a 1 (21 trials) or a 2 (33 trials). Additionally, because some subjects were tested immediately following completion of the DCDB while others were not (and thus had more prior experience interacting with both experimenters), we also fitted mixed models including an interaction between experimenter role and DCDB participation. Each of these interaction terms (playfulness \times experimenter role; DCDB participation \times experimenter role) was tested individually and retained for the final model if the P value for the interaction was < 0.05 . We assessed the effects of these interaction terms using the 'Anova' function from the 'car' package (Fox & Weisberg, 2019) to produce analysis of deviance tables using Type II Wald chi-square tests. In cases in which an interaction is included in the final model, we report the strata-specific effects of experimenter role across the levels of the moderating variable(s). If the P value for the interaction was ≥ 0.05 , we omitted the interaction term, as well as the candidate moderating variable, given that the effect of this variable was not of interest outside the context of an interaction. In each case, decisions to retain or omit interactions in the final models were corroborated by results from likelihood ratio tests, which we ran using the 'anova' function to compare nested models (R Core

Team, 2020). The effect of each decision to retain or omit interaction terms on the coefficients that remain in the models is reflected in the statistics reported in the Results section.

All models with continuous dependent measures (i.e. proximity, physical contact and eye contact) were fitted using the 'lmer' function with an identity link function and gaussian error distribution from the 'lme4' package (Bates et al., 2015). Models predicting the toy offering and directed licking measures were fitted using the 'glmer' function; we specified a log link function and poisson error distribution for the toy offering models and a logit link function and binomial error distribution for the directed licking models due to the count (toy offering) and binary (directed licking) nature of these dependent measures. We assessed the effects of the predictors using the 'Anova' function from the 'car' package (Fox & Weisberg, 2019) to produce an analysis of deviance table using Type II Wald chi-square tests. For post hoc analyses of interactions, we used the 'emmeans' function from the 'emmeans' package (Lenth, 2020) to conduct t tests between estimated marginal means, using Dunn-Sidak correction for the appropriate number of comparisons. We ensured model assumptions were met by visually examining diagnostic plots to check for normality of residuals and linearity of the fit. After examining diagnostic plots from models using untransformed outcome variables, we used a square-root transformation for the physical contact and eye contact variables to improve the normality of the residuals.

RESULTS

Proximity

Subjects spent significantly more time in proximity to the player (mean \pm SE = 12.41 \pm 0.51 s) as compared to the bystander (6.80 \pm 0.44 s; $\chi^2_1 = 72.93$, $P < 0.001$; Fig. 2) during the interruption period, with a medium effect size ($d = 0.67$). No significant interactions were identified between experimenter role and toy possession in the play period ($\chi^2_1 = 1.03$, $P = 0.31$) or between experimenter role and DCDB participation ($\chi^2_1 = 0.23$, $P = 0.63$).

Physical Contact

Overall, subjects spent more time in physical contact with the player (mean \pm SE = 1.77 \pm 0.22 s) as compared to the bystander (0.90 \pm 0.14 s; Fig. 2) during the interruption period. We identified significant interactions between experimenter role and toy possession in the play period ($\chi^2_1 = 9.37$, $P = 0.002$), as well as between experimenter role and DCDB participation ($\chi^2_1 = 4.00$, $P = 0.046$). Thus, we used estimated marginal means to assess strata-specific effects of experimenter preference (1) as a function of whether dogs did or did not take possession of a toy during the preceding play period and (2) across dogs that did and did not previously participate in the DCDB. These analyses revealed that dogs made significantly more physical contact with the player as compared to the bystander in all cases, with the exception of trials in which the dog had not previously participated in the DCDB, but did take possession of a toy during the play period (Table 1). An interaction contrast revealed that there was no significant difference in the magnitude of the effect of experimenter role based on whether subjects did or did not complete the DCDB ($t_{173} = 0.20$, $P = 0.84$). However, the effect of experimenter role (i.e. the tendency for subjects to make more physical contact with the player as compared to the bystander) was significantly larger during interruption periods that lacked toy possession in the prior play periods ($t_{185} = 2.34$, $P = 0.02$) with a medium effect size ($d = 0.74$).

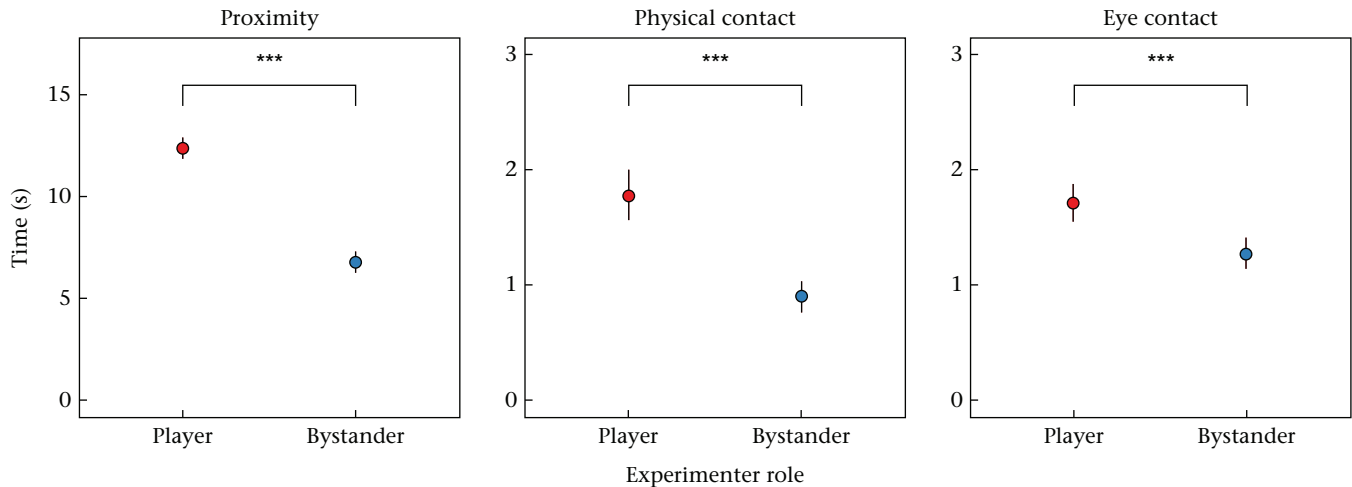


Figure 2. Time in seconds (mean \pm SE) that subjects spent in proximity to (left), in physical contact with (middle) and making eye contact with (right) each experimenter during the 30 s interruption periods. Asterisks denote significant differences.

Eye Contact

Subjects made significantly more eye contact with the player (mean \pm SE = 1.72 ± 0.16 s) as compared to the bystander (1.28 ± 0.14 s; $\chi^2_1 = 10.88$, $P < 0.001$; Fig. 2), with a small effect size ($d = 0.26$). No significant interactions were identified between experimenter role and toy possession in the play period ($\chi^2_1 = 0.48$, $P = 0.49$) or between experimenter role and DCDB participation ($\chi^2_1 = 0.10$, $P = 0.75$).

Toy Offering

Subjects offered a toy significantly more to the player (131 occurrences) as compared to the bystander (35 occurrences; $\chi^2_1 = 48.11$, $P < 0.001$; Fig. 3) during the interruption period, with a large effect size ($d = 1.32$). No significant interactions were identified between experimenter role and toy possession in the play period ($\chi^2_1 = 2.77$, $P = 0.10$) or between experimenter role and DCDB participation ($\chi^2_1 = 0.65$, $P = 0.42$).

Directed Licking

The number of trials in which subjects licked the player (80 trials) did not differ significantly from the number of trials in which subjects licked the bystander (69 trials; $\chi^2_1 = 1.31$, $P = 0.25$; Fig. 3) during the interruption period. No significant interactions were identified between experimenter role and toy possession in the play period ($\chi^2_1 = 0.06$, $P = 0.80$) or between experimenter role and DCDB participation ($\chi^2_1 = 0.79$, $P = 0.38$).

DISCUSSION

Our study aimed to determine whether dogs exhibit re-engagement behaviour – a proposed marker of joint intentionality – following the interruption of social play. Dogs initially engaged with a human in a social game designed to elicit coordinated joint activity while a second person passively watched. Upon interruption of this activity, we measured a range of potential re-engagement behaviours that dogs could direct at either their previous play partner or the passive bystander. While both experimenters did solicit the dog's attention prior to throwing the toys or continue the activity, importantly, neither experimenter actively encouraged the dog to retrieve the toys or continue the activity. This differed markedly from the play periods, in which the player (but not the bystander) continuously engaged the dog with dog-directed speech, always encouraging the dog to retrieve the toys when thrown. Overall, dogs spent significantly more time in proximity to and in physical contact with their previous partner relative to the bystander after the interruption. Additionally, dogs made significantly more eye contact with their partner and offered a toy to their partner significantly more than to the bystander. Taken together, these results suggest that dogs, similarly to human children, re-engage social partners when joint social play is interrupted.

This pattern of results fits well with previous work suggesting the importance of eye contact and object offering in studies of joint intentionality. For example, Tomasello and Moll (2010) argued that in studies of role reversal (another proposed behavioural marker of joint intentionality), looking to the partner's face in addition to holding out an object previously involved in a joint activity are crucial behavioural criteria indicative of a rich understanding of

Table 1
Strata-specific effects of experimenter preference from the physical contact measure during the interruption periods (1) as a function of whether dogs did or did not take possession of a toy during the preceding play period and (2) across dogs that did and did not previously participate in the DCDB

Toy possession	DCDB participation	Trials	Player-directed physical contact	Bystander-directed physical contact	<i>t</i>	<i>df</i>	<i>P</i>	<i>d</i>
Yes	Yes	80	1.70 \pm 0.41 s	0.40 \pm 0.17 s	2.66	570	.03	.39
Yes	No	194	1.43 \pm 0.23 s	1.26 \pm 0.22 s	1.42	570	.49	–
No	Yes	28	2.16 \pm 1.24 s	0.17 \pm 0.08 s	4.69	571	<.001	.98
No	No	26	4.21 \pm 1.13 s	0.51 \pm 0.20 s	3.45	571	<.001	.73

Number of trials, player-directed and bystander-directed physical contact (mean \pm SE), *t* values, degrees of freedom, *P* values and Cohen's *d* values for significant differences are included for each of the four contrasts.

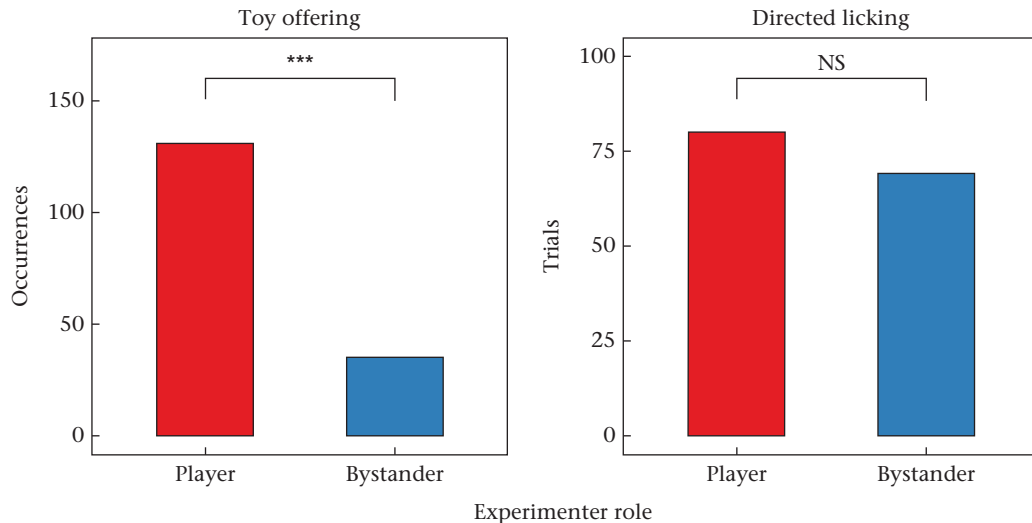


Figure 3. Total number of times subjects dropped a toy within one arm's length of each experimenter (left) and total number of trials in which subjects licked each experimenter at least once (right) during the 30 s interruption periods. Asterisks denote significant differences.

triadic activity. As 12- to 18-month-old human children (Carpenter et al., 2005) but not chimpanzees (Tomasello, Carpenter, & Hobson, 2005) exhibit these behaviours in experimental settings, they have been used to argue for the human uniqueness of joint intentions (Tomasello & Moll, 2010). While the present study was aimed at assessing re-engagement behaviour rather than role reversal, the finding that dogs directed significantly more eye contact and toy offering behaviour towards their previous partner relative to a bystander suggests that these behaviours are likely to be particularly strong indicators of attempted re-engagement of the triadic activity.

Our findings add to an emerging body of work that suggests that nonhuman animals may re-engage partners in interrupted joint activities in certain contexts. In addition to observational studies of nonhuman apes that have noted possible re-engagement behaviour (Gómez, 2010; Pika & Zuberbühler, 2008; Tanner & Byrne, 2010), recent empirical work has demonstrated that bonobos re-engage their previous partners after interruption of joint social grooming (Heesen et al., 2020). The present study is the first, to our knowledge, to experimentally demonstrate that any nonprimates exhibit re-engagement behaviour after interrupted joint activities and that any nonhuman animals re-engage partners specifically in the context of joint social play.

Importantly, our results contrast with some studies of nonhuman apes (MacLean & Hare, 2013; Tomasello, Carpenter, & Hobson, 2005; Warneken et al., 2006; Warneken & Tomasello, 2006) that found no, or limited, evidence for re-engagement behaviour or other behavioural markers of joint intentionality. In some of this previous experimental work, the authors noted that chimpanzees 'had little or no interest in the social games' with human partners, and in fact could not be induced to play some of the games at all (Warneken et al., 2006). This lack of motivation may have been due in part to the games' lack of ecological relevance (e.g. bouncing a ball on a trampoline) – these games appear better suited to developmental than comparative work (see MacLean & Hare, 2013 for evidence of higher levels of initial engagement from nonhuman apes in simpler social games with humans). In contrast, dogs readily engaged in the social game in our study, as indicated by toy possession on over 80% of the 328 trials. It is therefore possible that chimpanzees did not show re-engagement behaviour in previous experimental work because of a lack of initial engagement and motivation to participate in the activities

rather than an inability to form joint commitments. Supporting this interpretation, bonobos appear to re-engage conspecific partners in a more natural experimental context (Heesen et al., 2020). Experimental paradigms built on engagement with humans in social games are likely more ecologically relevant for dogs than nonhuman apes, allowing for more direct comparisons with previous developmental studies of human children (e.g. Kachel et al., 2018; Kachel & Tomasello, 2019). However, even in studies where chimpanzees and bonobos showed more initial engagement in social games with human partners, there was little evidence for re-engagement upon their interruption (MacLean & Hare, 2013). Accordingly, we argue that dogs present a uniquely powerful comparative model for the continued study of the cognitive mechanisms underlying joint activities due to their propensity to interact with humans in cooperative contexts and similar biological preparedness for cooperative communication (Bray, Gnanadesikan et al., 2021; Hare et al., 2002; MacLean et al., 2017; Salomons et al., 2021).

Our results also suggest a possible role of domestication in the evolution of behavioural patterns associated with joint intentionality. Based on evidence of re-engagement behaviour in bonobos, Heesen et al. (2020) recently suggested the possibility that the tendency to engage in joint commitments may be homologous in humans and bonobos. While our findings do not rule out the possibility that the capacity and/or propensity to form joint intentions is conserved among great apes (Heesen et al., 2021), they also suggest a different possibility: that the evolution of joint intentionality may be related to selection against aggression, a process implicated in human and bonobo evolution, as well as dog domestication. As a result of shared morphological, behavioural and cognitive traits – which are also present in domesticated canids, including experimentally domesticated foxes (Belyaev et al., 1985; Hare et al., 2005; Hare & Tomasello, 2005a, 2005b) – humans and bonobos have been hypothesized to have undergone self-domestication (Hare, 2016; Hare et al., 2012; Hare & Woods, 2020). As joint intentionality has been argued to rest on a sense of togetherness between individuals (Gilbert, 1990), it is plausible that selection against aggression helps promote the motivation requisite of desiring to do something together with others, separately from the capacity to understand others' intentions (which may be more widely observed across species). Currently, humans (Warneken et al., 2006, 2012), bonobos (Heesen et al., 2020) and

now domesticated dogs are the only species to have exhibited re-engagement behaviour in an experimental context, suggesting the possibility of convergent evolution. However, future work testing other great ape species as well as nondomesticated canids in ecologically relevant paradigms will be required to test this hypothesis.

Surprisingly, the extent of dogs' preferences for the player versus the bystander showed only limited evidence of moderation by engagement in the social game prior to the interruption period. Thus, while we found strong evidence for re-engagement behaviour in general, this phenomenon did not seem to depend on high levels of engagement with the toys during initial play. In fact, in the only model for which there was evidence of an interaction between behaviour during joint play and behaviour during the interruption periods, dogs showed a stronger preference for the player on trials in which they did not take possession of a toy during the play period. However, this effect occurred only among dogs who did not participate in a preceding test battery, and for only one of our five dependent measures, suggesting it is unlikely to be representative of a robust phenomenon. Similarly, our measure of engagement during the play period was formalized as whether the dog took possession of the toy during this time, but because we observed that dogs tended to interact with the experimenter in highly varied ways during play, it is possible that this measure did not robustly index dogs' interest or engagement in the activity. Given that dogs took possession of the toy in over 80% of the play periods, the lack of significant moderation effects may also be due in part to the relatively small sample of trials in which dogs were not engaged.

Importantly, our results do not necessarily indicate that dogs are capable of forming joint intentions with humans. One limitation of our study was that it did not directly control for some alternative explanations for re-engagement behaviour, such as social tool use (Warneken et al., 2012), whereby re-engagement is indicative of a desire to attain one's individual goal via the use of a social partner rather than a shared goal with a social partner. However, in our study, dogs were free to play on their own during the interruption period rather than reinitiating play with their previous partner, such that their partner was not necessary for goal attainment if the dog's goal was strictly to resume playing. Solitary play during the interruption period was commonly observed, but we did not attempt to quantify its occurrence in this study. Even so, it is possible that social play with a human partner is simply more rewarding than solitary play; under this explanation, dogs could have made re-engagement attempts out of a desire to initiate a more rewarding activity rather than to resume a joint commitment. The specificity of dogs' attempted re-engagement of their previous partner relative to a passive bystander provides some support for the existence of joint commitment, as does the emergence of this effect regardless of familiarity with the experimenters, as indexed by participation in a preceding test battery. However, future experimental work is needed to rule out this alternative explanation more conclusively.

Relatedly, nonsocial controls in future work will be crucial to interpreting whether the re-engagement behaviours we observed are indicative of joint intentionality. For example, would dogs show similar behaviours towards nonagentic ball-throwing machines that abruptly stop working? We would intuitively predict some of these same behaviours to emerge in such a case, which underscores the need for caution in concluding the presence of joint intentions based on re-engagement behaviours alone. However, directly analogous behaviours (e.g. gazing, toy offering) underlie much of the nonverbal evidential support for the capacity for joint intentions in young children, so researchers must take care to draw consistent theoretical conclusions from analogous behaviours

regardless of whether they are observed in humans or nonhuman animals. It is also possible that dogs may direct more or different re-engagement behaviours towards agents versus nonagents, which may shed light on the cognitive mechanisms underlying these behaviours in each case.

Our sample consisted entirely of retrievers from a population of assistance dogs in training. While previous work found that adult dogs from this population are no more skilled at following human social cues than a heterogenous sample of pet dogs or retrievers from a military working dog population (MacLean & Hare, 2018), it remains an open question whether our findings extend to other breeds or populations given this population's history of purposeful selection for work with humans. A handful of recent studies have documented breed differences in dog cognition and assessed their biological bases (Gnanadesikan, Hare, Snyder-Mackler, Call et al., 2020; Gnanadesikan, Hare, Snyder-Mackler, & MacLean, 2020; Horschler, Hare et al., 2019; MacLean et al., 2019). It is therefore reasonable to expect some degree of variation in re-engagement behaviour across breeds, which may be assessed by testing a heterogenous sample of pet dogs in a similar task. Additionally, it remains unknown how early these behaviours emerge in development and how they relate temporally to the ontogeny of other cooperative communicative skills in dogs. We hope to address these open questions in future research.

In summary, our results suggest that dogs exhibit a key behavioural marker of joint intentionality. Whether the re-engagement behaviour that we observed ultimately indicates the capacity for joint intentions in dogs remains an open question; however, similar behaviour in human children has been richly interpreted and subsequently used to argue for the human uniqueness of joint intentionality. Future work probing the cognitive mechanisms that support this behaviour in dogs will help to address evolutionary hypotheses about the cognitive building blocks of human ultrasociality, as well as unanswered questions about whether cooperative behaviour in other animals may also be subserved by joint intentions.

Data Accessibility

Data are available as Supplementary material.

Author Contributions

All authors contributed to Writing – Review & Editing. **D.J.H.:** Conceptualization, Data Curation, Formal Analysis, Investigation, Methodology, Visualization and Writing – Original Draft. **E.E.B.:** Conceptualization, Project Administration and Resources. **G.E.G.:** Conceptualization, Investigation and Methodology. **M.B.:** Conceptualization, Investigation and Methodology. **K.M.L.:** Project Administration and Resources. **B.S.K.:** Project Administration and Resources. **E.L.M.:** Conceptualization, Data Curation, Formal Analysis, Methodology, Supervision and Visualization.

Funding

This research was supported in part by grants from the Office of Naval Research (ONR N00014-17-1-2380 and N00014-20-1-2545) to E.L.M. D.J.H. was supported by a Haury Dissertation Fellowship from the School of Anthropology at the University of Arizona. G.E.G. was funded by the U.S. National Science Foundation Graduate Research Fellowship Program (DGE-1746060); any opinions, findings and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the U.S. National Science Foundation.

Declaration of Interest

We declare no conflict of interest.

Acknowledgments

We thank Julia Kemper, Thomas Kile, Lindsey Lang and Tegan Wambold for their help with data collection for pilot studies, as well as Elizabeth Carranza and Alex Evans for their help with coding. We are also grateful to the staff of Canine Companions for Independence for accommodating research with their assistance dogs in professional training at both the Oceanside, CA and Santa Rosa, CA campuses.

Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2021.11.007>.

References

- Arre, A. M., & Horschler, D. J. (2021). Swimming and diving as social play in juvenile rhesus macaques (*Macaca mulatta*). *Behaviour*, 158(6), 529–546. <https://doi.org/10.1163/1568539X-bja10074>
- Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Belyaev, D. K., Plyusnina, I. Z., & Trut, L. N. (1985). Domestication in the silver fox (*Vulpes fulvus* Desm): Changes in physiological boundaries of the sensitive period of primary socialization. *Applied Animal Behaviour Science*, 13, 359–370.
- Ben-Aderet, T., Gallego-Abenza, M., Reby, D., & Mathevon, N. (2017). Dog-directed speech: Why do we use it and do dogs pay attention to it? *Proceedings of the Royal Society B: Biological Sciences*, 284(1846), 20162429.
- Bettle, R., & Rosati, A. G. (2020). The primate origins of human social cognition. *Language Learning and Development*, 17(2), 79–95.
- Boesch, C. (1994). Cooperative hunting in wild chimpanzees. *Animal Behaviour*, 48, 653–667.
- Bratman, M. E. (1992). Shared cooperative activity. *Philosophical Review*, 101, 327–341.
- Bray, E. E., Gnanadesikan, G. E., Horschler, D. J., Levy, K. M., Kennedy, B. S., Famula, T. R., & MacLean, E. L. (2021). Early-emerging and highly heritable sensitivity to human communication in dogs. *Current Biology*, 31(14), 3132–3136.e5.
- Bray, E. E., Gruen, M. E., Gnanadesikan, G. E., Horschler, D. J., Levy, K. M., Kennedy, B. S., Hare, B. A., & MacLean, E. L. (2020). Cognitive characteristics of 8-to-10-week-old assistance dog puppies. *Animal Behaviour*, 166, 193–209.
- Bray, E. E., Gruen, M. E., Gnanadesikan, G. E., Horschler, D. J., Levy, K. M., Kennedy, B. S., Hare, B. A., & MacLean, E. L. (2021). Dog cognitive development: A longitudinal study across the first 2 years of life. *Animal Cognition*, 24, 311–328. <https://doi.org/10.1007/s10071-020-01443-7>
- Brown, J. L. (1983). Cooperation: A biologist's dilemma. *Advances in the Study of Behavior*, 13, 1–37. [https://doi.org/10.1016/S0065-3454\(08\)60284-3](https://doi.org/10.1016/S0065-3454(08)60284-3)
- Burkart, J. M., Allon, O., Amici, F., Fichtel, C., Finkenwirth, C., Heschl, A., Huber, J., Isler, K., Kosonen, Z. K., Martins, E., Meulman, E. J., Richiger, R., Rueth, K., Spillmann, B., Wiesendanger, S., & van Schaik, C. P. (2014). The evolutionary origin of human hyper-cooperation. *Nature Communications*, 5, 4747. <https://doi.org/10.1038/ncomms5747>
- Burkart, J. M., Hrdy, S. B., & van Schaik, C. P. (2009). Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology*, 18, 175–186. <https://doi.org/10.1002/evan.20222>
- Butterfill, S. (2012). Joint action and development. *Philosophical Quarterly*, 62, 23–47. <https://doi.org/10.1111/j.1467-9213.2011.00005.x>
- Carpenter, M., Tomasello, M., & Striano, T. (2005). Role reversal imitation and language in typically developing infants and children with autism. *Infancy*, 8, 253–278. https://doi.org/10.1207/s15327078in0803_4
- Clutton-Brock, T. H., & Parker, G. A. (1995). Punishment in animal societies. *Nature*, 373, 209–216. <https://doi.org/10.1038/373209a0>
- Fehr, E., & Fischbacher, U. (2004). Social norms and human cooperation. *Trends in Cognitive Sciences*, 8, 185–190. <https://doi.org/10.1016/j.tics.2004.02.007>
- Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Thousand Oaks, CA: Sage.
- Gácsi, M., Györi, B., Virányi, Z., Kubinyi, E., Range, F., Belényi, B., & Miklósi, Á. (2009). Explaining dog wolf differences in utilizing human pointing gestures: Selection for synergistic shifts in the development of some social skills. *PLoS One*, 4, 4–9. <https://doi.org/10.1371/journal.pone.0006584>
- Gergely, A., Faragó, T., Galambos, Á., & Topál, J. (2017). Differential effects of speech situations on mothers' and fathers' infant-directed and dog-directed speech: An acoustic analysis. *Scientific Reports*, 7, 13739. <https://doi.org/10.1038/s41598-017-13883-2>
- Gilbert, M. (1990). Walking together: A paradigmatic social phenomenon. *Midwest Studies in Philosophy*, 15, 1–14.
- Gnanadesikan, G. E., Hare, B., Snyder-Mackler, N., Call, J., Kaminski, J., Miklósi, Á., & MacLean, E. L. (2020). Breed differences in dog cognition associated with brain-expressed genes and neurological functions. *Integrative and Comparative Biology*, 60, 976–990. <https://doi.org/10.1093/icb/icaa112>
- Gnanadesikan, G. E., Hare, B., Snyder-Mackler, N., & MacLean, E. L. (2020). Estimating the heritability of cognitive traits across dog breeds reveals highly heritable inhibitory control and communication factors. *Animal Cognition*, 23(5), 953–964. <https://doi.org/10.1007/s10071-020-01400-4>
- Gómez, J. C. (2010). The ontogeny of triadic cooperative interactions with humans in an infant gorilla. *Interaction Studies*, 11, 353–379.
- Gräfenhain, M., Carpenter, M., & Tomasello, M. (2013). Three-year-olds' understanding of the consequences of joint commitments. *PLoS One*, 8(9), Article e73039. <https://doi.org/10.1371/journal.pone.0073039>
- Hare, B. (2016). Survival of the friendliest: *Homo sapiens* evolved via selection for prosociality. *Annual Review of Psychology*, 68, 155–186. <https://doi.org/10.1146/annurev-psych-010416-044201>
- Hare, B. (2017). Domestication experiments reveal developmental link between friendliness and cognition. *Journal of Bioeconomics*, 20, 159–163. <https://doi.org/10.1007/s10818-017-9264-9>
- Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science*, 298, 1634–1636. <https://doi.org/10.1126/science.1072702>
- Hare, B., Call, J., Tomasello, M., & Trut, L. (2001). Do chimpanzees know what conspecifics know? *Animal Behaviour*, 61, 139–151. <https://doi.org/10.1006/anbe.2000.1518>
- Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R., & Trut, L. (2005). Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Current Biology*, 15, 226–230. <https://doi.org/10.1016/j.cub.2005.07.003>
- Hare, B., & Tomasello, M. (2005a). Human-like social skills in dogs? *Trends in Cognitive Sciences*, 9, 439–444. <https://doi.org/10.1016/j.tics.2005.07.003>
- Hare, B., & Tomasello, M. (2005b). The emotional reactivity hypothesis and cognitive evolution. *Trends in Cognitive Sciences*, 9, 464–465. <https://doi.org/10.1016/j.tics.2005.08.010>
- Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, 83, 573–585. <https://doi.org/10.1016/j.anbehav.2011.12.007>
- Hare, B., & Woods, V. (2020). *Survival of the friendliest: Understanding our origins and rediscovering our common humanity*. New York: Random House.
- Heesen, R., Bangerter, A., Iglesias, K., Neumann, C., Pajt, A., Perrenoud, L., Guéry, J.-P., Rossano, F., & Genty, E. (2021). Assessing joint commitment as a process in great apes. *iScience*, 24(8), 102872. <https://doi.org/10.1016/j.isci.2021.102872>
- Heesen, R., Bangerter, A., Zuberbühler, K., Rossano, F., Iglesias, K., Guéry, J., & Genty, E. (2020). Bonobos engage in joint commitment. *Science Advances*, 6, 1–11.
- Heesen, R., Genty, E., Rossano, F., Zuberbühler, K., & Bangerter, A. (2017). Social play as joint action: A framework to study the evolution of shared intentionality as an interactional achievement. *Learning & Behavior*, 45, 390–405. <https://doi.org/10.3758/s13420-017-0287-9>
- Herrmann, E., Call, J., Hernandez-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science*, 317, 1360–1366. <https://doi.org/10.1126/science.1146282>
- Horschler, D. J., Hare, B., Call, J., Kaminski, J., Miklósi, Á., & MacLean, E. L. (2019). Absolute brain size predicts dog breed differences in executive function. *Animal Cognition*, 22, 187–198. <https://doi.org/10.1007/s10071-018-01234-1>
- Horschler, D. J., Santos, L. R., & MacLean, E. L. (2019). Do non-human primates really represent others' ignorance? A test of the awareness relations hypothesis. *Cognition*, 190, 72–80. <https://doi.org/10.1016/j.cognition.2019.04.012>
- Horschler, D. J., MacLean, E. L., & Santos, L. R. (2020a). Do non-human primates really represent others' beliefs? *Trends in Cognitive Sciences*, 24, 594–605.
- Horschler, D. J., MacLean, E. L., & Santos, L. R. (2020b). Advancing gaze-based research on primate theory of mind. *Trends in Cognitive Sciences*, 24, 778–779.
- Horschler, D. J., Santos, L. R., & MacLean, E. L. (2021). How do non-human primates represent others' awareness of where objects are hidden? *Cognition*, 212, 104658. <https://doi.org/10.1016/j.cognition.2021.104658>
- Johnston, A. M., Byrne, M., & Santos, L. R. (2017). What is unique about shared reality? Insights from a new comparison species. *Current Opinion in Psychology*, 23, 30–33. <https://doi.org/10.1016/j.copsyc.2017.11.006>
- Kachel, U., Svetlova, M., & Tomasello, M. (2018). Three-year-olds' reactions to a partner's failure to perform her role in a joint commitment. *Child Development*, 89, 1691–1703. <https://doi.org/10.1111/cdev.12816>
- Kachel, U., Svetlova, M., & Tomasello, M. (2019). Three- and 5-year-old children's understanding of how to dissolve a joint commitment. *Journal of Experimental Child Psychology*, 184, 34–47. <https://doi.org/10.1016/j.jecp.2019.03.008>
- Kachel, U., & Tomasello, M. (2019). 3- and 5-year-old children's adherence to explicit and implicit joint commitments. *Developmental Psychology*, 55, 80–88. <https://doi.org/10.1037/dev0000632>
- Kaminski, J., Call, J., & Tomasello, M. (2008). Chimpanzees know what others know, but not what they believe. *Cognition*, 109, 224–234. <https://doi.org/10.1016/j.cognition.2008.08.010>

- Kano, F., Call, J., & Krupenye, C. (2020). Primates pass dynamically social anticipatory-looking false belief tests. *Trends in Cognitive Sciences*, 24, 777–778.
- Krupenye, C., & Call, J. (2019). Theory of mind in animals: Current and future directions. *Wiley Interdisciplinary Reviews: Cognitive Science*, 10(6), e1503. <https://doi.org/10.1002/wics.1503>
- Lampe, M., Bräuer, J., Kaminski, J., & Virányi, Z. (2017). The effects of domestication and ontogeny on cognition in dogs and wolves. *Scientific Reports*, 7, 1–8. <https://doi.org/10.1038/s41598-017-12055-6>
- Lenth, R. (2020). *emmeans: Estimated marginal means, aka least-squares means* (Version 1.4.6). <https://github.com/rvlenth/emmeans>.
- Lewis, L. S., & Krupenye, C. (2021). Theory of mind in nonhuman primates. In B. L. Schwartz, & M. J. Beran (Eds.), *Primate cognitive studies*. Cambridge University Press.
- MacLean, E. L., & Hare, B. (2013). Spontaneous triadic engagement in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 127, 245–255. <https://doi.org/10.1037/a0030935>
- MacLean, E. L., & Hare, B. (2015). Dogs hijack the human bonding pathway. *Science*, 348, 280–281. <https://doi.org/10.1126/science.aab1200>
- MacLean, E. L., & Hare, B. (2018). Enhanced selection of assistance and explosive detection dogs using cognitive measures. *Frontiers in Veterinary Science*, 5, 236. <https://doi.org/10.3389/fvets.2018.00236>
- MacLean, E. L., Herrmann, E., Suchindran, S., & Hare, B. (2017). Individual differences in cooperative communicative skills are more similar between dogs and humans than chimpanzees. *Animal Behaviour*, 126, 41–51. <https://doi.org/10.1016/j.anbehav.2017.01.005>
- MacLean, E. L., Snyder-Mackler, N., Bridgett, M., & Serpell, J. A. (2019). Highly heritable and functionally relevant breed differences in dog behaviour. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20190716. <https://doi.org/10.1098/rspb.2019.0716>
- Marticorena, D. C. W., Ruiz, A. M., Mukerji, C., Goddu, A., & Santos, L. R. (2011). Monkeys represent others' knowledge but not their beliefs. *Developmental Science*, 4, 1406–1416. <https://doi.org/10.1126/scisignal.2001449.Engineering>
- Martin, A., & Santos, L. R. (2014). The origins of belief representation: Monkeys fail to automatically represent others' beliefs. *Cognition*, 130, 300–308. <https://doi.org/10.1016/j.cognition.2013.11.016>
- Melis, A. P., & Semmann, D. (2010). How is human cooperation different? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 2663–2674. <https://doi.org/10.1098/rstb.2010.0157>
- Michael, J., Sebanz, N., & Knoblich, G. (2016a). The sense of commitment: A minimal approach. *Frontiers in Psychology*, 6, 1–11. <https://doi.org/10.3389/fpsyg.2015.01968>
- Michael, J., Sebanz, N., & Knoblich, G. (2016b). Observing joint action: Coordination creates commitment. *Cognition*, 157, 106–113. <https://doi.org/10.1016/j.cognition.2016.08.024>
- Moll, H., & Tomasello, M. (2007). Cooperation and human cognition: The Vygotskian intelligence hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362, 639–648. <https://doi.org/10.1098/rstb.2006.2000>
- Nagasawa, M., Kikusui, T., Onaka, T., & Ohta, M. (2009). Dog's gaze at its owner increases owner's urinary oxytocin during social interaction. *Hormones and Behavior*, 55, 434–441. <https://doi.org/10.1016/j.yhbeh.2008.12.002>
- Nagasawa, M., Mitsui, S., En, S., Ohtani, N., Ohta, M., Sakuma, Y., Onaka, T., Mogi, K., & Kikusui, T. (2015). Oxytocin–gaze positive loop and the coevolution of human–dog bonds. *Science*, 348(6232), 333–336.
- Pika, S., & Zuberbühler, K. (2008). Social games between bonobos and humans: Evidence for shared intentionality? *American Journal of Primatology*, 70, 207–210. <https://doi.org/10.1002/ajp.20469>
- R Core Team. (2020). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Range, F., Marshall-Pescini, S., Kratz, C., & Virányi, Z. (2019). Wolves lead and dogs follow, but they both cooperate with humans. *Scientific Reports*, 9, 2–11. <https://doi.org/10.1038/s41598-019-40468-y>
- Range, F., & Virányi, Z. (2015). Tracking the evolutionary origins of dog–human cooperation: The 'canine cooperation hypothesis'. *Frontiers in Psychology*, 6, 1–10. <https://doi.org/10.3389/fpsyg.2015.00582>
- Ross, H. S., & Lollis, S. P. (1987). Communication within infant social games. *Developmental Psychology*, 23, 241–248. <https://doi.org/10.1037/0012-1649.23.2.241>
- Salomons, H., Smith, K. C. M., Callahan-Beckel, M., Callahan, M., Levy, K., Kennedy, B. S., Bray, E. E., Gnanadesikan, G. E., Horschler, D. J., Gruen, M., Tan, J., White, P., vonHoldt, B. M., MacLean, E. L., & Hare, B. (2021). Cooperative communication with humans evolved to emerge early in dogs. *Current Biology*, 31(14), 3137–3144. e11.
- Searle, J. R. (1979). What is an intentional state? *Mind*, 88, 74–92. <https://doi.org/10.1093/mind/LXXXVIII.1.74>
- Stevens, J. R., Cushman, F. A., & Hauser, M. D. (2005). Evolving the psychological mechanisms for cooperation. *Annual Review of Ecology, Evolution, and Systematics*, 36, 499–518. <https://doi.org/10.1146/annurev.ecolsys.36.113004.083814>
- Tanner, J. E., & Byrne, R. W. (2010). Triadic and collaborative play by gorillas in social games with objects. *Animal Cognition*, 13, 591–607. <https://doi.org/10.1007/s10071-009-0308-y>
- Tomasello, M. (2016). Précis of a natural history of human thinking. *Journal of Social Ontology*, 2, 59–64. <https://doi.org/10.1515/jso-2015-0041>
- Tomasello, M. (2018). How children come to understand false beliefs: A shared intentionality account. In *Proceedings of the National Academy of Sciences of the United States of America* (Vol. 115, pp. 8491–8498). <https://doi.org/10.1073/pnas.1804761115>
- Tomasello, M., & Carpenter, M. (2007). Shared intentionality. *Developmental Science*, 10, 121–125. <https://doi.org/10.1111/j.1467-7687.2007.00573.x>
- Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences*, 28, 675–691. <https://doi.org/10.1017/S0140525X05000129>
- Tomasello, M., Carpenter, M., & Hobson, R. P. (2005). The emergence of social cognition in three young chimpanzees. *Monographs of the Society for Research in Child Development*, 70(1), 1–152.
- Tomasello, M., & Moll, H. (2010). The gap is social: Human shared intentionality and culture. In P. M. Kappeler, & J. B. Silk (Eds.), *Mind the gap* (pp. 331–349). Berlin: Springer. <https://doi.org/10.1007/978-3-642-02725-3>.
- Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, 46, 35–57.
- Tuomela, R. (2002). Collective goals and communicative action. *Journal of Philosophical Research*, 27, 27–64. https://doi.org/10.5840/jpr_2002_33
- Tuomela, R., & Miller, K. (1988). We-intentions. *Philosophical Studies*, 53, 367–389.
- Udell, M. A. R., Spencer, J. M., Dorey, N. R., & Wynne, C. D. L. (2012). Human-socialized wolves follow diverse human gestures. And they may not be alone. *International Journal of Comparative Psychology*, 25, 97–117.
- Virányi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy, D., & Miklósi, Á. (2008). Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). *Animal Cognition*, 11, 373–387. <https://doi.org/10.1007/s10071-007-0127-y>
- Warneken, F., Chen, F., & Tomasello, M. (2006). Cooperative activities in young children and chimpanzees. *Child Development*, 77, 640–663. <https://doi.org/10.1111/j.1467-8624.2006.00895.x>
- Warneken, F., Gräfenhain, M., & Tomasello, M. (2012). Collaborative partner or social tool? New evidence for young children's understanding of joint intentions in collaborative activities. *Developmental Science*, 15, 54–61. <https://doi.org/10.1111/j.1467-7687.2011.01107.x>
- Warneken, F., & Tomasello, M. (2006). Altruistic helping in human infants and young chimpanzees. *Science*, 311, 1301–1303.
- West-Eberhard, M. J. (1975). The evolution of social behavior by kin selection. *Quarterly Review of Biology*, 50, 1–33.
- Wynne, C. D. L. (2021). The indispensable dog. *Frontiers in Psychology*, 12, 656529. <https://doi.org/10.3389/fpsyg.2021.656529>