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Collaborative interactions between humans and domestic dogs (*Canis familiaris*)

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Abstract

Domestic dogs (*Canis familiaris*) are ideal subjects for the comparative study of collaboration: they form stable social groups, engage in cooperative behaviour, and are characterised by human-like social skills. Moreover, dogs understand when human communication is intended for them, they obtain information about the emotional valence of human facial expressions and vocalisations, and readily form attachment bonds with humans. It has been hypothesised that, during the domestication process, dogs have been selected for collaborative activities with humans and evolved some human-like social skills as an adaptation to life with humans.

However, collaborative interactions between dogs and humans are understudied and not well understood. The aim of this research is to explore dogs' behaviour in contexts seen as the building blocks for successful collaboration: *informative* communication, *reputation* forming, and *other-regarding preferences*. In the first chapter of the thesis I review the literature on these topics. In Chapter 2, I explore the applicability to dogs of an experimental method for the comparative study of informative communication. In Chapter 3, with a simplified protocol, I provide evidence that dogs have some level of understanding of the relevance of the target for a human partner. Chapter 4 investigates reputation forming in dogs, suggesting that they do not take into account their previous experience about a human partner's skilfulness when they communicate to request human help. In Chapter 5, I use a novel apparatus for the study of other-regarding preferences, confirming that, in a food sharing situation,

dogs do not act altruistically towards humans but are rather motivated by the expectation of obtaining the food reward. Finally, in Chapter 6 I discuss the findings in the light of the current literature. The research presented in this PhD provides evidence that dogs may possess some of the building blocks of collaboration but not others. Specifically, they may have some understanding of the relevance of a target of communication for a human partner. However, there is no evidence that dogs' can use reputation judgments in collaborative contexts as flexibly as humans or chimpanzees, and in terms of other-regarding preferences, dogs do not appear to act altruistically towards humans when food is involved. Overall, the current results may be taken as a confirmation that dogs' human-like social skills may represent a specialisation to receive human communication.

Content list

Declaration

Whilst registered as a candidate for the above degree, I have not been registered for any other research award. The results and conclusions embodied in this thesis are the work of the named candidate and have not been submitted for any other academic award.

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Journal articles:

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Kaminski, J., & **Piotti, P.** (2016). Current Trends in Dog-Human Communication: Do Dogs Inform? *Current Directions in Psychological Science*, *25*(5), 322-326.

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Piotti, P., Kaminski, J. (2015) Do dogs use communication helpfully? Poster presentation. Ethodogs workshop "Social relationships and cognitive competences in the domestic dog: bridging science and education", Erice, Italy.

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Piotti, P., (2016, November) La comunicazione del cane nella cooperazione: che cosa ne sappiamo? (Dog communication in cooperative contexts: what do we know?) Invited speaker at the "III Congresso Gentle Team: la scienza in campo" (3rd Gentle Team Congress: the science in the field), Alfiano Natta, Italy

Piotti, P. (2016, January) Dog Cognition and Research. Invited lecture at Brinsbury Campus, Chichester College, United Kingdom.

Piotti, P. (2015, March) Helpful dogs? Invited lecture at Sparsholt College, United Kingdom.

Chapter 1. General Introduction

Introduction

Humans are considered the most collaborative species among primates: they form social groups where they collaborate with unrelated individuals, even when they do not expect to meet them again, in complex and flexible ways (Henrich et al., 2005; Melis & Semmann, 2010). Here *collaboration* is used as an umbrella term to indicate any form of behaviour that is beneficial to others, regardless the costs for the individual (Melis & Semmann, 2010); the same use will be made of the term *helpful*, which often has a similar meaning in the literature. A distinct meaning will be given to the term *pro-sociality*, i.e. voluntary behaviour performed with the intent to benefit others at no costs for the actor (Jensen, Vaish, & Schmidt, 2014), which differs from *altruism*, i.e. behaviour that benefits others at a cost for the actor (Fehr & Fischbacher, 2003). *Cooperation* is used to indicate collaborative activities performed and based on the formation of a common goal for the actor and its partners (Warneken & Tomasello, 2007).

It has been suggested that collaborative social interactions have a crucial role in the development of humans' cognitive skills (Vygotsky, 1978). Some authors proposed the so-called *Vygotskian intelligence hypothesis*, suggesting that social collaboration might have driven the evolution of unique aspects of human cognitive skills required to form human complex society (Dunbar, 2009;

Tomasello, Carpenter, Call, Behne, & Moll, 2005; Waller & Dunbar, 2005). As a consequence, some suggest that some types of collaborative behaviour may be unique to the human species.

One example is *informative* communication. Several species have been observed to use certain communicative behaviours, called *referential*, i.e. gestures that are performed to indicate an external entity. This is the case for the human *pointing* gesture, which emerges in human children around 10 months of age, when infants start to point towards out-of-reach objects (Camaioni, 1992). Similar gestures are observed in other species, especially when the animal interacts with humans, such as captive chimpanzees (*Pan troglodytes*) (Leavens, Hopkins, & Bard, 1996), dolphins (*Tursiops truncatus*) (Xitco, Gory, & Kuczaj, 2004; Xitco, Gory, & Kuczaj II, 2001), and dogs (*Canis familiaris*) (Hare, Call, & Tomasello, 1998; Miklósi, Polgárdi, Topál, & Csányi, 2000). However, humans are considered the only species able to communicate with informative motives, i.e. to indicate something that the receiver, but not the actor, has an interest in, and only for the benefit of the receiver (Liszkowski, Carpenter, Striano, & Tomasello, 2006). According to some authors, this is because human communication is *intrinsically cooperative* (Grice, 1975), i.e. the receiver when interpreting communication, will make the assumption that the actor has cooperative motives and expectations (Grice, 1989). There is currently no evidence of informative communication in non-human animals, and one of the aims of this thesis is to investigate this in dogs (Chapters 2 and 3).

Another area of interest is *reputation* forming. Reputation refers to the perception that an individual has of another's intentions and common behaviour (Russell, Call, & Dunbar, 2008). Reputation is particularly relevant to collaborative behaviour, because it may explain the existence of altruistic behaviour toward unrelated individuals that are not expected to meet again (Nowak, 2006). Some authors argue that it is surprising that collaborative interactions occur so commonly in the animal kingdom (Abdai & Miklósi, 2016): according to the theory of natural selection (Darwin, 1859), evolution relies on the survival of the fittest and individuals compete with each other. Therefore, it is very difficult to explain the existence of altruistic behaviours directed to non-kin, as they benefit the receiver at a cost for the actor (Axelrod & Hamilton, 1981; Moore, 2016; Nowak, 2006; Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012). Trivers (1971) suggests a possible mechanism, called *direct reciprocity*, where individuals that have repeated encounters are more likely to help those who have helped them in the past. However, humans often help others when there is no possibility for a direct reciprocation. In these cases, helping creates a good reputation that will be rewarded by others, a mechanism called *indirect reciprocity* (Nowak & Sigmund, 1998b). Empirical evidence on indirect reciprocity indicates that humans who are more helpful are also more likely to receive help (Wedekind & Milinski, 2000). It is hypothesised that reputation allows for the evolution of collaboration through indirect reciprocity (Nowak & Sigmund, 1998b). However, it is debated to what extent the ability to choose a partner for collaboration based on reputation is shared among human and non-human species (Abdai & Miklósi, 2016; Alexander, 1987; Melis, Hare, & Tomasello, 2006; Vail, Manica, & Bshary, 2014). Humans are highly relevant social partners for dogs (Nitzschner, Melis, Kaminski, & Tomasello, 2012), however there are no studies in the literature on dogs' ability to use reputation judgements when requesting human help. Therefore, the first step of my research in this direction is to investigate whether the phenomenon occurs in dogs (Chapter 4).

Another area of interest is the investigation of pro-social (Jensen et al., 2014) and altruistic (Fehr & Fischbacher, 2003) behaviour (often regarded to as other-regarding preferences) through food-sharing paradigms. In the abovementioned reciprocal altruism theory, Trivers proposed some prerequisites of altruism toward non-kin: the benefits to the recipient surpass the costs to the actor; the two individuals are bound by a stable relationship with frequent interactions; the individuals can recognize partners and their behaviour to avoid exploitation by non-cooperators (Trivers, 1971). These prerequisites can be satisfied through very simple mechanisms: the *tit-for-tat*, i.e. one individual copies the actions of the other (Axelrod & Hamilton, 1981) or associative learning strategies, i.e. if the recipient exploits helping actions, the actor changes strategy (Nowak & Sigmund, 1993). Because these are very simple strategies, which do not require complex and elaborated cognitive abilities, they can explain the evolution of reciprocity in non-human animals (Yamamoto & Tanaka, 2009). However, the human collaborative system might be unique in the animal kingdom in that humans show altruistic behaviour without any immediate benefit or expectations for future reciprocation (Fehr & Fischbacher, 2003; Melis & Semmann, 2010). One of the most common methods for the comparative study of altruistic behaviour is the so-called *bar-pulling paradigm*: animals are put in pairs in adjacent cages and can feed either themselves or a partner by pulling a bar. This test leads to several responses including, potentially, altruistic behaviour (Colman, Liebold, & Boren, 1969). The paradigm was very recently adapted to dogs (Dale, Quervel-Chaumette, Huber, Range, & Marshall-Pescini, 2016; Quervel-Chaumette, Dale, Marshall-Pescini, & Range, 2015; Quervel-Chaumette, Mainix, Range, & Marshall-Pescini, 2016), however, the designs have limitations in relation to the level of training and number of testing conditions, which I address in Chapter 5.

As it appears from this introduction, one recurring interest for researchers is whether human's level of collaboration is unique (Fehr & Fischbacher, 2003; Gómez, 2007; Melis et al., 2006; Moore, 2016; Yamamoto & Tanaka, 2009). Comparative research has tried to address this concept traditionally focusing on the comparison between humans and other primates. The idea was to investigate the evolution of collaboration by looking at species homologous to humans, i.e. characterised by a common ancestor, such as the chimpanzees. Such studies initially appeared to indicate that either a certain level and complexity of altruism is unique to human beings, or it was present in an ancestor common to humans and chimpanzees but not other animals (Melis & Semmann, 2010; Warneken & Tomasello, 2009a). For example, human children altruistically share information with others, while chimpanzees only communicate to request something that they have an interest in (Bullinger, Zimmermann, Kaminski, & Tomasello, 2011). Similarly, children were observed to help an experimenter in a wide range of tasks (Warneken, Chen, & Tomasello, 2006; Warneken & Tomasello, 2007). Chimpanzees only helped a human partner but only in the simplest tasks, such as handling an object that was out of the reach of the experimenter (Tomasello & Warneken, 2006), or in activities that did not involve sharing food (Tomasello & Warneken, 2006; Warneken et al., 2006; Warneken & Tomasello, 2009b).

However, in the recent years researchers have focused on species more distantly related to humans and new interest is rising on studies on analogous species, i.e. that do not share common ancestors, but rather common abilities with humans (Miklósi, Topál, & Csányi, 2004). Such studies are leading to previously unexpected findings, useful both to psychologists and ethologists (Hare & Tomasello, 2005; Miklósi et al., 2004), and show that certain cognitive skills that are not unique of our species but shared with other non-human animals, e.g. corvids (Clayton & Emery, 2005) or canids (Miklósi & Topál 2013). Dogs came into focus for their ability to understand the social human behaviour (Cooper et al., 2003; Miklósi et al., 2004). Similarities with humans in physiology, neurobiology, social behaviours, and the fact that dogs have been domesticated and have been living in close contact with humans for more than 30.000 years, make dogs good models for the study of human social cognitive abilities and underlying mechanisms (Miklósi, Topál, & Csányi, 2007; Overall, 2000; Thalmann et al., 2013). Furthermore, dogs present some social cognitive abilities observed in humans but not in any other non-human species (Hare & Tomasello, 2005; Lakatos, Soproni, Dóka, & Miklósi, 2009; Miklósi, Pongrácz, Lakatos, Topál, & Csányi, 2005; Tomasello & Kaminski, 2009). Dogs are the typical example of a species analogous to humans: it has been hypothesised that, during a unique domestication history, dogs have evolved specific social and communicative skills for interacting with humans because they share with human beings the ecological niche of the human social environment (Miklósi et al., 2004).

One hypothesis, the *Domestication Hypothesis* (Hare, Brown, Williamson, & Tomasello, 2002; Miklósi, Kubinyi, Topál, & Gácsi, 2003), states that dogs might have evolved human-like social and communicative skills as a form of convergent evolution (Hare & Tomasello, 2005). Cases of convergent evolution with humans are rare and extremely useful for the study of inheritable traits and the selective pressures, that shaped them (Hare & Tomasello, 2005; Miklósi et al., 2004). In the case of dogs, one possibility is that some of their social skills are a specific adaptation to the human social environment: human social systems might have posed the principal adaptation pressure for the evolution of the domestic dog, leading to the development of certain human-like social cognitive skills (Hare et al., 2002; Miklósi et al., 2003). Therefore, understanding the functioning and limits of dogs' social intelligence may significantly contribute to our understanding of the evolution and function of social cognitive skills in general (Cooper et al., 2003; Miklósi et al., 2004).

More recently, another non-exclusive hypothesis has been proposed, i.e. the *Canine Cooperation Hypothesis* (Range & Virányi, 2013, 2014, 2015). This hypothesis suggests that dogs' social skills towards humans evolved and are actually mediated by the high level of social attentiveness, tolerance, and consequent high cooperativeness of a common ancestor of dogs and wolves. In fact, these skills, which are preconditions for successful cooperation, are still present in wolves and might have provided a good basis for the evolution of dog-human cooperation (Range & Virányi, 2015). For example, wolves show increased attentiveness to conspecifics and are better at learning from them, compared to identically raised dogs (Range & Virányi, 2014). In this view, relevant skills were transferred onto dog-human interactions as dogs, during the domestication process, became less fearful of humans (Range & Virányi, 2015). Additionally, similarly to wolves, dogs can form stable social groups and can show forms of cooperation, e.g. raising their offspring (Pal, 2005) or defending their territory (Bonanni, Natoli, Cafazzo, & Valsecchi, 2011).

These two evolutionary mechanisms are not mutually exclusive, and might both explain the socio-cognitive skills that we currently see in dogs (Range & Virányi, 2015). Due to dogs' human-like skills, and the unique adaptation to the human environment, the study of collaborative interactions in the domestic dogs may increase our understanding of the underlying cognitive mechanisms of collaboration in general and the selective pressures that may shape the evolution of collaboration. However at this stage, this area of research is largely understudied in this species and evidence in the literature is very limited. It is often the case of testing whether certain behaviours are present in the species at all. The aim of this PhD thesis is therefore primarily to establish whether, and to what extent, dogs present behaviours that are considered as the building blocks for successful collaboration, such as informative communication, reputation forming or food sharing (Kaplan & Hill, 1985; Tomasello, 2007; Trivers, 1971). My main interest was to investigate interactions between dogs and humans in order to establish what might indicate collaboration. The second aim was to infer what dogs might take into account in such interactions and, potentially, their underlying motivations.

In the following chapters, I will discuss the three main areas that I have introduced: informative communication, reputation forming, and altruism and pro-sociality. Informative communication (Chapter 2 and 3), a specific type of communication that is thought to be unique to humans (Liszkowski et al., 2006), is largely understudied in other species—one study investigated chimpanzees

(Bullinger et al., 2011) and another on dogs (Kaminski, Neumann, Bräuer, Call, & Tomasello, 2011). Chapter 4 focuses on the effect of reputation judgment on dogs help requests to humans. There is quite a large body of research involving dogs, related to this topic (Abdai & Miklósi, 2016; Freidin, Putrino, D'Orazio, & Bentosela, 2013; Nitzschner, Kaminski, Melis, & Tomasello, 2014; Nitzschner et al., 2012). Surprisingly, however, none of the studies looked at dogs' ability to recognise the skilfulness or the efficiency of their partner when they are in need of help. This is a relevant skill (Nowak & Sigmund, 1998a) that has been investigated in several non-human animals, such as chimpanzees (Melis et al., 2006), elephants (Plotnik, Lair, Suphachoksahakun, & de Waal, 2011), and fish (Vail et al., 2014). Chapter 5 investigates other-regarding preferences through food sharing. The topic is widely researched in primates, often with contradicting results. As a recent review suggests, there are several technical difficulties which might bias the findings and make it difficult to adapt research apparatuses and protocols to different species (Marshall-Pescini, Dale, Quervel-Chaumette, & Range, 2016). There are currently three papers investigating other-regarding preferences in dogs (Dale et al., 2016; Quervel-Chaumette et al., 2015, 2016). However, these could only investigate one type of collaborative behaviour, giving a limited picture. Moreover, the adapted paradigms and protocols heavily rely on training for the dogs to understand the contingencies of testing conditions. This makes it difficult to infer the underlying cognitive mechanisms and tease apart helpful intents from lower level mechanisms, such as expectation of rewards. Therefore, I proposed a novel apparatus and protocol that does not require formal training for the dogs to understand the testing conditions (Chapter 5).

Informative communication in dogs?[1]

Dogs have remarkable social skills, which are considered to be to some extent functionally equivalent to those of humans (Kaminski & Marshall-Pescini, 2014). Dogs, like human infants, are very good at following visual, gestural cues provided by humans, such as pointing or gazing at a specific target (Hare & Tomasello, 1999; Soproni, Miklósi, Topál, & Csányi, 2001). Without the need of any formal training (Hare & Tomasello, 1999), and at a very young age (Riedel, Schumann, Kaminski, Call, & Tomasello, 2008), dogs' ability to use human gestures to find a hidden reward is comparable to that of young children in similar settings (Lakatos et al., 2009; Topál, Gergely, Erdohegyi, Csibra, & Miklósi, 2009).

In addition, when following human pointing, dogs tend to outperform their closest living relative, the wolf (*Canis lupus*), even when both species are raised in identical conditions (Virányi et al., 2008). Unless wolves receive extensive and prolonged training (Udell & Wynne, 2008), they do not reach as readily the same skills as dogs when it comes to using human communicative gestures (Gácsi, et al., 2009; Miklósi et al., 2003; Virányi et al., 2008). Finally, dogs do not seem to be as good at following cues to hidden food provided by other dogs,

[1] Based on the published manuscript:
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rather than humans, in an experimental setting (Hare & Tomasello, 1999; Shyne, Singer, & Jameson, 2012).

Taken together, this evidence led to the so-called Domestication Hypothesis, which proposes that dogs' human-like social skills derive from dogs' unique evolutionary past with humans and are an adaptation to life with humans (Hare et al., 2002). Dogs were the first species to be domesticated (Skoglund, Ersmark, Palkopoulou, & Dalén, 2015), and one possibility is that later during the domestication process humans selected dogs for activities, such as hunting and herding, that required skill at following human cues (Kaminski & Nitzschner, 2013). One hypothesis is therefore that dogs adapted to life in the human environment by developing specific social skills for interacting with humans (Hare et al., 2002; Miklósi et al., 2003). This hypothesis is further supported by the finding that dog breeds selected for work in continuous visual contact with human partners (e.g., sheepdogs, gun dogs) are more successful in following the human pointing gesture than dogs that are selected for independent work (e.g., hounds, underground-hunting dogs, livestock guard dogs, sled dogs) or non-purebred dogs (Gácsi, McGreevy, Kara, & Miklósi, 2009b).

Dogs also have the ability to referentially produce communicative behaviours e.g. in order to guide a human toward a certain object (Miklósi et al., 2000). These behaviours are described as *showing* behaviour, which includes gaze alternation and attention-getting behaviours that dogs use to indicate a referent (Miklósi et al., 2000). The showing behaviour fulfils the criteria for intentionality and referentiality as they have been introduced for primates (Gaunet & Deputte, 2011; Leavens, 2004). Specifically, dogs produce this behaviour in the absence of an audience; they alternate gazes between the human and the referent; they use attention-getting behaviours, e.g. vocalizations (Miklósi et al., 2000); and they take into account the attentional state of their audience (Gaunet & Deputte, 2011; Marshall-Pescini, Colombo, Passalacqua, Merola, & Prato-Previde, 2013).

Dogs' flexible use of interspecific communication with humans leads to questions about the cognitive mechanisms underlying such skills. One question is whether dogs understand the informative nature of human communication or, rather, interpret it as imperative, i.e. telling them where to go and/or what to do (Kaminski et al., 2011b; Kaminski & Nitzschner, 2013; Topál et al., 2009b). The question is particularly relevant given that informative communication has been described as a uniquely human form of communication (Liszkowski et al., 2006; Liszkowski, Carpenter, & Tomasello, 2008; Tomasello, Carpenter, & Liszkowski, 2007; van der Goot, Tomasello, & Liszkowski, 2014).

In human communication, imperative communication has the goal of obtaining something for the self by influencing someone's behaviour, e.g. a child pointing at an object that he or she wants to obtain (Camaioni, Perucchini, Bellagamba, & Colonnesi, 2004). From a cognitive perspective, it requires the child to conceive of the other person as an animate *agent of action*—something like a *social tool* (Camaioni et al., 2004). By contrast, declarative communication has the goal of sharing attention and interest with others and influencing someone's attentional focus by directing it to another object (Camaioni et al., 2004) or to the self (Moore & Corkum, 1994). From a cognitive perspective, declarative pointing is thought to require some understanding of others' mental states, e.g. others' intentions (Camaioni et al., 2004). Informative pointing is defined as a subtype of declarative gestures, which specifically refers to communicative acts produced with the intent to inform others about things they want or need to know (Liszkowski et al., 2006). Several cognitive skills need to be in place for informative pointing to occur. Tomasello et al. (2007) suggested that there needs to be a mutual understanding of the signaller's intention to communicate. This is often signalled through so-called *ostensive cues*, such as eye contact and high-pitched voice (Csibra & Gergely, 2009). There also needs to be an understanding of referential intention, which is required for the receiver to understand that he or she has to attend to a specific referent, and finally, there needs to be a motivation to be helpful and to provide information to the other (Tomasello et al., 2007).

Dogs' human-like social skills make them a good candidate for exploring whether human forms of communication are indeed unique (Kaminski et al., 2011b). Since dogs' social skills appear to be a specialisation to the communicative interaction with humans specifically, research in this area has primarily focused on dog-human communication. In order to be able to understand the informative aspect of communication, dogs would need to possess the cognitive skills required for such communication: an understanding of the communicative intent (e.g., sensitivity to ostensive cues), a referential understanding of communication (Tomasello et al., 2007) , and informative (helpful) motives.

There is some evidence that might suggest that dogs understand intent—more specifically, communicative intent. Dogs seem to perceive human actions as goal- directed, in that dogs differentiate human actions from the "actions" of an inanimate object, i.e. a box (Marshall-Pescini, Ceretta, & Prato-Previde, 2014)—although if a robot performs certain actions, dogs seem to accept it quickly as a *goal-directed* being, which suggests that dogs might attend to actions rather than intentions (Abdai, Gergely, Petró, Topál, & Miklósi, 2015). When it comes to dogs' understanding of humans' psychological states, results are not unanimous. Dogs seem to understand something about a human's current perspective, but this does not seem to lead to an understanding of humans' psychological states (Heberlein et al., 2017; Kaminski et al., 2009; Maclean, Krupenye, & Hare, 2014; Viranyi, Topál, Miklósi, & Csányi, 2006). Dogs do, however, seem to attend to humans' communicative intent. For example, dogs differentiate gestures made with communicative intent from random movements that resemble pointing gestures (Kaminski, Schulz, & Tomasello, 2012). Different ostensive cues, such as eye contact and tone of voice, seem to help dogs identify when a human has the intent to communicate (e.g., Scheider, Grassmann, Kaminski, & Tomasello, 2011; Téglás, Gergely, Kupán, Miklósi, & Topál, 2012).

The idea that dogs might have some understanding of the referential nature of human communication was suggested by a study showing that dogs followed a human's gaze toward a certain target only when it was preceded by ostensive cues (Téglás et al., 2012). Dogs are also sensitive to the order in which ostensive and referential signals (gestures) are given during a communicative interaction with humans. When the ostensive cues are given before the gesture, dogs attend to the gesture more than when it is the other way around. This may indicate that during the presentation of the ostensive cues, dogs are already forming referential expectations (Tauzin, Csík, Kis, & Topál, 2015). Finally, dogs also use gaze alternation in a referential way during situations that require social referencing, i.e. seeking information from another individual regarding a target (Marshall-Pescini et al., 2013). However, when they see a human pointing and the referent of the gesture is later moved, dogs reach the location that the human indicated rather than the actual object. This suggests that they may understand pointing as a general indication of where to go rather than what to do (Tauzin et al., 2015b)—see also Kaminski & Nitzschner (2013), for a discussion of this point.

Finally, the central question is whether dogs act based on cooperative/helpful motives. Dogs' ability to follow human pointing might be partly based on their ability to understand the cooperative element of human communication in a way that other nonhuman animals do not (Kirchhofer, Zimmermann, Kaminski, & Tomasello, 2012). For example, a direct comparison of dogs' performance in an object-choice task to that of chimpanzees, humans' closest relative, showed that dogs were especially skilled at finding hidden food when they could follow human social cues (i.e., the pointing gesture), whereas chimpanzees performed better when they could use physical, non-social cues, i.e. the noise made when a cup holding the food was shaken (Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006). Furthermore, dogs are outstandingly good at following a point specifically when the gesture is used in cooperative contexts, i.e. when the human partner points to help the dog find a food reward (Hare & Tomasello, 1999) or is used to request a dog's help in retrieving an object (Kirchhofer et al., 2012). Dogs have also evolved the predisposition to use gaze to communicate with humans when facing unsolvable problems, suggesting that they expect humans' help (Miklósi et al., 2003). Moreover, dogs do not outperform chimpanzees in non-communicative social contexts, meaning that dogs' skills do not seem to extend to all social interactions but may be limited to cooperative, communicative contexts (Wobber & Hare, 2009). This suggests that dogs' social skills possibly rely on a special receptiveness to human cooperative communication (Kirchhofer et al., 2012), which seems to depend on a sensitivity to humans' ostensive referential signals (Topál et al., 2009a).

In a study conducted by Bräuer, Schönefeld, and Call (2013), dogs were trained to open a door by pushing a button. Dogs needed to be prompted to push the button by human communication and would not push it spontaneously. Moreover, there is evidence that in communicative contexts, dogs differentiate between objects based on their owners' preference for one over the other, rather than their own selfish interest (Turcsán, Szánthó, Miklósi, & Kubinyi, 2014). Additionally, dogs have the general motivation to act cooperatively in response to humans' requests. When asked to indicate the location of a hidden object, dogs indicated things that a person, but not they themselves, had an interest in; however, they then did not differentiate between an object the person was interested in versus an object the person was not interested in (Kaminski et al., 2011a). There is evidence that dogs interpret human communications as directives (Kaminski et al., 2011a; Scheider, Kaminski, Call, & Tomasello, 2013), such as a command to fetch, irrespective of the object (Kaminski et al., 2011a). This suggests that dogs' helpful indications may partly depend on the effect of social facilitation, which can suppress the dog's own preferences—for example, when following human pointing, dogs chose a less preferred food reward indicated by a human over a reward that they preferred but that was not indicated (Pongrácz, Hegedüs, Sanjurjo, Kovári, & Miklósi, 2013).

Overall, the evidence suggests that dogs may possess some of the skills necessary for the understanding of communication as information. There is, however, not enough evidence suggesting that dogs act with helpful motives when interacting with others, and, in addition, there is not much evidence for dogs' understanding of humans' mental state, i.e. human perspective and state of knowledge (Heberlein et al., 2017; Kaminski et al., 2011a; Maclean et al., 2014). According to a *mentalistic* approach, this is necessary for declarative communication to be possible (Tomasello et al., 2007). Some authors, however, have challenged this mentalistic view, arguing for a non-mentalistic basis of human preverbal communication (Csibra & Gergely, 2009, 2013; Leavens, 2004; Leavens, Russell, & Hopkins, 2005; Moore, 2013, 2014). The hypothesis here is that infants' early pointing may be aimed at gaining positive emotional reactions rather than directing the attention of others to external objects, and therefore the understanding of others' attention is not necessary (Moore & Corkum, 1994). Also, Gergely and Csibra (2009) suggested that human communication may rely on *natural pedagogy* (i.e., it is characterized by a series of elements that allow and facilitate the transfer of knowledge). Specifically, even very young children are sensitive to ostensive cues indicating to others that they are addressed in the communication (Csibra & Gergely, 2009). Such cues create referential expectations in the receiver (Csibra & Volein, 2008), which allow him or her to interpret the communication as conveying information that is relevant and generalizable (Csibra, 2003; Csibra & Gergely, 2009, 2013). This way, the understanding of others' states of mind is not required for successful declarative communication. Thus, the authors suggested that nonhuman animal communication might be more comparable to human communication than is thought by others (Csibra & Gergely, 2009).

The currently available evidence on dog communication suggests that dogs possess some of the cognitive building blocks that need to be in place for an individual to communicate informatively: dogs seem to have some understanding of humans' communicative intent (Kaminski et al., 2012; Scheider et al., 2011; Téglás et al., 2012) and, in some situations, seem to show helpful motives and have an expectation for humans to act helpfully (Bräuer, Bös, Call, & Tomasello, 2013; Hare & Tomasello, 1999; Kaminski et al., 2011a; Kirchhofer et al., 2012; Miklósi et al., 2003). Findings on dogs' understanding of humans' mental states (Heberlein et al., 2017; Kaminski et al., 2009; Maclean et al., 2014; Viranyi et al., 2006) and their understanding of referentiality (Tauzin, Csík, Kis, Kovcs, & Topál, 2015; Tauzin et al., 2015b; Téglás et al., 2012) are still controversial, however, and as of yet there is no convincing evidence that dogs show the tendency to communicate with a motive to inform (Kaminski et al., 2011a).

The studies described in Chapters 3 and 4 will focus on some aspects that remain unclear, such as dogs' understanding of the referential nature of communication (Kaminski et al., 2011a; Kaminski & Nitzschner, 2013; Tauzin et al., 2015b; Topál et al., 2009b)—that is, understanding the relevance of the referent for the receiver—and will further investigate to what extent helpful motives drive dogs' communication with humans (Kaminski et al., 2011a).

Reputation forming in dogs

Reputation can be defined as the ability to gain "knowledge about an individual's typical behaviour based on knowledge of that individual's past behaviour" (Russell et al., 2008). Reputation is of particular interest in the study of human collaborative behaviour since, from an evolutionary point of view, it is difficult to explain collaboration when there is no expectation for reciprocation of favours (Wedekind & Milinski, 2000). One possibility is that an individual's reputation may be monitored and taken into account by others in future social interactions (Fehr & Fischbacher, 2004; Hauser, McAuliffe, & Blake, 2009; Trivers, 1971). For example, Wedekind and Milinski (2000) asked human adults to play a game where they could repeatedly give money and receive from others, but never interacted directly, so could not reciprocate favours. However, the participants, had access to receivers' *image scoring*, i.e. how the individual was perceived by the group – which can also be defined as reputation. The authors found that an individual's altruistic behaviour improved the individual's image scoring, and that individuals with higher scoring received higher donations. The authors concluded that image scoring affects *indirect reciprocity* (Alexander, 1987) and this may play role in the evolution of cooperation, for example in large groups (Nowak, 2006; Nowak & Sigmund, 1998a, 1998b; Wedekind & Milinski, 2000). Different studies often use different terminology, therefore Abdai and Miklósi determined three criteria for *reputation based judgements*: an individual "(1) assigns different values (positive, negative) to particular behavioral patterns (e.g., helping, hindering) that are performed in a social interaction (e.g., problem solving), (2) associates these behaviors with specific individuals (partnership values) and (3) shows different behaviors (e.g., avoidance or preference) toward others based on the overall value which has been associated with them" (Abdai & Miklósi, 2016, p. 2).

The mechanisms connecting collaboration with reciprocity appear to be rooted very early in the development of human beings. For example, Olson and Spelke (2008) investigated various forms of reciprocation in 3.5-year-old children, who have limited experience with complex cooperative networks. Already at this age, children are more likely to give to individuals known for being generous rather than selfish ones (Olson & Spelke, 2008). One interesting question is whether indirect reputation influences collaborative choices in non-human animals as well. Comparative research has provided two possible hypotheses.

One hypothesis is that mechanisms based on reputation were possibly present in a common ancestor of humans and their closest relative, the chimpanzee (Melis et al., 2006). This hypothesis is supported by studies comparing human and non-human primates. For example, a study investigated a group of semi-free ranging chimpanzees, which were given a chance to recruit a conspecific partner for an activity that required solving a problem cooperatively in order to obtain food. The chimpanzees had a direct experience with potential partners, i.e. they interacted with the partners trying to solve the problem, and showed to prefer a partner very effective at solving the problem compared to a non-effective one (Melis et al., 2006). Another study compared children with chimpanzees, bonobos (*Pan paniscus*) and orang-utans (*Pongo pygmaeus*) to compare their abilities in forming an opinion about others based on direct and indirect experiences (i.e. observations of third party interactions). According to the study, the ability to form direct and indirect reputation judgment is present in children and at least some other great apes. Specifically, orang-utans and 2.5-year-old human children prefer approaching a human experimenter that acted nicely towards them, rather than a "mean" experimenter. Orang-utans, chimpanzees and 2.5-year-old children could also form an opinion about an experimenter taking into account how they interacted towards third parties (Herrmann, Keupp, Hare, Vaish, & Tomasello, 2013).

Another hypothesis is that choosing collaborative partners based on reputation is advantageous in social groups (Abdai & Miklósi, 2016; Nowak & Sigmund, 1998a, 1998b; Wedekind & Milinski, 2000). It may contribute to survival by avoiding harmful individuals as well as choosing the most appropriate partner for cooperative activities (Abdai & Miklósi, 2016). Therefore, indirect reciprocity and reputation forming may evolve in certain species based on their ecological needs (Vail et al., 2014). Indirect reciprocity may be relevant not only in human society but possibly also in some primates, social canines and other groups (Abdai & Miklósi, 2016; Alexander, 1987; Nowak & Sigmund, 1998a). Computer models confirm that individual selection may favour recipients that have helped others in the past because they gain the image of valuable collaborative partners (Nowak & Sigmund, 1998a). Comparative research also provides examples from non-primates animals. For example, coral trouts (*Plectropomus leopardus*) can determine appropriately when a situation in a hunting context requires a collaborator and then they choose the most efficient collaborator (Vail et al., 2014). Similar results were observed in a group of elephants (*Elephas maximus*), which could learn to coordinate with a partner in a task requiring two individuals to simultaneously pull two ends of the same rope to obtain a reward. The elephants also inhibited the pulling response if the arrival of a partner was delayed or the partner lacked access to the rope, which suggests that they recognised the role of the partner in the cooperative task (Plotnik et al., 2011). These have been interpreted as examples of convergent evolution dictated by the selective pressures of the species' ecological niche (Plotnik et al., 2011; Vail et al., 2014).

It is possible that one mechanism, or a combination of the two, mediates the evolution of indirect reciprocation and reputation judgement in a species. Dogs are the ideal subjects to investigate these possibilities. It has been hypothesised that during domestication, dogs adapted to a specific environment, the human niche (Hare & Tomasello, 2005; Miklósi et al., 2003). During this process, dogs have been selected for cooperating with humans in activities such as hunting and herding (Clutton-Brock, 1995; Hare et al., 2002; Ruusila & Pesonen, 2002). Humans are highly relevant social partners for dogs (Nitzschner et al., 2012). For example, dogs coordinate behaviourally with humans in problem solving situations (Bräuer et al., 2013a; Ostojić & Clayton, 2013). Dogs have also evolved communicative strategies to request human's help, the *looking back behaviour* (Miklósi et al., 2003). This has been observed by investigating dogs and wolves raised in identical conditions, i.e. both highly socialised to humans. In a study, authors observed dogs and socialised wolves' behaviour during a so-called *unsolvable task*: during this test, the subject is initially given a chance to learn that they can retrieve some food from below a container by pulling a rope. After a few successful retrievals, the apparatus is altered so that the rope is stuck and food becomes inaccessible—i.e. the task becomes *unsolvable*. Dogs and wolves are presented with the unsolvable task in the presence of a human partner and the results indicate that dogs readily look at the human to request help, while socialized wolves do not (Miklósi et al., 2003). Given the examples above, it may be expected that dogs evolved strategies to predict human behaviour in order to determine a preferred partner during social interactions, such as cooperative activities or when they are in need of human help (Nitzschner et al., 2012). The first step of the study of indirect reciprocation in dogs is to comprehend the level of flexibility in dogs' ability to form an opinion about humans.

The literature indicates that dogs form preferences for specific human partners based on their past behaviour; however, it seems to be important for dogs to have a direct experience with the partners (Nitzschner et al., 2012). For example, in one study, dogs had direct experience with two experimenters: a *nice* experimenter who interacted with the dog in a friendly way, and an *ignoring* experimenter, who walked the dog within a room, but ignored it. At the end of these direct experiences, the dogs clearly preferred approaching and spending more time with the nice experimenter (Nitzschner et al., 2012). The authors then tried to replicate the same results but gave the dog an indirect experience of two experimenters: one was nice towards a third party (another dog), while the other was ignoring. This time, the dogs that observed the interactions did not form a preference for either of the two experimenters. The authors concluded that dogs are able to form a reputation about humans based on their direct experience only

(Nitzschner et al., 2012). Another possibility could be that, for the dogs observing the interaction, their direct experience of being ignored by the experimenters had a greater impact than the indirect experience (Abdai & Miklósi, 2016).

Overall, research on dogs' ability to judge third party interactions has provided contradicting results. For example, in two studies, the dogs were given a chance to witness an exchange between a human receiver and a *generous* experimenter, who gave food to the receiver, and a *selfish* experimenter, who offered the food and then withheld it before the receiver could take it (Kundey et al., 2011), or refused to donate the food (Marshall-Pescini, Passalacqua, Ferrario, Valsecchi, & Prato-Previde, 2011). After these demonstrations, the dogs could either approach the two experimenters or get some food given by them. If the dog approached or accepted the food from one of the two human partners, this was considered a preference choice. The dogs preferred the generous experimenter and the authors interpreted this behaviour as the ability to make a reputation-like inference for human strangers from indirect experience (Kundey et al., 2011; Marshall-Pescini et al., 2011). Kundely et al. (2011) replicated the results also when visual social cues, i.e. face-to-face contact, were reduced, and when the giving partner was an inanimate self-propelled agent. Marshall-Pescini et al. (2011) included a control condition, where there was no receiver but the donors acted exactly as before. In this control condition, dogs did not choose the generous experimenter as often and the authors concluded that this indicates that the dogs were using third-party interactions to gain information about the donors and predict their potential future behaviour. Although these findings were promising, later studies provided more parsimonious explanations. For example, Freiding and colleagues (2013) demonstrated that *local enhancement* mechanisms were driving dogs' choices. In their study, the generous and selfish experimenters swapped places right after the demonstration and before the dog could approach them. The authors found that after this manipulation the dogs either choose randomly between the location of the generous exchange and that of the selfish exchange, or they went to the last location that had been visited by the receiver. The authors suggested that possibly in theirs and previous research, dogs associated the receiver's reaction to the experimenters' location rather than the features of the person in itself—i.e. local enhancement, rather than reputation forming, could possibly explain the dogs' behaviour (Freidin et al., 2013). This conclusion has been replicated by Nitzschner et al. (2014), who found that the critical factor leading dogs' choice was the location where the generous exchange took place, not the person. These authors pointed out that allowing the dogs to receive food during the test might bias them. Therefore, similarly to Marshall-Pescini et al. (2011), dogs were not given food by the experimenters. Nitzschner et al. (2014) observed that, as a consequence, the dogs switched preference in their approaching behaviour after the first test trial (from the generous to the selfish experimenter), most likely because the generous experimenter did not give food and the dogs tried to check whether the other person might do. The authors concluded that this change of strategy is an indication that the dogs had no problems in discriminating between the two persons and could therefore exclude this point as a potential limitation.

The previous examples suggest that dogs may be able to form an opinion about humans, providing that they can gain information through direct experience (Nitzschner et al., 2012). Moreover, they highlight the importance of controlling for potential confounds which may bias dogs' choice, such as food associations with one person rather or the other or local enhancement (Nitzschner et al., 2014).

The research presented so far regards dogs' abilities to discriminate humans based on their reputation. However, there is very little research on dogs' ability to use such information when they are in need of a collaborative partner. Two studies have looked into the topic. Horn et al. (2012) tested dogs playing with a problem solving toy, after letting them experience that sometimes the toy could be empty and sometimes it could somehow get stuck. Prior to testing, dogs also experienced that a certain experimenter (a *filler*) could refill the toy when it was empty, while another experimenter (a *helper*) could fix it when it was blocked. The authors analysed looking behaviours of the dogs during the tests and their proximity to each experimenter. Their results indicated that the dogs spent more time with the filler and they interpreted this finding as an indication that dogs recognised the role of the filler and flexibly adjusted their human-directed behaviour to the current problem (Horn et al., 2012). However, it should be noted that the dogs in the Horn et al.'s (2012) study first approached the helper, regardless of the problem. The authors suggest this may be caused by a difficulty in understanding the contingencies of the physical problem the dogs were exposed to (Horn et al., 2012).

Petró, Abdai, Gergely, Topál, and Miklósi (2016) employed *unanimated objects* (i.e., robots) instead of humans as partners for the dogs, in order to try and replicate the findings by Horn et al. (2012). Their study aimed to understand whether dogs are able to detect skilfulness or the specific role played by the human in a particular situation, e.g. either refilling a toy or fixing it, forming expectations about their partners' behaviour based on previous experiences with them. Their findings indicated that the dogs could indeed select the appropriate partner when facing a problem situation; however, the authors suggested that the most parsimonious interpretation was that the dogs associated the action of either unanimated object with the specific location where the food was hidden (Petró et al., 2016).

It is still unclear whether dogs can recognize skilfulness and take it into account when requesting help, especially from humans (Horn et al., 2012). For example, it is possible that dogs do not understand the physical contingencies of the task at hand. However, it may as well be that dogs were moved by more parsimonious food-partner associations (Petró et al., 2016).

One way to answer this question could be to investigate the effect of *skilfulness* and the *quality of the interaction* between the dog and human partner (e.g. a nice or an ignoring partner) on dogs' help request behaviours, such as the looking back behaviour (Miklósi et al., 2003).

Other-regarding preferences in dogs

Based on the costs and benefits of helpful acts, researchers have defined two forms of helpful behaviour: pro-social behaviour, i.e. voluntary behaviour that benefits others (Jensen et al., 2014), and altruistic behaviour, i.e. behaviour that benefits others at a cost for the actor (Fehr & Fischbacher, 2003; Tomasello, 2009). In order to investigate helpful motives, often referred to as *other-regarding preferences* (Burkart, Fehr, Efferson, & van Schaik, 2007; Quervel-Chaumette et al., 2015; Stevens, 2010), food sharing has been largely studied in primates in natural settings (Feistner & McGrew, 1989; Jaeggi & Gurven, 2013; Kaplan & Hill, 1985). *Food sharing* is defined as "the un-resisted transfer of food from one food-motivated individual to another" (Feistner & McGrew, 1989; Jaeggi & Gurven, 2013, p. 1) and is seen as a sign of helpful motivation (Smith & Bird, 2000). Empirical research in laboratory settings has focused on the comparison between humans and other primates with the scope of disentangling the mechanisms that explain this form of collaboration (Tomasello, 2009). For example, researchers found that chimpanzees do not provide food to a conspecific (Jensen, Hare, Call, & Tomasello, 2006; Silk et al., 2005) unless they are actively solicited to do so (Melis et al., 2011). On the contrary, humans are thought to have an innate predisposition for other-regarding preferences (Hepach, Vaish, & Tomasello, 2013).

A large body of evidence on other-regarding preferences in non-human animals derives from the bar-pulling paradigm, originally designed for monkeys

(Colman et al., 1969). A subject (donor) is initially trained to operate a food delivery system, which allows it to obtain a reward and/or giving it to a partner (receiver). The test and the apparatus have been adapted to several different species, including various non-human primates (Bullinger, Burkart, Melis, & Tomasello, 2013; Burkart et al., 2007; Cronin, Schroeder, Rothwell, Silk, & Snowdon, 2009; Stevens, 2010), parrots and corvids (Schwab, Swoboda, Kotrschal, & Bugnyar, 2012), and dogs (Dale et al., 2016; Quervel-Chaumette et al., 2015, 2016). In some test designs, the donor can choose between different collaborative outcomes, while in others they are presented with one potential outcome and their response, or lack of, is measured (Colman et al., 1969). In order to test whether the donors act with the intention to benefit the receiver, several studies also compare pro-social and altruistic conditions with control conditions, in which the receiver is not present or cannot access the delivered reward (Bullinger et al., 2013; Burkart et al., 2007; Cronin et al., 2009; Cronin, Schroeder, & Snowdon, 2010; Lakshminarayanan & Santos, 2008; Massen, Luyten, Spruijt, & Sterck, 2011; Melis et al., 2011; Silk et al., 2005; Stevens, 2010; Takimoto, Kuroshima, & Fujita, 2010; Vonk et al., 2008).

Two main theories explain the possible mechanisms that make dogs good co-operators, both with humans and other dogs. According to the Domestication Hypothesis (Hare et al., 2002; Miklósi et al., 2003), dogs might have adapted to life with humans following a unique domestication process. Dogs are the most ancient domesticated species, with this process being dated around 33,000 years ago (Ovodov et al., 2011; Skoglund et al., 2015; Thalmann et al., 2013; Wang et al., 2015). During this process, dogs were used for a number of collaborative activities which involved being skilful at cooperating and communicating with humans (Clutton-Brock, 1995; Ruusila & Pesonen, 2002). Another non-exclusive possibility is described in the Canine Cooperation Hypothesis, according to which dog-human cooperation is mediated by the high level of cooperativeness, social attentiveness and tolerance present in dogs' ancestors (Range & Virányi, 2015).

There are several example of dogs' ability to cooperate. For example, in a recent study, dogs were put in a situation where they could help a human partner to reach a goal, i.e. try to open a door by pushing a button (Bräuer et al., 2013b). The dog knew how to open the door but the human did not. The authors found that the dogs helped only if the human explicitly communicated with them to request help. However, when dogs helped, they continued to do so over trials without receiving any reward (Bräuer et al., 2013b). This result was later interpreted as the dogs being highly motivated to help, while having problems inferring the human's goal if this was not communicated explicitly (Bräuer, 2015). However, it could be argued that dogs did not act with helpful motives but responded to a human command to perform a trained task. In another study, dog dyads could obtain some food by acting cooperatively in a problem-solving situation and the two dogs could then share the spoils after they solved the problem. The authors observed that the dogs coordinated their actions to solve the problem, but did not tend to share; one of the partners often monopolized food, even if it was presented in two bowls (Bräuer et al., 2013a). A similar study found dogs coordinated their actions with humans in order to solve a problem—however, altruistic or pro-social tendencies were not investigated (Ostojić & Clayton, 2013).

Finally, two recent studies used a version of the bar-pulling paradigm with dogs (Quervel-Chaumette et al., 2015, 2016). The authors attempted to design a test taking into account some of the main issues commonly related to this paradigm (Marshall-Pescini et al., 2016a). One known risk is to over-train the animals, which may inflate altruistic responses; in order to overcome this, the authors designed a test relying on the extinction of a trained behaviour (Quervel-Chaumette et al., 2015). In both studies, the dogs were presented with an apparatus with two bars and had 5 seconds to choose between an *altruistic* bar, which would reward only the receiver, and a *no-reward* bar, which did not deliver food to the donor or the receiver. In the Quervel-Chaumette et al. study (2015), dogs were tested alone and in the presence of conspecific partners (familiar and unfamiliar dogs). In the Quervel-Chaumette et al. (2016), dogs were tested with a human partner as receiver. Authors also included control conditions, in which the social partner was in the room but had no access to the food. Finally, they had *knowledge probe* trials, in which food was made accessible to the donor, to assess whether the subject understood when they could access the food and the location and the food delivery. In the first study, when the receiver was another dog, the dogs chose to pull the altruistic bar rather than the no-reward bar; they preferred to pull it when it delivered food to the *familiar* receiver rather than a *stranger*, but only when this had access to the food. There was no difference in the dogs' altruistic pulling when the donor was alone or when the receiver (both stranger and familiar) had no access to the food, and dogs pulled the least for the stranger dog (Quervel-Chaumette et al., 2015). Unfortunately, the design of this study did not allow for a comparison between the donors' choices towards the partners in the no-reward condition. This issue might be increased by the short duration of the testing trials (5 seconds): as the authors admitted, donors were distracted by the presence of the stranger dog, which might relate with the very low frequency of pulls, and that was even lower than when the stranger receiver was in the room but had no access to the apparatus and was therefore more distant from the receiver (Quervel-Chaumette et al., 2015). The authors explain that the time interacting with the stranger was limited; therefore, it is possible that with more time available dogs would decide to pull in the presence of the stranger. In the second study (Quervel-Chaumette et al., 2016), the authors adopted the same apparatus and study design, however the receivers were familiar and unfamiliar human partners. The dogs' in the study did not act pro-socially towards the human partner, and familiarity did not influence the rate of food delivery. Because the humans were required to avoid interacting with the dogs, the authors suggested that this might have inhibited the dogs, thus causing the discrepancy in the results from the previous study (Quervel-Chaumette et al., 2016).

These two examples of research on other-regarding preferences in dogs are very promising; however, they present some limitations. For example, one problem is the high level of training required for the dogs to understand the testing conditions. This makes it impossible to rule out more parsimonious explanations, such as food expectation. Therefore, it is necessary to adopt a design where dogs do not need formal training to understand the conditions they are presented with. This would have the additional benefit of allowing for testing different levels of helpful situations, from selfish to altruistic.

Thesis outline

Chapter 2: Showing behaviour towards a hidden tool in selfish and altruistic contexts

The first question of interest of this thesis is whether dogs use informative communication (Kaminski et al., 2011a). This ability is thought to be unique to humans (Tomasello et al., 2007). There is evidence from comparative research that human infants use communication to inform, while humans' closest relative, the chimpanzee, only uses communication to *request* (Bullinger et al., 2011). The aim of this study was to replicate the study by Bullinger et al. (2011) using dogs as subjects. Dogs were initially trained to discriminate two objects through experiencing that one could be used as a tool to retrieve food from an apparatus, while the other object (a *distractor*) did not work. The dogs were then tested in two conditions: in a *selfish* condition, the tool was used to deliver the food to the dog; in a *helpful* condition it was used to deliver the food to the owner of the dog. During a short absence of the owner, the experimenter would hide the tool and the distractor. The owner would then return and indicate that he/she was looking for an object in order to elicit dogs' communicative responses. Only a small percentage of the dogs in the sample was able to complete the training and could be tested. Moreover, the analysis of dogs' showing behaviour (Miklósi et al., 2000) revealed that dogs did not discriminate between the two objects during the test. It is possible that food created a distraction for the dogs, therefore it was necessary to design a different protocol that did not require the use of food, whilst allowing to assess dogs' ability to discriminate across stimuli and to investigate their helpful motives in a communicative context.

Chapter 3: Do dogs provide information helpfully?

The chapter describes the protocol that was designed following the study in Chapter 2. The main question of Chapter 3 is whether dogs would use the showing behaviour (Miklósi et al., 2000) to communicate helpfully: i.e. to inform an ignorant human about the location of a target that the human, but not the dog, is interested in. Such informative intent could imply that dogs understand the human's goals and need for information and have the motivation to communicate helpfully (Kaminski et al., 2011a; Tomasello et al., 2007). The chapter develops across two studies. Study 1 investigated whether dogs would abandon a hidden dog toy to indicate either an object *useful* for a human partner, a *random* novel object or an *empty* container. They did, although they indicated the random object or the empty container more than the useful object. This might suggest that dogs were driven by an egocentric motivation to interact with the novel targets. However, *neophilia* (Kaulfuß & Mills, 2008) might also have masked dogs' helpful intents. To prevent this, in Study 2, dogs had initial access to both objects. In order to simplify the task, dogs were also expected to indicate only one object (useful or random). In this study, dogs established joint attention with the human in both conditions. However, in response to the human's vocal communication, dogs showed the useful object more persistently than the random object, demonstrating that they understood the objects' relevance to the human. Two non-exclusive conclusions can be drawn from these findings. These results might suggest that informative motives could possibly underlie dogs' showing behaviour. Also, dogs might have indicated the hidden object because they interpreted it as being the target of the human's search. This would be consistent with taking into account the objects' relevance, without necessarily implying that dogs understood the human's state of knowledge.

Chapter 4: Do dogs form an opinion about humans based on skilfulness?

This chapter investigates whether dogs are affected by their previous experience with a human partner when requesting the human's help. Reputation formation is crucial for social, and especially cooperative, interactions. It is well established that dogs evaluate humans based on their direct experience (Nitzschner et al., 2012), however this has been mainly tested in contexts where humans were either nice or not towards the dog (Heberlein, Turner, Range, & Virányi, 2016; Nitzschner et al., 2012). The literature on dogs' use of human skilfulness in a help-request context is very limited and findings are controversial (Horn et al., 2012; Petró et al., 2016). This chapter is developed through two studies. The aim of the chapter was to investigate reputation formation in dogs, based on their direct experience with human partners and their understanding of skilfulness. Dogs experienced the partner being skilled or not and either nice or not towards them. In Study 1, dogs observed two demonstration types. A skilful experimenter succeeded in solving a puzzle and obtaining food for the dog, while an unskilful experimenter failed, though food was dropped inconspicuously. The demonstrations were followed by an unsolvable task (Miklósi et al., 2003): dogs were presented with a container baited with food that was inaccessible, while the experimenters stood either side of it. Referential looks (Smith & Litchfield, 2013) towards each experimenter were recorded as a measure of dogs' help requests (Miklósi et al., 2003). Dogs who looked referentially did not look at the skilful experimenter above chance. There was also no overall difference in the frequencies of looks towards skilful and unskilful experimenter or in their duration. These results suggest that dogs might not take skilfulness into account when they form an opinion about humans or when they look referentially at humans for help. However, it is possible that dogs could not discriminate between the two experimenters within this specific context. To rule out these two possibilities, in Study 2 dogs were exposed to one demonstration only, comparing the results between subjects. A two-by-two design was adopted, with the experimenter either acting nicely towards the dog or ignoring it (quality of interaction variable) and either helping the dog in a skilful way or not helping it at all (skilfulness variable). To further reduce carryover effects, dogs experienced only one demonstration, immediately followed by one unsolvable task trial. Again, results indicated no significant differences across groups in the latency, duration or frequency of looks towards the experimenter during the unsolvable task. However, dogs that received a skilful demonstration tended to look longer at the experimenter, compared to dogs that did not receive any demonstration, with a trend towards significance. The results of these two studies seem to indicate that dogs do not take skilfulness into account when using the looking back behaviour to request human help. This conclusion is supported by recent findings suggesting that dogs' preference in looking at a human partner based on their skills might in fact be driven by more parsimonious explanations, such as association with food (Petró et al., 2016). However, the possibility that dogs might take into account skilfulness when interacting with a social partner in other contexts is not yet excluded. Another possible way to investigate this is to explore partner choice in a cooperative context. The paradigms for the study of cooperation in dogs are currently affected by several limitations. Therefore, the following chapter, focuses on the investigation of a novel paradigm that can be adapted e.g. for the study of partner choice during cooperation, other regarding preferences, and joint-goals.

Chapter 5: Relationship and human regarding preferences in dogs

This chapter explores dogs' other-regarding preferences through the use of a variation of the bar-pulling paradigm (Colman et al., 1969) designed to tackle some of the limitations of the procedures in previous studies (Dale et al., 2016; Marshall-Pescini et al., 2016a; Quervel-Chaumette et al., 2015, 2016). Specifically, there was no formal training involved in the process of exposing the dogs to the test conditions. This allowed investigating, within the same test, selfish, altruistic, and pro-social behaviour, as well as including control conditions for social facilitation biases. The results of this study suggest that dogs do not act pro-socially or altruistically towards human partners; moreover, the relationship they have with the human partner (i.e. a stranger human or their owner) has no effect on their other regarding preferences. Some of these results have been confirmed by a recent study, which was however limited to one testing condition (Quervel-Chaumette et al., 2016). This chapter concludes with the discussion of the benefits of the novel paradigm, such as a more complete assessment of other regarding preferences in dogs and decreased risk of confounding biases.

Chapter 6: General discussion

The main findings and their implications are discussed in the light of the current literature. I suggest that the results of this thesis provide further evidence confirming the possibility that dogs' human-like social skills may represent a specialisation to receive human communication

Chapter 2. Showing behaviour in selfish and altruistic contexts

Chapter overview

Dogs have outstanding skills when it comes to communicating with humans and became a subject of interest for comparative research. Similar to children and chimpanzees' pointing gesture, dogs are able to direct a human's attention to a specific target by using the so-called showing behaviour. It is not known whether dogs use the showing behaviour only to selfishly indicate a target they are interested in, like chimpanzees do, or whether they can also communicate to inform, i.e. for the benefit of their partner and with helpful intents, like children do. In this study we tested a paradigm used in children and chimpanzees for the comparative study of informative communication. After initial training to discriminate a useful *tool*, used to retrieve some food, from a random *distractor* object, dogs were tested in a situation where the dog's owner searched for the tool either to retrieve the food for him/herself (*helpful* condition) or for the dog (*selfish* condition). The results indicate that, despite the training, the dogs could not discriminate between the two objects at the time of testing.

Introduction

Dogs are particularly good at understanding human communication, such as a pointing gesture performed by a human partner (Hare et al., 1998; Miklósi et al., 1998). Dogs are also very skilled at producing communicative behaviours. For example, their showing behaviour (Miklósi et al., 2000) satisfies some of the operational criteria for referential and intentional communication provided by Leavens et al. (2004; 2005): dogs use visual orienting (gazing alternation) between a partner and distant objects, and attention getting behaviours (vocalisation) (Miklósi, Polgárdi, Topál, & Csányi, 2000), they are influenced by the attentional status of an observer (Gaunet & Deputte, 2011).

One question of interest is whether dogs are able to communicate to inform, i.e. to communicate to an ignorant human the location of a target that the human, but not the dog, is interested in (Kaminski et al., 2011a). This would imply that dogs understand the human's goals and need for information, and have the motivation to communicate helpfully (Kaminski et al., 2011a). For these reasons, such an ability has been so far considered unique of human beings (Behne, Liszkowski, Carpenter, & Tomasello, 2012; Liszkowski et al., 2006, 2008; van der Goot et al., 2014).

One study looked at whether dogs would communicate helpfully to inform an ignorant human. The authors let the dog witness a series of objects being hidden: objects that the dog had an interest in (i.e. a toy), objects that a human partner had an interest in (i.e. everyday objects that the partner had used while the dog could see it), or random distractors (i.e. objects that the partner had ignored). Then the human partner, naïve to the hiding location, would search for the objects that he/she needed while the dog had no interest in. The authors observed that the dogs indicated the location of an object more frequently when it was something they wanted rather than when it was something the human wanted. The dogs did indicate objects that they had no interest in, however, they could not differentiate between objects useful for the human partner versus a random useless object. The authors concluded that dogs had some helpful motivation when communicating with humans, but there was no evidence of informative motives (Kaminski et al., 2011). It cannot be excluded that the human objects were not sufficiently relevant to the dogs, for them to discriminate between useful object and random distractor.

Another paradigm was designed specifically for the comparative study of informative communication, by looking at the pointing gesture in human infants and chimpanzees (Bullinger et al., 2011). In this study, chimpanzees and infants were given the opportunity to point for a hidden tool in two contexts. In one context (selfish or *for-me* condition) it was made clear that the tool would be used to retrieve a reward for the pointing subject, whereas in the other context (helpful or *for-you* condition) it was clear that the tool would be used to retrieve the reward for the experimenter. The chimpanzees pointed reliably only for their own benefit, whereas the human children pointed reliably both for themselves and the experimenter (Bullinger et al., 2011).

Interestingly, the dogs in the study by Kaminski et al. (2011) did not stop indicating the location of the hidden object, even when they had no interest in it, which suggests they had some helpful motives. However, it is possible that the dogs did not discriminate the two objects based on their relevance for the human partner. Given that food is a primary resource for dogs, it is possible that the paradigm by Bullinger et al. (2011) would be better understood by dogs. Using such a paradigm would also allow direct comparison across three species: dog, humans, and chimpanzees. There is controversial evidence that dogs could understand the use of a tool in order to retrieve a reward: in a study by Viranyi et al. (2006) dogs were required to indicate either a hidden toy or a tool (a stick) that they had witnessed being used to retrieve the toy from a out-of-reach location. The dogs very rarely showed the toy and the authors concluded that these results reflected dogs' difficulties in recognizing the role of the stick in getting the toy; however, they did not exclude this skill altogether and suggested that the time they gave to the dogs was insufficient to establish the relationship between the stick and the toy (Viranyi et al., 2006). It is therefore possible that, with adequate training, dogs could recognize the role of a tool in retrieving a reward.

The aim of the current study was, therefore, to assess whether dogs would learn the role of a tool to retrieve a reward from a feeding apparatus. We were also interested in measuring how dogs' showing behaviour towards the location of the tool varied based on whether the apparatus was used for the benefit of the dog (selfish context) or for the benefit of the owner (helpful context).

Ethical statement

All procedures performed in the study were in accordance with the ethical standards of the institutions at which the studies were conducted (Max Planck Institute for Evolutionary Anthropology and University of Portsmouth).

The study was carried out in strict accordance with the recommendations in the ASAB/ABS guidelines for the use of animals in research and was approved by the University of Portsmouth Animal Ethics Committee (Animal Welfare and Ethical Review Body) (Appendix A: Ethical approval for the studies in Chapters 2 & 3). Informed consent was obtained from the dog owners for their dogs to participate in the study.

Methods

The general procedure consisted of a *warm-up*, a *demonstration phase*, a *training phase*, and a *test phase.* The warm-up allowed the dogs to understand that they could receive a treat if they explored an object placed on the floor by the experimenter. In the demonstration phase, dogs witnessed an experimenter operate a food delivery apparatus using a tool (a stick) and received the food. In the training phase, the dogs were trained the dogs to discriminate between the tool (stick), that, and a random distractor object (an empty CD container). Demonstration and training were repeated in blocks of six trials each, until the dog reached a pre-determined learning threshold. At this point, the dog entered in the test phase, where the food delivery apparatus was repeatedly used by their owner, some times for the benefit of the dog (*selfish* conditions) and some times for the benefit of the owner (*helpful* conditions). After each time the owner used the apparatus, he/she briefly left the room; then an experimenter hid the tool and the distractor object in two different boxes, and quickly left the room. The owner returned and pretended to look for the tool while talking to the dog, in order to elicit a showing behaviour in response.

Participants

Overall, 33 adult pet dogs (16 males, 17 females) were included in the study. The sample included 8 crossbreed dogs (Appendix B: Subjects' demographic information for Chapter 2). Dogs were aged between 1 and 8 years ($M = 4$, $SD = 2$).

Apparatuses

The food delivery apparatus was based on the one described in Bullinger et al. (2011) and consisted of a Plexiglas box (31 x 31 x 31 cm) with a mechanism inside (Figure 2.1). The mechanism worked in such a way that it was possible to fill it by dropping a food pellet in a hole on the top of the apparatus. By inserting the stick in another hole on the top of the apparatus, it was possible to push a series of levers that would push the food pellet through a tube on the side of the apparatus, so that it would fall on the floor, accessible to the dog. The apparatus was made out of Plexiglas to give the dog a chance to see how it worked.

Figure 2.1. The food delivery apparatus used in the test.

The apparatus was made of Plexiglas so that the mechanism was visible to the dogs. The experimenter used the apparatus while making sure that the dog could see her action and inside the apparatus itself.

Experimental area

The study took place in two different laboratories (at the Max Plank Institute of Evolutionary Anthropology and at the University of Portsmouth), however the rooms were arranged to be as similar as possible. In both laboratories, the testing area (2.3 x 5 m) was an empty room, divided in two parts by a wire and/or Plexiglas fence (Figure 2.2a), so that one side of the room was not accessible to dogs, but dogs were able to see clearly what happened there. The owner had access to this smaller area through a moving gate.

The testing apparatus was placed on the floor attached to the fence. The tube from which the food was ejected could be positioned so that it either opened towards the dog's side of the room (selfish condition) or towards the owner's side of the room (helpful condition). Therefore, depending on the position of the tube it could be predicted where the food would fall.

In the part of the room that was accessible to the dog, two shelves were placed on the wall opposite to the fence at 1.80 m from the ground. On each shelf was placed an opaque plastic box (52 x 32 x 22 cm) that was used as hiding place during the test phase (Figure 2.2d).

Figure 2.2. Experimental room setup and methods.

a) Experimental area: the side of the room accessible to the owner and the apparatus and that accessible to the dog were separated by a fence made with wire and Plexiglas so that the area was visible to the dog. b) Warm up phase: the experimenter stood in front of the dog on the same position where she would later train the dog. The handler sat on a chair and held the dog by the collar, while the experimenter was showing an object to the dog. c) Demonstration phase: the experimenter used the tool to operate the apparatus, while ignoring the distractor. d) Training phase: the tool and the distractor were placed on the floor for the dog to choose between them. The chosen object was then used by the experimenter to attempt using the apparatus.

Procedure

The demonstration phase took place over different sessions of 1 hour each, until the dog learnt to discriminate between the tool and the distractor. For the warm-up and the demonstrations, the dog was taken to the testing area by the experimenters while the owner waited in a separate room. Once the dog had completed the training, it entered into test phase, which required the participation of the owner.

Warm-up

The aim of this phase was to familiarise the dog with the training procedure, i.e. to choose an object. After taking the dog to the experimental area and giving it a few minutes to habituate to the room, one experimenter (handler) sat on a chair and held the dog by the collar. The other experimenter stood in front of them (Figure 2.2b), 1 meter away, showing the dog an object (a black piece of plastic) and placing it immediately on the ground in front of her. The experimenter then touched the object while talking to the dog, to attract its attention to the object. The handler released the dog, which was rewarded as soon as it reached the object within a head's distance. The procedure was repeated in blocks of six trials until the dog walked immediately up to the object as soon as it was released for 5 out 6 trials. With each repetition, the experimenter interacted less and less with the dog and at the final stage she only called the dog by its name, saying "Look!". At the end of the warm-up the dog had a break. At the end of the break the experimenter placed the apparatus on the floor on the spot she had been standing before and started with the *demonstration phase.*

Demonstration

At the beginning of each trial of this phase, the handler sat on the chair holding the dog by the collar. The experimenter then baited the food box, calling the dog if needed, and placed the tool and the distractor on the floor nearby the apparatus. While ignoring the distractor, she took the tool and encouraged the dog to sniff it; she then used the tool to operate the apparatus (Figure 2.2) and let the dog have the treat.

Training

During this phase the dogs were trained to discriminate between the tool and the distractor. As in the previous phases, the handler sat on the chair holding the dog. The apparatus was on the floor in same place as during the demonstration. The experimenter baited the apparatus making sure that the dog was paying attention. She then took the two objects and walked in front of the dog. After calling the dog and saying “Look!”, as she had done in the *warm-up*, she placed the two objects on the floor at her sides. The handler immediately let the dog go. Whenever the dog made a choice (i.e. fetched, tried to fetch or went near one of the two objects), the experimenter picked it up and try to use it on the apparatus. If the dog chose the tool then it could eat the treat that was retrieved; otherwise, the experimenter would say “It’s not working” and the trial would be over. If the dog did not make a choice within 30 seconds, the experimenter removed the objects and the food, ending the trial.

Dogs passed the learning threshold if they chose the tool in 5 out of 6 trials, for a maximum of 12 total trials. If the dog did not pass the threshold, another training block was repeated for a maximum of 2 times.

For each subject, the placement of the objects on the left hand side and the right hand side was semi-randomised across trials in a pre-determined order, so that the target tool was never placed in the same location for more than two consecutive trials.

Test phase

Once the dog was trained, it was invited for the test phase, which involved the owner and took place on a separate day. The test consisted of 4 blocks, each preceded by a filler trial. On the test day, the owner was given standardised video instructions regarding the procedure; then, the experimenter walked into the experimental room with the owner and the dog. The test started with a *filler trial*, immediately followed by one *test block*.

Filler: the filler trial introduced the dog to the upcoming outcome of the test block (i.e. the testing condition) and it was performed at the beginning and in the middle of a test block (i.e. every two test trials). The filler trial was identical to the demonstration, however, the apparatus was either in the dog's side of the room (selfish condition) or the owner's side of the room (helpful condition). The tube that the treats dropped from was turned towards the corresponding side of the room. Upon entering the room, the dog was let off leash. Then, the owner and the experimenter walked near the apparatus (crossing the gate as necessary). The owner operated the apparatus using the tool, and either the dog (selfish condition) or the owner (helpful condition) received the food. If the owners received the food, he/she picked it up and pretended to eat it. The first test trial then started without interruption.

Test block: As soon as the dog ate the food or the owner pretended to eat it, the experimenter baited again the apparatus, making sure that the dog was watching. Then the owner pretended to receive a phone call, walked across the gate and left the room, as in Kaminski et al. (2011), leaving the dog with the experimenter and waiting out of the door of the experimental room. While ensuring that the dog was watching, the experimenter hid the tool and the distractor in the opaque boxes, placing one object in each box. The experimenter always hid the object in the right box first, then the one in the left box. She then knocked at the door where the owner was waiting. The owner counted 15 seconds, so that the experimenter had the time to leave through another door and the two would not meet. The owner then entered the room and searched for the tool, according to a similar procedure to that described in Kaminski et al. (2011) and Bullinger et al. (2011):

Phase 1: upon entering, the owner looked at the location where the tools previously had been, then walked up to the chair and sat down (this took about 5 seconds). He/she rose his/her arms, palms up, frowned, looked around and said "Hmm, that's strange. It was there, and now it's gone. I don't understand it." and repeatedly mentioned the dog's name. While doing so, the owner remained seated the entire time (about 10 seconds). The owner did not ask specifically for the object.

Phase 2: the owner began to ask the dog specifically by addressing the question directly, "Where is it? Where has it gone?", for 15 seconds while producing the same arm and shoulder movements and repeatedly mentioning the dog's name. Again the owner remained seated the entire time.

Phase 3: the owner stood up and looked around while remaining silent for about 5 seconds.

The owner was not informed of the location of the tool and was not able to see the objects inside the opaque containers. At the end of this search, the owner tried to guess the location of the tool, relying on the dog's behaviour. The owner chose only one of the two shelves and looked for the target tool; he/she did not go to the other shelf.

Similar to Kaminski et al. (2011), if the owner found the object he/she picked it up saying "Wow, there it is! Great!"; otherwise he/she just made a gesture as lifting his/her arm and shoulder and say "Oh too bad it is not here!". He/she did the same upon finding the distractor. If the owner could not make a guess about the location of the tool based on the dog's behaviour, he/she just lifted his/her arms and shoulders saying "Too bad, we can't find it". If the owner found the tool, he/she then used it to operate the apparatus and let the dog have the food, or the owner pretended to eat the food, depending on the condition. After one of these possible events, the owner called the experimenter back into the room and then the trial was over. Dogs had a break at the end of each block.

Test trials were blocked in groups of 4 identical trials each, arranged in an AB design. During A blocks selfish condition trials were performed, during B blocks helpful condition trial were performed, for a total of 16 experimental trials (8 for each condition). Dogs were allocated to two counterbalancing groups, so that half of the dogs started with the A block and the other half started with the B block.

The hiding places were determined according to a pre-determined order to counterbalance potential carryover effects across sessions. Each object was hidden at least once in every hiding place. The allocation of the 2 hiding places was randomised in such a way that the owner could not guess the location based on previous trials; that is, within one block each object could be hidden in the same hiding place twice (Kaminski et al., 2011).

Behaviour analysis

Digital video footage was taken from all trials and the software Avidemux version 2.6 was used to record dogs' behaviour during testing. The software was set to a sensitivity of .10 seconds.

The amount of time spent in the area below each of the two hiding places (selfish and helpful) was recorded. Since the hiding locations were at two corners of the room, a circle with a diameter of 1.50 meters was drawn on the floor so that it was possible to code the dog's position within the circle. The decision of the owner at the end of each trial was also recorded.

Statistical analysis

Data were analysed using IBM SPSS Statistics version 22. The Kolmogorov-Smirnov test for normality revealed that the data were not normally distributed, thus non-parametric tests (two tailed) were used. In order to avoid pseudo-replication (Hurlbert, 1984), measures were averaged across test trials for each dog before performing the statistical analysis. Therefore, for every variable measured and each condition, the mean value across the test trials was used. The only exception to this was the owners' decision, which was calculated as the percentage of trials where the owner found the tool based on the total trials where owners decided to look in a box.

Results

Only 8 dogs (24%) passed the training threshold, moved to the test and were included in the statistical analysis (Appendix B: Subjects' demographic information for Chapter 2).

On average, the owners looked into a box in 44% of the helpful trials and 56% of the selfish trials. One sample Wilcoxon test showed that in both conditions, the percentage of trials where the owner found the tool did not differ from chance level, set at 50% (Table 2.1.).

Table 2.1. Median of the percentage of trials where the owner found the tool

Conditions	*Mdn*	*Interquartile range*	*z*	*p*
Helpful condition	50	0.00-54.17	- .85	.396
Selfish condition	37	18.75-66.67	- .85	.391

Note: Results of one sample Wilcoxon rank-sum test ($N = 8$)
Both tests had a small effect size: $r_{helpful} = -.30$; $r_{selfish} = -.30$

Wilcoxon matched pairs signed rank test also revealed that dogs did not prefer spending time in proximity to the tool in either of the two conditions; they also did not prefer being in proximity of the distractor in either condition (Table 2.2.)

Table 2.2. Effect of condition on the time spent near the hiding locations

	Helpful condition		Selfish condition			
Variables	*Mdn* (s)	*Interquartile range*	*Mdn* (s)	*Interquartile range*	*z*	*p*
Time near tool	37.75	31.62-49.12	36.50	33.88-38.38	.56	.575
Time near distractor	29.25	25.12-34.12	28.50	25.25-39.88	-.42	.674

Note: Results of matched pairs Wilcoxon signed rank test (N = 8)
Both tests had a small effect size: r_{tool} = .14; $r_{distractor}$ = -.01

In order to assess whether dogs still discriminated the tool and the distractor, the time spent in proximity of the two was also compared. Wilcoxon matched pairs signed rank test revealed that, in neither condition did dogs prefer spending time in proximity of the tool (helpful: z = 1.40, p = .161; selfish: z = -.91, p = .362) in both cases there was a small size effect ($r_{helpful}$ = .35; $r_{selfish}$ = .23).

Discussion

In this study, we tested whether the procedure used by Bullinger et al. (2011) to train subjects to discriminate between a tool, that could be used to obtain food from an apparatus, and another object serving as random distractor could be applied to dogs. We were then interested in assessing whether dogs would indicate the tool to their owner both when the dog would gain the food reward once the tool was used and when the owner would get the reward. It was not possible to code looking behaviour (i.e. “showing”), which is the most form of indication used by dogs that can be found in the literature. However, the dog’s position relative to a target has been reported in the literature as used referentially as well (Gaunet, Steiger and Deputte, 2011) and has therefore been investigated in this study.

The dogs in our study did not indicate the tool more often when they benefitted from its use (selfish condition) or when the owner did (helpful condition). Further analysis also revealed that, at the time of testing, dogs did not have any preference for the tool over a random distractor. As such, our results could not confirm whether the dogs used communication helpfully or not, because it did not appear that the dogs had retained the training at time of testing. However, the sample size was very small and the small size effects suggest that the findings of this study should be taken cautiously.

Nevertheless, some considerations can be made to explain why such a small proportion of the dogs was able to learn the task and why the dogs did not seem to discriminate between the two objects at the time of testing. It is possible that this training procedure was too complicated for the dogs, as suggested by the fact that only 24% of the subjects passed the learning threshold. Dogs were trained by letting them experience the effect of the use of the tool with the apparatus (i.e. obtaining food), versus the distractor. In order to be considered trained, dogs had to choose the tool over the distractor in 5 out of 6 trials. Such threshold was set based on the study by Bullinger et al. (2011) and proved to be successful in 15-month-old children and chimpanzees. However, the proposed training protocol may be too complex for dogs. There is some evidence that dogs find easier to follow a human gesture, rather than a token (Udell, Giglio, & Wynne, 2008) or physical cues, such as the rattling noise of food in a container (Bräuer et al., 2006), which suggests that possibly it is difficult for dogs to understand the physical contingencies of objects.

Another possibility is that dogs did not retain the learning between the time of training and the testing. The learning threshold in this study, in terms of correct trials, was defined based on the threshold used in the study by Bullinger et al. (2011); however, in the case of children and chimpanzees, training did not require a long time, therefore the test was performed immediately after. On the contrary, in the current study there was a gap of few days between training and testing, which was due to the length of the training. It is also possible that the training threshold employed here was too flexible. For example, in a study involving dogs, a successful threshold had been 85% success rate (Fukuzawa et al., 2005).

It is also possible that the dogs did not need to understand the contingencies of the apparatus used in the study in order to pass the training threshold, but they did need it to understand the test procedure; this may have led to the discrepancy between training and testing results. Specifically, the dogs might have associated the tool with the food in order to discriminate between the two objects during the training, rather than understanding that it was necessary to retrieve the food.

One could argue that one possible problem in the test was dogs' difficulty to remember the location of the hidden objects once these were out of their views. This, however, should not be the case as the experimenter ensured that the dogs paid attention while she was hiding each object. In the literature on object permanence, dogs have demonstrated the ability to search accurately for visibly displaced objects, as long as they are not invisibly displaced (Gagnon & Doré, 1992; Triana & Pasnak, 1981; Miller et al., 2009). It can therefore be expected that dogs could successfully find the hidden objects.

Finally, it is possible that the presence of food was more of a distraction for the dogs during the test. It is possible that, during the training some of the dogs could discriminate between the two objects, because they were both visible. However, once the objects were not visible anymore, the dogs were distracted by the presence of the treats in the apparatus (which was one the floor and therefore more accessible) and were not interested in indicating the hidden objects.

The findings of the current study do not exclude the possibility of helpful communication in dogs. However, it is also not possible to draw conclusive results from this study. In order to further investigate helpful communication in dogs, it is necessary to simplify the procedure, for example avoiding the use of food. Helpful motives in dogs might also be better investigated by observing whether dogs would abandon a reward in order to communicate with humans. The study could therefore be repeated avoiding training, but rather investigating whether dogs' communication about a hidden object takes into account the context it was used by a human partner.

Chapter 3. Do dogs provide information helpfully? [2]

Chapter overview

The results of Chapter 2 indicate that the presence of food may be too distracting for the dogs when trying to explore informative communication. Additionally, it may be too difficult for the dogs to keep track both of the various outcomes of use of the tool (selfish vs helpful) and the location of the hidden objects. Therefore, the studies in this chapter build from the previous results, focusing on the primary aim, i.e. investigating the possibility of informative communication in dogs. The study has been conducted without the use of food, and dogs will be given a chance to understand the relevance of the objects based on the context they were used by a human partner. As in the previous study, the main variable measured will be dogs' communicative signal produced to direct the attention of humans towards outside entities, a behaviour often referred to as showing behaviour. There is currently no evidence that dogs communicate helpfully, i.e. to inform an ignorant human about a target that is of interest to the

[2] Based on the published manuscript:
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human but not to the dog. Communicating with a helpful motive is particularly interesting because it might suggest that dogs understand the human's goals and need for information. In Study 1, we assessed whether dogs would abandon an object that they find interesting in favour of an object useful for their human partner, a random novel distractor, or an empty container. Results showed that it was mainly self-interest that was driving the dogs' behaviour. The dogs mainly directed their behaviour towards the object they had an interest in, but dogs were more persistent when showing the object relevant to the human, suggesting that to some extent they took the humans interest into account. Another possibility is that dogs' behaviour was driven by an egocentric motivation to interact with novel targets and that the dogs' *neophila* might have masked their helpful tendencies. Therefore, in Study 2 the dogs had initial access to both objects, and were expected to indicate only one (relevant or distractor). The human partner interacted with the dog using vocal communication in half of the trials, and remaining silent in the other half. Dogs from both experimental groups, i.e. indicating the relevant object or indicating the distractor, established joint attention with the human. However, the human's vocal communication and the presence of the object relevant to the human increased the persistency of showing, supporting the hypothesis that the dogs understood the objects' relevance to the human. We propose two non-exclusive explanations. These results might suggest that informative motives could possibly underlie dogs' showing. It is also possible that dogs might have indicated the location of the hidden object because they recognised it as the target of the human's search. This would be consistent with taking into account the objects' relevance, without necessarily implying that the dogs understood the human's state of knowledge.

Introduction

Dogs are particularly good at understanding human communication, for example they can find hidden food following communicative cues provided by humans (Hare et al., 1998; Miklósi et al., 1998; Miklósi & Soproni, 2006). This was demonstrated in a series of studies using the so-called object-choice task. In this task a piece of reward is hidden underneath one of several containers, and afterwards a human indicates the correct container to the dog by e.g. pointing at it (Hare et al., 1998; Miklósi et al., 1998; Soproni, Miklósi, Topál, & Csányi, 2002). Dogs demonstrated to be extremely skilful in following this gesture both from a very young age and without the need for any explicit training (Gácsi, McGreevy, Kara, & Miklósi, 2009a; Hare et al., 2002, 1998; Riedel et al., 2008). When compared to their closest living relative, the wolf, dogs performed better even when both species were raised under identical conditions (Hare et al., 2002; Miklósi et al., 2003; Virányi et al., 2008) unless wolves received extensive and prolonged training (Gácsi, McGreevy, et al., 2009b; Udell, Dorey, & Wynne, 2008).

The reasons for dogs' outstanding abilities in inter-specific communication with humans are thought to depend on dogs' unique evolutionary history (Hare et al., 2002; Miklósi et al., 2004). Dogs are the most ancient domesticated species (Thalmann et al., 2013; Wang et al., 2015) and it has been hypothesised that humans bred them selectively for certain activities, such as hunting and herding (Clutton-Brock, 1995), where it was important for dogs to be particularly skilful at following human communication (Kaminski & Nitzschner, 2013). One hypothesis is therefore that, as an adaptation to life with humans, dogs developed specific socio-communicative skills for interacting with humans (Hare et al., 2002; Hare & Tomasello, 2005; Miklósi et al., 1998, 2004).

Dogs seem to be flexible not only in how they use communicative signals coming from humans but also in their production of communicative behaviours towards humans, such as the one described as showing behaviour (Hare et al., 1998; Miklósi et al., 2000). The term showing behaviour summarises actions like gaze alternation and other communicative signals through which dogs indicate a hidden object or food to a human (Miklósi et al., 2000). There is evidence that showing behaviour fulfils all the criteria required for identifying intentionality and referentiality as they had been introduced for primates (Leavens, 2004; Leavens et al., 2005). Specifically, dogs do not indicate in the absence of an audience, they alternate gazes between the human and the referent, they use attention getting behaviours (e.g. vocalisations) (Miklósi et al., 2000) they take into account the attentional state of their audience (Gaunet & Massioui, 2014; Marshall-Pescini et al., 2013), and finally they show persistence and elaboration when their communication is not successful (Leavens et al., 2005).

Dogs' flexible use of inter-specific communication with humans raises researchers' interest in the cognitive mechanisms underlying such skills. One question that is currently understudied is to what extent dogs communicate to truly inform a human partner about the hidden object. In the infant literature, the informative intent (Liszkowski et al., 2008; Savalli, Ades, & Gaunet, 2014) is described as a subtype of declarative communication (i.e. communicating to share an experience or influence someone's mental state), as opposed to imperative communication (i.e. communicating to obtain an object or influence someone's behaviour) (Bates, Camaioni, & Volterra, 1975; Camaioni, 1992; Moore & D'Entremont, 2001). Some consider human communication to rely on mechanisms unique to humans (Grice, 1975; Tomasello, 2007; Tomasello et al., 2007). One is the presence of a common ground, i.e. a body of knowledge, beliefs and suppositions that two speakers believe they share with each other (Clark, 1996; van der Goot et al., 2014). Forming a common ground with another individual might require to some extent the ability to make inferences about the other individual's mental states. The other is a unique cooperative tendency, which humans expect when they communicate (Tomasello, 2007). Some authors consider these to be uniquely human traits and the reason why humans, from a very young age, can successfully infer the location of a hidden toy from following an adult's pointing gesture, while humans' closest relatives, the chimpanzees, fail to do so (Behne et al., 2012). Children also produce pointing helpfully to inform others about the location of a relevant object without expecting anything in return, as opposed to chimpanzees, who would not produce pointing gestures unless there is something in it for them (Bullinger et al., 2011; Liszkowski et al., 2006).

However, other authors have challenged the idea that declarative pointing requires the understanding of another individual's mental state or goals, or the presence of a common ground, and argue for explanations of preverbal human communication that do not require the understanding of internal state (Gómez, 2007; Leavens, 2004; Leavens et al., 2005; Moore & Corkum, 1994; Moore, 2013). Gergely and Csibra suggest two mechanisms that do not require the understanding of mental states. The first mechanism suggests that children understand actions, including communication, in a referential and teleological way, i.e. they can link others' behaviour to a certain object, and they interpret actions as directed to a certain goal (Csibra, 2003, 2010; Csibra & Gergely, 2007; Gergely & Csibra, 2003). The second mechanism implies that human communication relies on natural pedagogy, i.e. it is characterised by a series of elements that allow and facilitate the transfer of knowledge. Specifically, humans, from a very young age, are sensitive to ostensive cues indicating that they are addressed in the communication, have referential expectations after observing ostensive cues, and interpret ostensive-referential communication as conveying information that is relevant and generalizable (Csibra, 2003; Csibra & Gergely, 2009). Similar mechanisms are thought to be possible, to a certain degree, in non-human animals (Csibra & Gergely, 2009; Gergely & Csibra, 2003; Moore, 2013; Moore, Mueller, Kaminski, & Tomasello, 2015), including dogs (Topál et al., 2006; Topál, Kubinyi, Gácsi, & Miklósi, 2005; Topál et al., 2009b).

Kaminski and colleagues (Kaminski et al., 2011a) tested whether dogs produce informative communicative behaviours by confronting dogs with a situation during which the humans and the dogs' motivation to receive the hidden object varied. They showed that dogs indicate the location of a hidden object to a human if the dogs had a selfish interest in the hidden object, but not if only the human had an interest in it. Humans' and dogs' interest in the object was determined by the context and by who interacted with the object before it was hidden. Either only the dog interacted with the object (e.g. a dog toy), or the human and the dog interacted with the object, or only the human interacted with the object. Afterwards a second person hid the object while the first person left the room. The first person then returned and asked the dog to find the object.

Dogs communicated the location reliably only if they had an interest in the hidden object. In a follow up study, two objects were hidden at the same time. One was an object that the human had an interest in and the dog had seen the human use, while the other was a distractor object that the human ignored entirely. In this case, the dogs did not distinguish between the two objects. This result suggests that either dogs do not have the motivation to attend to the humans needs, or lack the cognitive capacity to understand the human's lack of knowledge and need for information (Kaminski et al., 2011a). Kaminski and colleagues' study suggests that there is of yet no evidence that dogs understand the informative element of communication (Kaminski et al., 2011a) despite their unique skills in communicating with humans (Topál, Kis, & Oláh, 2014). Indeed, dogs could possibly interpret human communication (e.g. pointing) as an imperative, i.e. the human is directing them on where to go (Tomasello, 2007) or what to do (Gómez, 2005; Kaminski et al., 2011a). In this scenario dogs would also produce their communicative behaviours towards humans without any intent of influencing the humans' state of mind. If dogs' communication were either a request or a response to a command to fetch, they would be communicating without necessarily understanding others' state of knowledge and goals (Kaminski et al., 2011b). However, the study by Kaminski and colleagues could not tease apart the possibilities that the dogs' behaviour was due to a lack of helpful motivation, or due to their inability to understand the need for information and the relevance of the object for the human partner (Kaminski et al., 2011a).

The current study therefore aims to further investigate dogs' collaborative and informative motives during communication. We also aimed at assessing dogs' ability to understand an object's relevance after they see a human partner using it. In Study 1, we examined whether dogs would abandon a hidden dog toy to indicate the location of another object that a human partner wanted. It is possible that the objects' novelty and the humans' requests, rather than relevance, influenced the dogs' choices in such situation. Therefore, in Study 2 we examined whether dogs are able to understand that the human partner wanted an object that she had previously used, over a distractor that she had previously ignored. If dogs are driven to use the showing behaviour based on an informative intent, then we would expect the dogs to show prevalently the object relevant to the human over a distractor, as suggested by previous research in infants (Liszkowski et al., 2006, 2008). On the contrary, if the motivation underlying dogs' communication is to request, or an attempt to respond to a human's command to fetch, as the results by Kaminski et al. (2011) would suggest, then we would expect dogs to either indicate only objects that they have an interest in or indicate equally any hidden object, without differentiation based on the object's relevance to the human partner.

Ethical statement

The studies were carried out in strict accordance with the recommendations in the ASAB / ABS guidelines for the use of animals in research and were approved by the University of Portsmouth Animal Ethics Committee, and were covered by the same approval as for the study in Chapter 2 (Appendix A: Ethical approval for the studies in Chapters 2 & 3. Dog owners were informed about the procedure involved and gave their permission for their dog to participate in the study.

Study 1

The general procedure of this study was modelled on the study designed by Kaminski and colleagues (Kaminski et al., 2011a). Dogs knew the location of a hidden dog toy and the content of a second hiding place (i.e. an object relevant for the human, an object useless for the human, or no object); we wanted to know if dogs would indicate the location of an object depending on the human's interest in the object. It was hypothesised that abandoning the dog toy in favour of indicating the relevant object suggested a motivation to help. More consistent indications towards the relevant object, rather than the other useless object (a distractor), would also indicate that dogs understood the objects' relevance for the experimenter.

Subjects

A sample of 29 adult dogs was recruited for this study. Four dogs had to be excluded from testing because they did not settle during the warm-up, and one dog was tested but excluded from subsequent analysis because of a procedural mistake. Dogs were recruited through the Dog Cognition Centre Portsmouth Register and through contacts with local dog training groups. The inclusion criteria for the study were that dogs had to be between 1 and 10 years old and had to be comfortable and relaxed while being separated from their owner for the duration of the test. In addition, the dogs had to be toy motivated. All dogs were normal family dogs that lived with their owners and had the training background typical for a pet dog. Some of the dogs had participated in other studies before, but not studies using an experimental paradigm similar to the one used here.

Twenty-four dogs, 16 males and 8 females, represented the final sample (Appendix C: Subjects' demographic information for Chapter 3). Twelve dogs were crossbreeds and twelve were pure breeds (according to the British Kennel Club Breed Groups, as defined by the British Kennel Club) these consisted of 6 Gundogs, 1 Hound, 1 Pastoral, 2 Terriers, 1 Working, 1 Utility). The age of the dogs ranged between 1.5 and 8 years (*M* = 3.8 years, *SD* = 1.7).

Methods

Testing took place in one of the rooms (3.70 m x 4.20 m) of the Dog Cognition Centre Portsmouth (DOCS). Two opaque containers (19 cm x 10 cm) were placed on the floor, one in the left and the other in the right corner of the room. A chair for the experimenter to sit on was placed equidistant to both containers (Figure 3.1). Different objects were used as hidden targets: a notepad, stapler or a dog toy.

Procedure

In order to allow the dogs to habituate with the environment and with the people involved, the dogs were first allowed to explore the experimental room. During this time both the experimenter and the helper interacted with the dog to ensure the dog was familiar with them, while avoiding playful interactions with the dog in an attempt to not create a play context for the dogs, which might have affected the study.

After this warm up the experimenter sat down on the chair provided and started writing notes, using the notepad (*relevant* object). The helper stood about a meter away from her while the dog was allowed to roam around freely. To ensure that the dog attended to the experimenter's activity, the experimenter and the helper now and then called the dog's attention and encouraged the dog to stay near them while avoiding indicating the notepad specifically at any time. During this demonstration, only the relevant object was in the room; the dog toy and the distractor were left outside and out of the view of the dog. The rationale behind this set up was to prevent dogs from being distracted by the other objects during the demonstration. At the end of the demonstration, the experimenter left the room and took the relevant object with her, placed it with the others in a container outside the room, and walked away. The set up therefore ensured that all objects were already out of the room before the hiding phase. This allowed the helper to take the objects to be hidden, while avoiding the experimenter seeing them.

Each dog was presented with 6 trials (two per condition: relevant, distractor, and no object) and each trial consisted of a demonstration, followed by a searching phase (described below). The dog was given a few minutes break at the end of each searching phase, before starting another trial, while the helper set up the room for the following trial. The demonstration in trial 1 lasted about 40 seconds, whilst demonstrations in trials 2–6 were reduced to about 20 seconds in order to prevent the dogs from losing interest. The order with which the demonstrations were administered was counterbalanced across dogs, so that each condition was presented in the first trial (with the longer demonstration) for a third of the dogs. After this time elapsed the experimenter left the room through door A (Figure 3.1) together with the helper. The helper then returned and, depending on the condition, hid one or two objects in the boxes provided.

"Relevant" condition: The helper returned to the room, holding the dog toy and the relevant object (notepad) in her hands. While ensuring that the dog was watching, the helper hid the dog toy in one container and the relevant object in the other container.

"Distractor" condition: The helper returned to the room holding a dog toy and the distractor (stapler) in her hands. While ensuring that the dog was watching, the helper hid the dog toy in one container and the distractor in the other container.

"No object" condition (baseline): The helper returned to the room holding only a dog toy in her hands. While ensuring that the dog was watching, the helper hid the dog toy in one of the two containers and showed the dog that the other container was empty.

The helper always baited the containers starting with the left one first. The location of objects was counterbalanced and semi-randomised across trials and conditions with the stipulation that the same type of object could not be in the same location in more than two consecutive trials. During the hiding phase the helper made sure the dog could see closely the objects that were hidden so that the dogs could recognise the object that they had observed earlier during the demonstration.

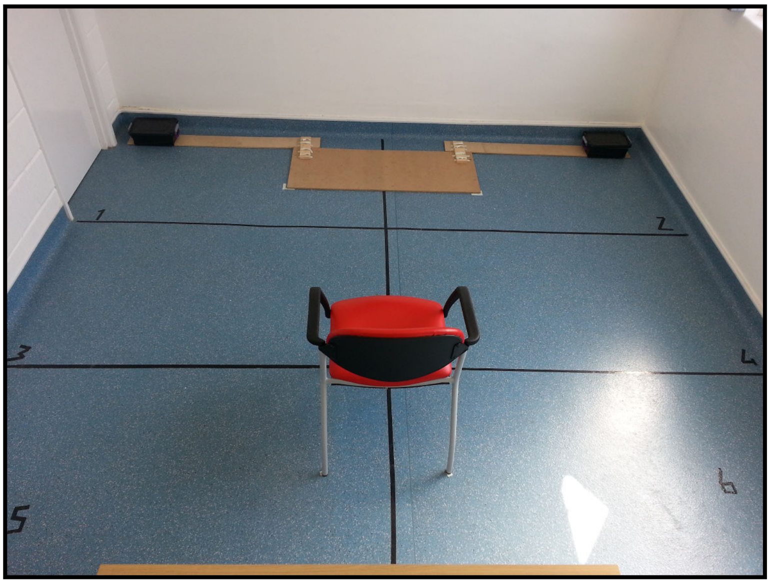

Figure 3.1. Testing room for Study 1.

A chair was placed in the testing room for the experimenter to sit on. Two opaque containers were positioned in front of the chair at the two corners of the room, so that the chair was equidistant from each container.

After the hiding was completed the helper left the testing room, cueing the experimenter to enter. The experimenter held a pen in her hand in an attempt to indicate that she was going to continue her previous activity. The experimenter then started searching the area around the chair for a few seconds as if she was looking for the notepad, which she needed for her activity. Upon not finding it, she sat on the chair and followed a pre-determined script, similar to that of Kaminski and colleagues (2011a), where the duration of each phase was determined using a timer:

Phase 1: the experimenter searched for the object for 20 s while performing the following activities: repeatedly lifting her arms and shoulders and saying ‘Hmm, that’s weird. It was there, and now it’s gone. I don’t understand.’ and repeatedly mentioning the dog’s name. In order to prevent influencing the dog by gazing at the containers, the researcher kept her gaze on the dog the entire time, as in Viranyi and colleagues’ procedure (Viranyi et al., 2006). While doing so, she remained seated the entire time.

Phase 2: the experimenter started formulating more specific questions, which were directed at the dog, “Where is it? Where has it gone?’” for 20 s while producing the same arm and shoulder movements, and repeatedly mentioning the dog’s name. Again, she looked only at the dog and remained seated.

Phase 3: the experimenter stood up while remaining silent for a few seconds and continued to look at the dog.

Phase 4: the experimenter tried to guess the location of the notepad based on the dogs’ behaviour and made a decision. If the experimenter found the notepad, she retrieved it saying “Wow, there it is! Great!”, and put it in her pocket without offering it to the dog or praising the dog in any way. If she did not find the notepad in the container that she opened, she closed the container without touching the content and saying “Oh, too bad! It’s not here”. If the experimenter could not infer where the object could be based on the dog’s behaviour, she just lifted her arms and shoulders saying “Too bad, we can’t find it”. Although the phrasing changed, the tone of the experimenter’s voice and her expressions were kept as similar as possible in all cases. After each of these possible events the trial was over; the experimenter took the dog out through door B, while the helper returned to the testing room and re-set the room for the next trial.

The overall design was a within subjects design where all dogs participated in all conditions and received 2 trials per condition summing up to 6 trials altogether. Trials were presented blocked by condition with the order of conditions counterbalanced across subjects.

Behaviour analysis

Digital video footage was taken from all trials and the Solomon Coder software (beta 091110, copyright 2006–2008 by András Péter, developed at ELTE TTK Department of Ethology, Budapest, Hungary) was used to record dogs' behaviour during testing. The software was set up with a sensitivity of .10 seconds.

The direction of gazing in the search phase was recorded on the basis of the orientation of the head of the dog. The frequency and duration of gazing toward three distinctive locations in the room was recorded: (1) gazing at the experimenter, (2) gazing at the box where the dog toy was hidden, (3) gazing at the target box (i.e. the other box). Gazes were also subjected to a sequential analysis. According to the definition of gaze alternation by Miklósi and colleagues (Miklósi et al., 2000), a gazing sequence consisting of two gazing units was recorded when gazing at the experimenter was followed directly by a gaze at one of the two boxes within 2 seconds or vice versa. Specifically, coders followed the rule that there could be a maximum gap of 2 seconds between the end of the first gaze in the alternation and the beginning of the following one. For example, if the dog looked at the box first and then at the experimenter, there could be no more than 2 seconds between the end of the look to the box and the beginning of the look to the experimenter.

Finally, the first hiding place that dogs indicated in the search phase (with their position, orientation of the body or orientation of the head) was recorded.

Since dogs' level of attention during the demonstration might vary, we also recorded the amount of time that dogs spent looking at the experimenter during the demonstration, i.e. the overall duration of looks to the experimenter in this phase. Looking was defined as the dogs head being oriented toward the experimenter and was recorded from the moment the experimenter started writing on the note-pad, to the moment she stood up to leave the room.

A random selection of the video material (20%) was coded by a second observer, naïve to the purpose of the study and to the content of the hiding boxes. The correlation between the two coders was calculated using Spearman r, and inter-coder reliability was assessed according to the limits given by Landis & Koch (1977).

Inter-observer reliability was substantial for the frequency of gazes to the dog toy ($r_s = .78$, $N = 28$, $p = .001$), the frequency of gazes to the target box ($r_s = .65$, $N = 28$, $p = .001$), the duration of gazes to the target box ($r_s = .72$, $N = 28$, $p = .001$), and the gaze alternations between the experimenter and the target box ($r_s = .75$, $N = 28$, $p = .001$). There was an excellent agreement on the duration of gazes to the dog toy ($r_s = .88$, $N = 28$, $p = .001$), the frequency of gaze alternations between the experimenter and the dog toy ($r_s = .80$, $N = 28$, $p = .001$), and the duration of gazes during the demonstration ($r_s = .82$, $N = 30$, $p = .001$).

Statistical analysis

Data were analysed using the statistical software R (R Development Core Team, 2015), with the packages *lme4* (D. Bates, Machler, Bolker, & Walker, 2015), *MuMIn* (Bartoń, 2016), and *lsmeans* (Lenth, 2015). A series of generalised linear mixed models (GLMM), fit by maximum likelihood (Laplace Approximation), were calculated for the variables measured. Models were first evaluated through an automated model selection process that generated a set of models with combinations of factors from a global model (which included all the effects in question), ranked them and obtained model weights using the Second-order Akaike Information Criterion (AIC) (Burnham & Anderson, 2003). The models with lowest AIC were evaluated with a likelihood ratio test against the corresponding null models (i.e. including only control factors). If the comparison was significant then Laplace estimated p-values were calculated for the different fixed effects of the model with lowest AIC (Baayen, 2008). Pairwise post-hoc comparisons were obtained from a Tukey test in the absence of interactions, while the least-squares of means method was used in case of interaction between categorical factors. If there was a significant interaction between fixed factors, only p-values for the interaction effects will be reported because the significance of main effects is uninterpretable in case of a significant interaction (Zar, 1999). All results have been reported with standard errors.

A GLMM (null model) with *logit* function was calculated with the binary response variable "indication of the target" (yes, no), and the nested random intercept factors "dog", "trial" and "toy side" (N = 144, number of subjects = 24). All the relevant fixed factors and interactions were included in the model (Appendix D: Model fitting additional information for Chapter 3). The model that yielded the lowest AIC comprised the fixed factors “condition” and “attention during demonstration”, without interaction.

A GLMM (null model) with *log* function was calculated with the response variable “frequency of gaze alternations” and the fixed factor “direction of the gaze alternation” (toy-box, target-box). The likelihood ratio test showed that the null model with a dog-specific slope for the factor “direction of the gaze alternation” yielded a significantly lower AIC. Therefore the nested random slope factors “dog”, “trial” and “toy side” (*N* = 144, number of subjects = 24) were included in the null model. All the relevant fixed factors and interactions were included in the model (Appendix D: Model fitting additional information for Chapter 3). The model that yielded the lowest AIC comprised the fixed factors “direction of the gaze alternation” and “trial”, without interaction.

The last GLMM (null model) with *logit* function was calculated with the response variable “duration of gazes (s)” weighted by the factor “duration of the trial (s)” and the fixed factor “direction of the gaze” (experimenter, toy-box, target-box, other). All the relevant fixed factors and interactions were included in the model (Appendix D: Model fitting additional information for Chapter 3 for details). The nested random intercept factors “dog”, “trial” and “toy side” (*N* = 144, number of subjects = 24) were included in the model. The model that yielded the lowest AIC comprised the factors “direction”, “condition” (relevant, distractor, no object), and “attention” (s), with a 3 level interaction.

Results

Overall, dogs first indicated the target on average in 47% of trials. There was a main effect of dogs' attention during the demonstration and the content of the target box, without any interaction, on the number of trials in which the dogs first indicated the target box ($GLMM_{Attention+Condition}$, $AIC_{NullModel} = 398.9$, $AIC_{FullModel} = 394.2$, $N = 24$, $\chi_{23} = 10.679$, $p = .013$). The probability of indicating the target increased with the time spent looking at the demonstration, with the dogs being more likely to choose the target first in the trials where they were more attentive to the demonstration (estimate $_{attention}$ ± SE = .028 ± .013, p = .030). Post-hoc Tukey revealed that when the relevant object was in the target box, compared to the distractor, dogs were less likely to indicate the target box, though this difference was not significant (estimate $_{relevant\text{-}distractor}$ ± SE = − .835 ± .093, p = .093). There was also no difference in the dogs' indications to the target box between the relevant object and the no object condition (estimate relevant-no object ± SE = − .728 ± .398, p = .160), or between the distractor object and the no object condition (estimate $_{distractor\text{-}no\ object}$ ± SE = .1071 ± .386, p = .958).

The analysis of gaze alternations indicated that overall the majority of the dogs alternated their gazes both between the experimenter and the dog toy (87%), and between the experimenter and the target box (75%), (McNemar test: p = 0.375). Also, there was no difference in the proportion of dogs that used gaze alternations to indicate the target in the relevant object (50%), in the distractor condition (67%), and no object condition (46%) (Cochran's Q test: T = 3.818, p = 0.148). There was a main effect of the factors "direction of the gaze alternation" and "trial" on the frequency of gaze alternations ($GLMM_{Direction+Trial}$, $AIC_{NullModel} = 708.0$, $AIC_{FullModel} = 697.2$, $N = 24$, $\chi_{21} = 11.135$, $p = .001$). The frequency of gaze alternations decreased overall with the progression of trials (estimate $_{trial}$ ± SE = − .131 ± .039, *p* = .001). Post-hoc Tukey test also revealed that dogs were more likely to show the toy more often than the target box (estimate $_{toy—target}$ ± SE = .731 ± .260, *p* = .001).

There was a significant effect with a 3 level interaction between the direction of the gaze, condition, and the attention during the demonstration, on the duration of dog gazes ($GLMM_{Direction*Condition*Attention}$, $AIC_{NullModel}$ = 38073.8, $AIC_{FulModel}$ = 37361.2, N = 24, χ_{227} = 752.6, *p* = .001). Dogs were more likely to gaze longer at the toy box when they were more attentive to the demonstration, both in the distractor condition (estimate $_{toy*distractor*attention}$ ± SE = .003 ± .001, *p* = .001) and in the relevant object condition (estimate $_{toy*relevant*attention}$ ± SE = .002 ± .001, *p* = .001). However the effect of attention and condition was different when dogs were gazing at the target. In the distractor condition, the dogs' gazes to the target box were shorter when dogs were more attentive to the demonstration (estimate $_{target*distractor*attention}$ ± SE = − .002 ± .001, *p* = .001). On the contrary, in the relevant object condition, gazes to the target box were longer when the dogs were more attentive to the demonstration (estimate $_{target*relevant*attention}$ ± SE = .003 ± .001, *p* = .001).

Discussion

One main finding of this study is that when the dogs paid more attention to the demonstration they were more persistent, i.e. longer, in showing the target if it contained the object relevant for the human, rather than a distractor. One possible explanation is that dogs were able to recognise the objects' relevance based on the demonstration that they witnessed, and that they took that into account when communicating with the experimenter. Such behaviour would be consistent with the definition of informative communication, and comparable to the behaviour of children in similar studies (Liszkowski et al., 2006).

However it should be noted that the frequency of gaze alternations varied only based on whether the dogs were gazing at the toy or the target box but not the condition (i.e. the target object was relevant or a distractor). Furthermore, though gaze frequency decreased with trials, the dogs clearly showed the toy more often than the target. This suggests that irrespective of condition, dogs could never ignore their own selfish interest for the dog toy in favour of the other objects.

One could argue that the frequency of gazes to the target did not change across conditions because dogs may find it difficult to discriminate across conditions the content of the box that did not contain the toy. It could be that because the objects in the target box are not relevant to dogs, they simply did not differentiate them in their communicative behaviour. Interestingly though the findings show that dogs clearly discriminated the content of the boxes overall and in the different conditions.

Attention also played a role in influencing the behaviour of the dogs. The level of attention during the demonstration affected the persistency of gazes to the target in a way that was consistent with the content's relevance (i.e. it increased in the relevant condition and decreased in the distractor condition). This could possibly suggest that attention aided the dogs' in understanding the relevance of the objects. Another explanation, which does not exclude the previous one, could be that more attentive dogs communicate more. It might be possible that attention to humans increases communication in dogs. Indeed, the number of trials in which the dogs first indicated the target increased with the attention, regardless of the condition. Moreover, gazes to the toy were more persistent when dogs were more attentive in the demonstration.

Finally, the experimenter's searching behaviour and utterance did not affect the dogs' overall indications. Dogs are sensitive to ostensive cues in ways very similar to children (Call, Bräuer, Kaminski, & Tomasello, 2003; Kaminski et al., 2012; Virányi, Topál, Gácsi, Miklósi, & Csányi, 2004), which is something quite unique among non-human species (Gácsi et al., 2009). Cues such as eye contact and high pitch voice appear to help dogs understanding that communication is directed at them (Call et al., 2003; Kaminski et al., 2012) and help to initiate and maintain communication (Csibra, 2010; Király, Csibra, & Gergely, 2013; Topál et al., 2014). Therefore it would be expected that the human's high pitch voice would increase dogs' communication. One possible explanation could be that dogs' overall orientation used to measure the first indication was not necessarily a communicative behaviour, but rather reflected dogs' focus of attention. Since dogs were distracted by the presence of the toy and their own interest in it, they did not orientate much towards the target box.

Since it is possible that the dogs' preference for the dog toy, or the novel object (Kaulfuß & Mills, 2008) was simply inhibiting their overall behaviour, we conducted a follow up study in which only one object per dog was hidden and it was either an object the human needed or a distractor. Moreover, both objects were in the room and accessible to the dog from the beginning of the trial. The effect of the ostensive cue *high pitch voice* was also investigated systematically.

Therefore, for each dog, the experimenter searched for the hidden object in silence for half of the trials, and talked with a high pitch voice in the other half.

Study 2

In this follow up study dogs witnessed one of two objects being hidden in the room that was either relevant to the experimenter (*relevant* group) or was not (*distractor* group). The object that was not hidden was taken out of the room by the helper. We also manipulated whether the experimenter used certain ostensive cues (high pitched voice) during her search or not.

Subjects

A sample of 51 dogs was recruited in this study. Dogs were recruited through the Dog Cognition Centre Portsmouth Register and through contacts with local dog training groups. The inclusion criteria were identical to those in Study 1. Some of the dogs had participated in other studies before, but not in studies using an experimental paradigm similar to the one used here. None of the dogs had participated in Study 1.

Forty-eight dogs took part in this study, 24 dogs per condition (Appendix C: Subjects' demographic information for Chapter 3 an additional dog was recruited but excluded from testing because of aggression, and two additional dogs were tested but excluded from analysis because of procedural mistakes. In both groups 17 of the dogs were males and 10 of the dogs were crossbreeds. Pure breed dogs were classified according to the British Kennel Club Breed Groups, as defined by the British Kennel Club. In the relevant group, the pure breed dogs consisted of: 7 Gundogs, 1 Hound, 2 Pastoral dogs, 1 Terrier, 2 Working dogs, 1 Toy. In the distractor group, the pure breed dogs consisted of: 6 Gundogs, 2 Pastoral dogs, 1 Terrier, 3 Working dogs, and 2 Utility. The age of the dogs ranged between 1 and 10 years in the relevant group (*M* = 4.1 years, *SD* = 2.8), and between 1 and 9.5 years in the distractor group (*M* = 4.3 years, *SD* = 2.4).

Methods

The study followed a procedure similar to that of Study 1, with the difference that now only one object was hidden in one of three possible locations and that object was either relevant to the experimenter (notepad) or not (stapler).

Testing took place in one of the rooms (4.60 m x 4.20 m) of the Dog Cognition Centre Portsmouth (DOCS). Three opaque containers (19 cm x 10 cm) were placed on the floor: one in the left, one on the middle and the other in the right corner of the room. A bench for the experimenter to sit on was placed in the middle of the three containers and at a distance of 2.70 m to two of the containers and at a distance of 2.60m of the third (Figure 3.2). Two different objects were used as hidden targets: a notepad (relevant object) and a stapler (distractor).

Figure 3.2. Testing room for Study 2.

A bench was positioned in the middle of the testing room. Three opaque containers (one on the left, one in front and one on the right of the bench) were positioned so that each of them was at the same distance from each other and from the bench. The two objects, relevant and distractor, were positioned on the bench before the dog entered the testing room.

Like in Study 1, the procedure started with a warm-up phase. After the warm-up the dog was led out of the room by the helper and the experimenter. The dog and the experimenter re- entered the room and the experimenter sat down on the bench. The two objects, the notepad and the stapler, were lying on the bench. The experimenter ignored the stapler, and picked up the notepad to write her notes. In order to make sure the dog noticed her activity, the researcher continuously mumbled to herself while being busy writing. If the dog moved far away, the experimenter called for the dog's attention to ensure he returned while never specifically indicating the notepad. After using the notepad for 30 sec (measured with a timer) the experimenter said something like "Oh, I need to leave, you wait here!" and left the room through door A while leaving the notepad on the bench.

After the experimenter left the room, the helper entered through the same door, went straight to the bench and picked up the notepad and the stapler. Then, making sure that the dog was watching, she hid one of the two objects depending on the condition while holding on to the other object. Dogs were randomly assigned to one of the two conditions:

Relevant condition: the helper hid the relevant object (the notepad) in one of the three boxes while catching the dog's attention by talking to him while hiding the object.

Distractor condition: the helper hid the distractor (the stapler) in one of the three boxes while catching the dog's attention by talking to him while hiding the object.

The helper always started the baiting of the containers by opening the containers to the left, then the middle one and finally the one on the right. While opening all containers she kept the dog's attention by talking to the dog but did not pay more attention to any of the containers over the others. After the hiding was completed, the helper left the room through door B (Figure 3.2), taking with her the object she had not hidden, and leaving the dog in the testing room.

After the helper had left, the experimenter returned through door A, and started the search following the exact same protocol as in Study 1.

The study followed a mixed design. The between subjects variable was the group that dogs were allocated to. Within each group it was then varied whether the experimenter talked to the dog in a high-pitched voice while searching, *vocal trials*, or not, *silent trials* (within subject variable). Vocal and silent trials were presented blocked with half of the dogs in each group starting with vocal trials and the other half starting with silent trials. Dogs in each group (relevant and distractor) received three vocal and three silent trials summing up to six trials altogether. The location where the object was hidden was counterbalanced and semi-randomised following a double Latin square design so that during each block (silent and vocal) the object was hidden once in each container and the possible combinations were counterbalanced across the subjects. After the searching phase had elapsed the experimenter had to take a decision on which container to check. Again this was identical to the protocol used in Study 1. After making a choice the trial was over, the experimenter guided the dog out of the room and the helper entered the testing room to rearrange it for the following trial.

Behavioural analysis

We recorded the frequency of gazes towards two distinctive locations in the room: (1) gazing at the experimenter, (2) gazing at the box where the target object was hidden (target box). As in Study 1, gazes were subjected to a sequential analysis and gaze alternations were recorded.

As in Study 1, the duration of looks toward the experimenter during the demonstration phase were also recorded.

Again, in order to assess inter-coder reliability a random selection of the video material (20%) was coded by a second observer, naïve to the purpose of the study and to the content of the hiding boxes. The correlation between the two coders was calculated using Spearman r. Inter-observer reliability was moderate for the frequency of gazes to the target box ($r_s = .44$, $N = 58$, $p = .001$) and the duration of gazes to the target box ($r_s = .53$, $N = 58$, $p = .001$). There was an excellent agreement on the frequency of gazes to the experimenter ($r_s = .86$, $N = 58$, p = .001), the duration of gazes to the experimenter ($r_s = .90$, $N = 58$, p = .001), and the duration of gazes during the demonstration ($r_s = .88$, $N = 59$, p = .001).

Statistical analysis

Data were analysed using the statistical software R (R Development Core Team, 2015), with the packages *lme4* (Bates et al., 2015), *MuMIn* (Bartoń, 2016), and *lsmeans* (Lenth, 2015). A modelling approach (GLMM) was used for the analysis of the data using the same procedure applied to Study 1. All results have been reported with standard errors.

A GLMM (null model) with *log* function was calculated with the count response variable “gaze alternations” (number of gaze alternations toward the target box), and the nested random intercept factors “dog”, “counterbalancing group” and “trial” (N = 288, number of subjects = 48). All the relevant fixed factors and interactions were included in the model (Appendix D: Model fitting additional information for Chapter 3). There were no significant main effects or interactions, therefore the null model was retained.

Another GLMM with *logit* function was calculated with the response variable "duration of gazes (s)", weighted by the factor "duration of trials (s)" (null model). The random intercept factor "dog" (N = 48) was included in the null model. All the relevant fixed factors and interactions were included in the model (Appendix D: Model fitting additional information for Chapter 3for details). The model that yielded the lowest AIC comprised the fixed factors "direction" (experimenter, empty-boxes, target-box, other), "condition" (relevant, distractor), and "communication" (silent, vocal), with a 3 level interaction.

Results

Nearly all dogs alternated their gazes between the experimenter and the target box (92% in the relevant group, 100% in the distractor group), with no significant difference between the two groups (Fisher's exact test, p = .49).

The analysis of the frequencies indicated that the number of gaze alternations was not influenced by the condition ($GLMM_{Condition}$, AIC = 637.1, N = 48, χ_{21} = 1.764, p = .184), or the communication ($GLMM_{Communication}$, AIC = 638.3, N = 48, χ_{21} = .609, p = .435). Therefore any variation in the frequency of gaze alternations was due to individual differences ($AIC_{NullModel}$ = 636.9).

There was an effect, with a 3 level interaction, of the direction of the gaze, the content of the target box (condition), and the communication on the duration of dog gazes ($GLMM_{Direction*Condition*Communication}$, $AIC_{NullModel}$ = 54038.0, $AIC_{FullModel}$ = 52465.9, N = 48, χ_{215} = 1602, p = .001). The factor "attention" during the demonstration did not improve the model and was therefore not included (GLMM$_{Direction*Condition*Communication+Attention}$, AIC = 52467.9, N = 48, χ_{21} = 0, p = .995). Gaze duration was more likely to increase when dogs were gazing at the target (compared to an empty box), in the relevant group (compare to the distractor group), and in the vocal trials (compared to silent trials) (estimate $_{target*relevant*vocal}$ ± SE = .336 ± .098, p = .001) (Figure 3.3).

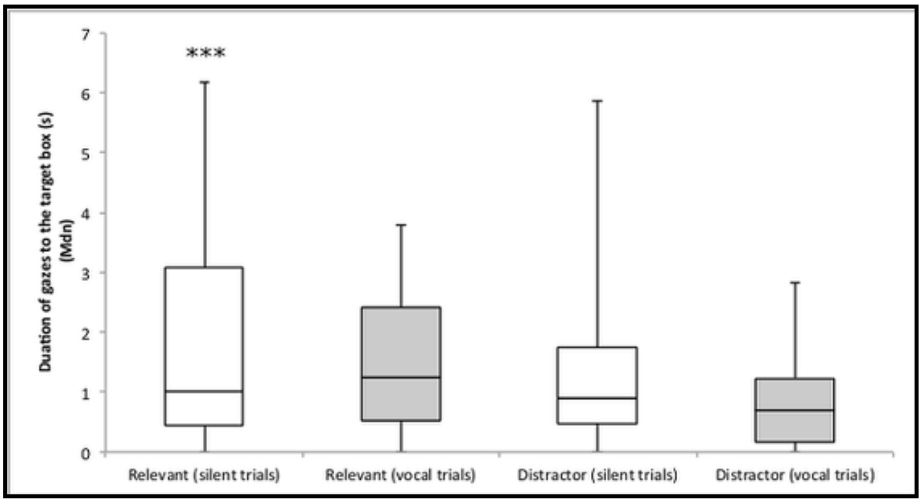

Figure 3.3. Effect of direction, condition, and communication on dogs' gazes.

The asterisks in the graph represents the significance of the estimate for the direction of the gaze x condition x communication with a 3 level interaction. Gaze persistency was more likely to increase when gazes were directed to the target, in the relevant group and in the vocal trials. A breakdown of the duration of gazes to the target, divided by condition and communication, is presented in the graph. The middle line in the box plots represent the median duration of gazes, the extremes of the boxes represent the lower and upper quartiles, and the error bars represent the minimum and maximum duration of gazes.

Discussion

The findings of this study showed that dogs seemed to differentiate between the objects that were hidden. Vocal trials and the presence of the relevant object led to more persistent, i.e. longer gazes directed to the target. This can possibly be an indicator that dogs differentiate the objects based on the human's interest in them and might mean that dogs communicative behaviour towards humans is underlined by a helpful motive, as it is similar to the infants' informative pointing described by Liszkowski and colleagues (Liszkowski et al., 2006, 2008). A more parsimonious explanation is that the high pitch voice used by the experimenter had an arousing effect on dogs (McConnell, 1990), thereby enhancing their communicative response. However, humans' ostensive cues, in this case high-pitched voice, initiate and maintain communication in dogs (Tauzin et al., 2015b; Topál et al., 2014).

Consequently, another possibility is that the experimenter's voice helped in establishing a communicative context or helped the dogs understanding the humans' need for information. Future research could further investigate how different types of ostensive cues affect dogs' communication. Recent results showed that temporal contiguity between human ostensive cues and referential signals (pointing) is necessary for dogs to understand the gesture. The manipulation of the temporal order in which ostensive cues and pointing were presented to the dog, in fact, allowed for the confirmation of the importance of ostensive signals preceding referential cues in communication-based knowledge acquisition processes in dogs (Tauzin et al., 2015a). Also eye contact with the owner increases dogs' attention getting behaviours (Ohkita, Nagasawa, Kazutaka, & Kikusui, 2016). The systematic manipulation of different ostensive cues (e.g. high pitch voice, eye contact), in association with their temporal manipulation (before and after searching behaviour) (Hill, 1965) may aid the understanding the role of high pitch voice upon dogs' behaviour in a cooperative-communicative context. Applying such an approach to a range of communicative and non-communicative contexts could possibly allow teasing apart the overall arousing effect of some ostensive cues (i.e. high pitch sounds) from the more context specific effects on dogs' communication.

General Discussion

The results of Study 1 show that dogs did not indicate preferentially the object needed by the experimenter. They rather indicated objects that they had an interest in (i.e. the toy or novel objects). However, the dogs' indications were more persistent when directed to the relevant object, and increased with the attention during the demonstration. These results are confirmed by those of Study 2 where, in the absence of a personal interest, dogs' indications towards an object relevant for the human were more persistent when compared to indications towards a distractor if the experimenter verbally addressed the dog. In the light of these results, there seems to be some evidence that dogs could be able to distinguish between objects based on a human's need for them. Interestingly, in both studies dogs used gaze alternation with similar frequency regardless of the relevance of the object, therefore indicating that objects' relevance may not affect the motivation of dogs to establish joint attention when communicating to humans. This result should however be considered cautiously, since the inter-coder reliability was low for the frequency of gases. It is possible that such low correlation between the two coders depended on the low frequency of the behaviour, associated with difficulty in coding it; or it could be possibly an indication that the reliability coder required more training.

The use of contingencies between the events observed by the dogs could be a more parsimonious mechanism that may as well possibly explain these results. Stimulus enhancement, caused by witnessing the experimenter interacting with the relevant object, could have directed the behaviour of the dogs. Such a possibility would imply that the dogs did not understand the relevance of the object to the experimenter. Although the helper manipulated both objects in all conditions in an attempt to control for this, the possibility cannot be completely excluded. However, the level of flexibility with which dogs use their showing behaviour (Gaunet & Deputte, 2011; Gaunet & Massioui, 2014; Gaunet, Steiger, & Deputte, 2012; Marshall-Pescini et al., 2013; Miklósi et al., 2000) makes this mechanism less likely to be the sole explanation for their communicative behaviour.

Another possible explanation for our results is that dogs' communication may be underlined by informative motives. Gaze alternations show dogs' intention to form joint attention with the experimenter (Miklósi et al., 2000), while the persistent gazes towards the relevant object may have been used to direct the experimenter's attention (Gómez, 2007). Such behaviour is consistent with the description of informative pointing provided by Liszkowski and colleague, where the pointer provides the information by directing the recipient's attention towards a target because of the recipient's relation to the target itself, rather than a personal interest (Liszkowski et al., 2006). For this to be possible dogs need to possess a number of skills. In order to understand the human's need for information, dogs need to recognise humans as intentional agents (Kaminski et al., 2011a), as well as have the motivation to use communication helpfully (Liszkowski et al., 2006). Dogs perceive the communicative intent in the human pointing, as demonstrated by their ability to distinguish an intentional communicative pointing from similar, non-communicative movements in the same direction (Kaminski et al., 2012). Moreover, Marshall-Pescini and colleagues (2014), using a habituation-dishabituation paradigm, were able to show that dogs appear to perceive human actions as goal-directed. Finally, dogs have been selected during domestication for being particularly skilful in interacting with humans in social and communicative situations (Cooper et al., 2003; Hare & Tomasello, 2005; Miklósi et al., 2004). There are indications that they have helpful motives when interacting with humans in general, such as during instrumental helping (Bräuer et al., 2013b), cooperative problem solving (Ostojić & Clayton, 2013), and complex cooperative interactions (Naderi, Miklósi, Dóka, & Csányi, 2001, 2002). Additionally, dogs also have the general motivation to act cooperatively in response to humans' requests (Kaminski et al., 2011a).

Another parsimonious explanation for our results could possibly be that dogs were indicating the hidden object to comply with a human request, as previously suggested by Kaminski and colleagues (2011a). It has been hypothesised that dogs interpret human referential behaviour as being about something but cannot make the connection to the specific object that is being referred to (Tempelmann, Kaminski, & Tomasello, 2014). It is possible that dogs interpret human search and ostensive cues as directives, e.g. a request to fetch or to find a hidden object (Gómez, 2005; Kaminski et al., 2011a).

Moore and Gomez propose that, in ape and infant pointing, imperative and declarative gestures could possibly share the common cognitive complexity of understanding behaviours as connected to targets through joint attention (Gómez, 2007; Gómez, Sarria, & Tamarit, 1993; Moore, 2013). The dogs in our study established joint attention in both conditions. Therefore this interpretation could be valid for dogs as well. This could imply that dogs possibly indicated the hidden object because they interpreted it as the target of the experimenter's search, especially in the case of the distractor group in Study 2, when the relevant object was not in the room and there were no other objects attracting the attention of the dogs. Such a mechanism is similar to that described by Csibra and Gergely, and according to the authors it does not require the understanding of others' mental states and is possible in non-human animals (Csibra, 2003; Csibra & Gergely, 2007; Gergely & Csibra, 2003). Nevertheless, the possibility of informative communication is not excluded. Specifically, the fact that dogs' showing behaviours were more persistent in the relevant condition, demonstrates that at least in the relevant condition, dogs took into account the relevance of the objects to the experimenter when communicating. This could not be explained by a more parsimonious mechanism, such as social enhancement. On the contrary, interpretations such those of Moore and Gomez do not require the understanding of humans' state of knowledge or the intent to influence the mental state of others. It would suffice for dogs to recognise the communicative context, e.g. through the human ostensive cues, and to identify the relevant object as the target of the human's search in order to indicate a target relevant for the receiver (Gómez, 2007; Moore, 2013).

In conclusion, while the current results could not demonstrate the presence of an informative intent in dogs' communication, they do not fully exclude this possibility, which needs further investigation. Specifically, this study provides some evidence that dogs may be able to recognise the relevance of an object for a human partner based on the context in which it was used. Further research should attempt to tease apart the elements driving dogs' understanding of objects' relevance. Coincidentally, the results add to the existing body of evidence indicating some level of a helpful motivation in dogs' communication, demonstrating that such helpful drive is easily masked by preponderant selfish interests. When more preferred objects were not present in the room (Study 2), dogs indicated targets that they had no interest in, without receiving any explicit reward. It may therefore be necessary to account for competing interests when investigating helpful motives in dogs.

Chapter 4. Do dogs form an opinion on humans based on skilfulness?[3]

Chapter overview

The results of Chapter 3 indicate that dogs might use gazes, and especially referential gazing, with helpful motives. There is evidence that dogs gaze at humans also as a strategy to request help when facing an unsolvable problem. According to the theory of indirect reciprocity, it should be expected that dogs would form a preference for requesting help from humans with a better reputation. There is evidence that dogs form reputation judgments about humans based on direct experience. This has been mainly tested in contexts where humans were either nice or not towards others. However, the theories of indirect reciprocity state that those individuals who are more helpful should be preferred. Therefore, in the current studies we investigated reputation formation based on seeing human partners being skilled or unskilled. The ability to distinguish

[3] Manuscript based on the paper under review:
Piotti, P., Spooner, R.M., Jim, H.-L., Kaminski, J. (submitted) Who to ask for help? Do dogs form an opinion on humans based on skilfulness? *Animal Cognition*

between skilful and unskilful individuals is highly relevant when selecting a partner for collaborative activities.

Thirty-two adult pet dogs observed 4 blocks of 2 demonstration types. A skilful experimenter succeeded in solving a puzzle and obtaining food for the dog. An unskilful experimenter failed, though food was dropped inconspicuously. Blocks were followed by unsolvable task trials: dogs were presented with a container baited with food that was inaccessible, while the experimenters stood either side of it. Referential looks towards each experimenter were recorded. Dogs who looked referentially did not choose the skilful experimenter above chance. There was also no overall difference in the frequencies of looks at the skilful vs the unskilful experimenter or their duration. In order to simplify the task, in a second study dogs only witnessed one type of demonstration, and tested immediately after in a single unsolvable task trial. Forty-eight Dogs were allocated to one of four groups, according to a two by two design: demonstrations could be either skilful or not-helpful (*skilfulness* variable) and nice or ignoring (*quality of interaction* variable). Again, dogs' look back behaviour did not increase in any of the conditions.

These results suggest that dogs might not take into account skilfulness when looking referentially at humans for help, or possibly could not use the information to evaluate them in this context.

Introduction

Reputation is the ability to gain knowledge about an individual's common behaviour through the individual's past behaviour (Melis & Semmann, 2010; Russell et al., 2008) to form a set of collective beliefs, perceptions, or evaluative judgments about someone (Emler, 1990; Sperber & Baumard, 2012). Reputation is considered a crucial element of cooperative interactions as it allow recruitment of the best collaborative partner (Wedekind & Milinski, 2000; Wu, Balliet, & Lange, 2016) and avoidance of exploitation (Axelrod & Hamilton, 1981). For example, humans monitor the roles of other individuals and choose future collaborators on the basis of individuals' past behaviour (Fehr & Fischbacher, 2004; Trivers, 1971). Starting from a very young age, they identify and recruit the most effective collaborators when they need help in solving a problem (Tomasello et al., 2005; Warneken et al., 2006) and they can form an opinion about others based both on their direct and indirect experience (Herrmann et al., 2013). There is some evidence that other primates, such as chimpanzees (Herrmann et al., 2013; Melis et al., 2006; Subiaul, Vonk, Okamoto-Barth, & Barth, 2008) and orang-utans, can identify and recruit a collaborative partner based on their direct experience and, to some extent, after observing third party interactions (Herrmann et al., 2013). Recently, comparative research showed that also species evolutionarily more distant from humans, such as fish (Vail et al., 2014), ravens (Asakawa-Haas, Schiestl, Bugnyar, & Massen, 2016), and dogs (Horn et al., 2012) form preferences in choosing their collaborative partners.

However, the cognitive mechanisms underlying this skill are still unclear (Asakawa-Haas et al., 2016).

Dogs are a species of particular interest for the comparative study of social skills, because of their unique ability to communicate with humans (Cooper et al., 2003; Miklósi et al., 2004). One hypothesis is that dogs' outstanding skills are the result of a unique domestication process (Hare et al., 2002, 2005; Miklósi et al., 2003), during which dogs adapted to life with humans and formed a specialization for communication with humans, especially in cooperative contexts (Bräuer et al., 2006; Reid, 2009). The literature indicates that dogs can form an opinion about humans based on their direct experience, such as interacting with someone nice versus someone ignoring them (Nitzschner et al., 2012). Results about dogs' ability to evaluate humans based on indirect experiences are more controversial (Chijiiwa, Kuroshima, Hori, Anderson, & Fujita, 2015; Freidin et al., 2013; Marshall-Pescini et al., 2011; Nitzschner et al., 2014). One area that is largely understudied is dogs' ability to take into account their opinion about humans in a collaborative context. There is evidence that dogs use a specific behaviour, called *looking back*, to seek for human help when they cannot solve a problem (Miklósi et al., 2003). Therefore, the look back represents an interesting behaviour that can be used to measure dogs' tendency to recruit human help. Horn et al. (2012) investigated whether dogs could discriminate two experimenters based on their skills (i.e. filling an empty food-toy, rather than unlocking the toy when it was blocked), and whether dogs would also use this *looking back* behaviour to request help from the most appropriate partner based on the problem at hand (i.e. an empty apparatus or a locked apparatus). While dogs looked back equally at either experimenter, the different amount of time spent close to the experimenters showed that dogs could possibly discriminate the two (Horn et al., 2012). It is also possible that the dogs did not look preferably at one of the two experimenters because both were helpful, in a way.

Petró et al. (2016) replicated the work by Horn et al. (2012) but substituted the human partners with *inanimate interactive agents*. In this study, dogs initially looked more at the most appropriate agent, based on the context (i.e. when a filler was required or when a helper was required), though the behaviour faded with trials. The authors concluded that the dogs most likely associated the action of either inanimate agent with the specific location where the food was hidden (Petró et al., 2016). It is therefore still not clear whether dogs can discriminate humans based on skilfulness and subsequently take it into account to request for help from the best collaborators.

In the current study, we adopted the original test that was designed to study canine help requests through the measure of the looking back behaviour, i.e. the *unsolvable task paradigm* (Miklósi et al., 2003). In the unsolvable task, dogs are initially given access to some food that they can retrieve from below a container, in the presence of a human partner; after a few successful retrievals, the apparatus is altered so that the food becomes inaccessible, thus the task becomes unsolvable. Dogs have been found to respond by looking back at the human, which has been interpreted as a request for help (Miklósi et al., 2003). There is evidence that the looking back behaviour during the unsolvable task is largely affected by past experience. For example, dogs trained for agility or water rescue, gaze more at humans compared to search and rescue dogs or untrained dogs (D'Aniello, Scandurra, Prato-Previde, & Valsecchi, 2015; Marshall-Pescini, Passalacqua, Barnard, Valsecchi, & Prato-Previde, 2009) and pet dogs gaze more than kennelled dogs (D'Aniello & Scandurra, 2016). Similarly, dogs kept as companion pets gaze more at their owner in a problem solving situation, compared to working dogs kept outside of the owner's house (Topál, Miklósi, & Csányi, 1997). However, it is yet not known how flexibly dogs can take into account their past experience with a human partner when requesting their help.

We designed two experiments to investigate the effect of direct experiences with humans on dogs' looking back behaviour. In Study 1, we examined whether dogs would preferably look at a skilful partner rather than an unskilful one, during the unsolvable task. It is however possible that dogs can only take into account other social elements of their interactions with humans, such as being nice (Nitzschner et al., 2012), rather than skilfulness. It may also be difficult for dogs to discriminate between two partners in the unsolvable task. Therefore, in Study 2, there was only one experimenter, who showed to be either skilful or unskilful, and either interacted to the dog in a friendly way or ignored the dog.

Ethical statement

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed involving animals were in accordance with the ethical standards of the institution at which the studies were conducted (the University of Portsmouth). The studies were carried out in strict accordance with the recommendations in the ASAB/ABS guidelines for the use of animals in research and were approved by the University of Portsmouth Animal Ethics Committee (Animal Welfare and Ethical Review Body, AWERB, approval n. 515a, Appendix G: Ethical approval for the study in Chapter 5). Informed consent was obtained from all the dog owners for their dog to participate in the study.

Study 1

The aim of this study was to investigate whether dogs can form an opinion about humans, based on their direct experience observing skilful and unskilful human partners during a problem-solving task, and subsequently recruit the best helper when they face an unsolvable task. Since dogs can form an opinion about humans based on their direct experience (Nitzschner et al., 2012), and dogs' gazing behaviour toward humans is influenced by previous collaborative experiences (D'Aniello et al., 2015; Marshall-Pescini et al., 2009), we expected the dogs to gaze more at the skilful experimenter during the unsolvable task. The overall study design was similar to Nitzschner et al. (2012). Dogs had different demonstrations with two experimenters (PP and RMS), One experimenter skilfully operated a *problem-solving toy*, while the other attempted but failed. Immediately afterwards, dogs were presented with the unsolvable task in the presence of the two demonstrators (test phase). The whole procedure was repeated four times, therefore dogs experienced four blocks of demonstrations and four tests overall.

Methods

Apparatuses and testing areas

Previous studies on reputation forming in dogs, indicate that dogs may associate a specific location with food, rather than choosing a human partner based on his/her characteristics (Nitzschner et al., 2014; Petró et al., 2016). Therefore, in the current study, two different apparatuses were used, for the demonstration phase and test phase, referred to as the problem-solving apparatus and the unsolvable task apparatus, and each phase took place in two different rooms of the Dog Cognition Centre Portsmouth (Figure 4.1).

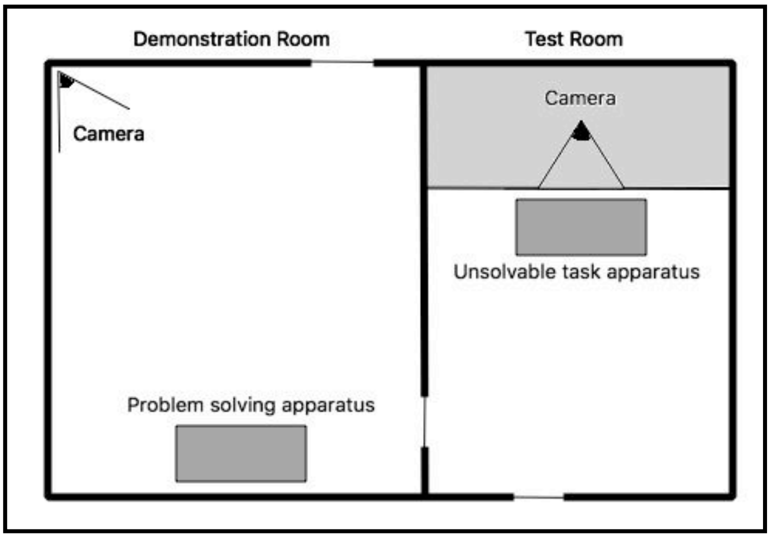

Figure 4.1. Testing rooms

The two rooms were connected by an internal door. The dark grey squares in each room represent the apparatuses. In the Test Room, the access to the light grey area was blocked through a fence and was inaccessible to the dog, so to facilitate the video recording.

The problem-solving apparatus (Figure 4.2) consisted of a wooden frame holding 3 plastic bottles with no lid, each containing one piece of dry dog food. The bottles needed to be turned upside down for the dog food to be released and a piece of cardboard, which acted as a divider obstructing the bottles' neck, had to be pulled out to release the treats.

Figure 4.2. Problem solving apparatus.

The apparatus consisted on a wood frame with three bottles on a rod that could rotate on their longitudinal axis. A piece of dry food is visible at the bottom of each bottle; a small wood partition was inserted transversally in the bottle. Therefore, in order to retrieve the food it was necessary to flip the bottle upside down and then pull the wood flap away.

The unsolvable task apparatus was a variation of the apparatus used in Miklósi et al. (2003). A piece of sausage was placed in a transparent plastic container that was attached to a wooden board. In the unsolvable task the container was covered with a metal basket attached to the board, so that the dogs could not remove it, and thus could not reach the food.

Participants

A sample of 32 pet dogs was used, including 8 females and 24 males (M_{age} = 4.43 years, Min_{age} = 1.00 year, Max_{age} = 10.00 years). Of these, 18 dogs (56%) were pure breeds (Appendix H: Subjects' information for Chapter 5). The inclusion criteria were for the dogs to be between 1 and 11 years old, to be able to visit the Dog Cognition Centre Portsmouth with their owner and be comfortable when separated from their owners. Dogs that had previous experience with the experimenters were excluded from the experiment. Some of the dogs had participated in other studies of the Dog Cognition Centre, however none of them were similar to the current study. Participants were recruited through the Dog Research Study Register of the University of Portsmouth and personal contacts.

Procedure

The overall procedure resembled that of Nitzschner et al. (2012). The dogs witnessed a series of demonstrations performed by two experimenters; each dog observed two types of demonstrations based on the experimenter's role, i.e. skilful or unskilful. Dogs were then tested with a variation of the unsolvable task, similar to that used by D'Aniello et al. (2015), in order to allow for having two experimenters in the room. The test phase of the unsolvable task is typically preceded by a few solvable trials, for the dogs to understand that they can access the food (Miklósi et al., 2003). In this study we did not want to distract the dogs after the demonstrations, therefore they were presented with the solvable trials as soon as they arrived. After that the dogs were exposed to the demonstrations and the unsolvable task trials. The 3 phases (solvable trials, demonstrations and unsolvable task) followed the procedure below:

Solvable trials: after the dog's owner agreed for their dog to participate in the study, a handler walked the dog across the Demonstration Room and took it to the Test Room (Figure 4.1), where there was a plastic container, fixed on a wooden board, containing some dog treats. The dog was allowed to eat the food and the handler refilled the container; this was repeated two more times. Then the handler took the dog outside, so that the experimenters could enter the rooms and prepare for the demonstrations. The handler and the dog waited nearby the demonstration room, in a spot from where the handler could see what happened inside the room through a window, but the dog could not.

Skilful and unskilful demonstrations: for each demonstration, only one experimenter was in the Demonstration Room, while the other waited in the Test Room. At the beginning of the first demonstration, the experimenter placed the problem-solving apparatus in position in the Demonstration Room, and refilled it as necessary, then she signalled the handler to enter the room. The handler walked the dog up to the apparatus and held it by its lead so that it was approximately a head's distance from the apparatus, i.e. the dog was close enough to the demonstration but not close enough to disrupt it. Both experimenters talked to the dog during the demonstration, to ensure it watched. During the skilful demonstrations the skilful experimenter helped the dog by performing the correct sequence of movements necessary to solve the problem and retrieve the food, which then the dog could then eat. On the contrary, in the unskilful demonstrations, the unskilful experimenter performed ineffective movements that could not solve the problem, i.e. the food was not retrieved from the bottles. It was necessary to ensure that dogs received the same amount of food during both demonstrations to avoid any food related bias. Therefore, after turning each bottle, the unskilful experimenter inconspicuously dropped three pieces of food from her pocket for the dog to find and eat them. This way the dogs received the same amount of food in both types of demonstrations and with similar timing. In order to control for odour cues, both experimenters had three pieces of food in their pocket during the demonstration. At the end of each demonstration, the experimenter said: "All done!" if it was a skilful demonstration or "I don't get it!" if it was unskilful; on this cue the handler walked the dog outside the room again, so that the two experimenters could exchange room unseen by the dog. The order of the demonstrations was counterbalanced, so that half of the dogs started with the skilful demonstration and the other half with the unskilful one. Also, PP was the skilful demonstrator for half of the dogs and RMS was for the other half. Demonstrations were presented in a semi-randomised order, with the stipulation that the same demonstration was not repeated more than twice in a row.

Unsolvable task trial: after the demonstrations, both the experimenters entered the Test Room and stood at the two sides of the apparatus. The handler led the dog into the room and placed a piece of sausage in the apparatus, then left the room for one minute. Since the dogs had previously experienced that food was accessible on the apparatus (solvable trials), they initially tried to reach the piece of sausage. Upon realising it was now out of their reach because of the metal basket, the dogs were expected to engage in other behaviours, including requests to the two experimenters (e.g. gaze alternations between the humans and the food). For the duration of the test, the experimenters stood still and kept their gaze on the food basket to ensure they did not influence the dog in any way (Figure 4.3). After the test the handler took the dog away for another demonstration; after the fourth test the study was over.

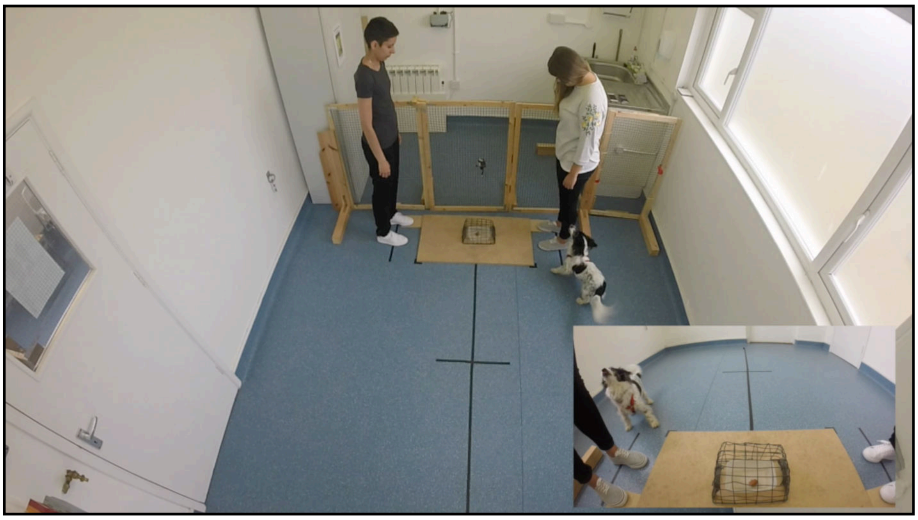

Figure 4.3. Impossible task, example of looking back behaviour

A *looking back* behaviour was recorded when the dog turned and lifted their head and/or eyes toward the head of one of the two experimenters.

Overall, the dogs experienced three solvable trials, followed immediately by 4 demonstration trials per experimenter (2 skilful and 2 unskilful) and the first unsolvable task trial. The dog then experienced a block of 2 additional demonstrations (1 skilful and 1 unskilful) followed by another unsolvable task trial. This block of 2 demonstrations and 1 unsolvable task trial was repeated three times, so that overall each dogs experienced 14 demonstrations and 4 unsolvable task trials.

Behaviour analysis

Digital video footage was taken for all trials and the Solomon Coder software (beta 091110, copyright 2006–2008 by András Péter, developed at ELTE TTK Department of Ethology, Budapest, Hungary) was used to record dogs' behaviour during testing. In order to reduce the possibility of unconscious biases, the video analysis was done by PP after the end of the study, ensuring that the information about the role of each experimenter was hidden during the coding.

Dog behaviour was measured from the moment the handler released the dog from the leash, and concluded when 60 seconds elapsed, which was right before the handler returned to the testing room. Dogs' looking behaviour was recorded based on the orientation of the head and/or eyes of the dog. As suggested by Smith & Litchfield (2013), the term gaze is avoided because it was not always possible to determine the direction of the eyes, but only the orientation of the head/nose of the dog. The term looking is used instead.

Looks toward two specific targets were recorded: 1) *looking at food* was recorded each time the head of the dog was directed towards the basket containing the food; 2) *looking back* was recorded when the dog turned and lifted their head and/or eyes toward the head of one of the two experimenters, and looks to the skilful and the unskilful experimenter respectively were recorded separately. As we were interested in dogs' help requests, we only recorded looks that were referential, according to the definition by Smith & Litchfield (2013), which we adapted to allow for the presence of two experimenters: i.e. looks included in a sequence between food and one or both experimenters (and vice versa). Only unbroken looks lasting at least 0.2 seconds were recorded and a gap no longer than 2 seconds from the end of each look and the beginning of the following one was allowed, as suggested by Gaunet and Deputte (2011) and Marshall-Pescini et al. (2009).

For each look, the latency to look (i.e. time between the beginning of the test and the dog orienting their head/eyes toward an experimenter or the food) was recorded, as were the frequency and duration of the looks. The first experimenter that dogs looked at was also recorded.

A random selection of the video material (20%) was coded by a second coder (RMS), naïve to the role of each experimenter at the time of coding. The correlation between the two coders was calculated using Spearman r, and inter-coder reliability was assessed according to the limits given by Landis and Koch (1977). Inter-observer reliability was excellent for the durations of looks to the experimenters (RMS: $r_s = 0.80$, $N = 24$, $p = 0.01$; PP: $r_s = 0.84$, $N = 24$, $p = 0.001$) and frequency of looks towards RMS ($r_s = 0.84$, $N = 24$, $p < 0.001$); it was substantial for the frequency of looks toward PP ($r_s = 0.76$, $N = 24$, $p < 0.001$)

and latency to look towards PP (r_s = 0.74, N = 24, p < 0.001); it was moderate for the latency to look toward RMS (r_s = 0.51, N = 24, p = 0.001).

Statistical analysis

Data were analysed using IBM SPSS Statistics version 22. The Kolmogorov-Smirnov test for normality revealed that the data were not normally distributed, thus non-parametric tests (two tailed) were used. Measures were averaged across trials for each dog before performing the statistical analysis, so for every variable measured, the mean value across the four test trials was used.

Results

Overall, 97% of the dogs looked at the experimenter at least in one of the trials. Trials where dogs never looked at the experimenter (14% of all trials) were excluded from further analysis.

The initial analysis was on the first experimenter that dogs looked at. For each dog, the percentage of trials where they looked at the skilful experimenter was calculated based on the number of trials where they did look at one of the two experimenters (one dog was excluded from the analysis because did not look at the experimenters). A one-sample Wilcoxon signed rank test was then performed on this value, and indicated that dogs choose the skilful experimenter below chance level, i.e. 50% of trials (*Mdn* = .50, *interquartile range* = .25-66, N = 31, z = -4.87, p < .001), with a large effect size (r = - .87). Size effects have been calculated according to Pallant (2007) and assessed using Crohen criteria (1988) of .1 = small effect, .3 = medium effect, .5 = large effect.

As it is possible that the duration of looking declined in the first trial, due to the passive behaviour of the experimenters, the duration of the first look in the first trial was also analysed separately (all dogs were considered in the analysis). Wilcoxon matched-pair signed rank test indicated no differences in the looking behaviour towards Skilful and Unskilful experimenter (N = 32; Mdn_{skil} = .00, interquartile range .00 – .60; Mdn_{unskil} = .00, interquartile range .00 – .60; z = -.03, p = .974, with a small size effect r = .001).

The following analysis regarded the duration, frequency and latency to look at each experimenter. Because it was possible that the dogs' help-seeking behaviour had declined across trials, the first trial has initially been analysed alone (dogs that did not look have been excluded from the analysis). Wilcoxon signed rank test showed that the looks towards the *skilful* and the *unskilful* experimenter did not differ for frequency, latency or duration; the effect size were small for frequencies and latencies tests but medium for the duration tests (**Table** 4.1.).

Table 4.1. Median duration of *looking back* at the skilful experimenter versus the unskilful experimenter during the first trial, results of related-measures Wilcoxon signed rank test (*N* = 27). P values have been corrected for multiple comparison using Bonferroni method. Effect sizes (*r*) were calculated dividing the test statistics by the square root of the number of observations (Pallant, 2007).

Skilful	Unskilful

	Mdn	*Interquartile range*	*Mdn*	*Interquartile range*	*z*	*p*	*r*
Frequencies	1.00	0.00-2.00	1.00	0.00-2.00	-.17	.861	-.02
Latencies (seconds)	35.40	12.8-60.00	33.00	14.80-60.00	.14	.885	.02
Durations (seconds)	1.20	0.00-2.50	1.40	0.00-5.00	.44	.656	.06

All subsequent analysis was performed on the data averaged across trials. The duration, frequency and latency of looking back indicated that dogs did not prefer the skilful experimenter over the unskilful one; the size effect was small for each measure (Table 4.2).

Table 4.2. Median measure across all trials of *looking back* at the skilful experimenter versus the unskilful experimenter (*N* = 32). P values have been corrected for multiple comparisons using Benjamini & Hochberg (1995) method. Effect sizes (*r*) were calculated dividing the test statistics by the square root of the number of observations (Pallant, 2007).

	Skilful		Unskilful				
	Mdn	*interquartile range*	*Mdn*	*Interquartile range*	*z*	*p*	*r*
Frequencies	1.00	0.50 – 1.50	1.00	0.50 – 1.50	-2.20	.082	-.28
Latencies (s)	37.33	19.11 – 53.98	36.60	22.09 – 52.98	.01	.992	-.01
Durations (s)	.60	.20 – 1.21	.57	0.38 – 1.34	-1.08	.422	-.13

Note: Results of matched sample Wilcoxon signed rank test (*N* = 32).

Discussion

This study investigated whether dogs would discriminate between the two humans solely on the basis of the level of skilfulness they demonstrated in the previous problem-solving situation. Our test paradigm was the unsolvable task. In this context, dogs typically look at humans to request their help to retrieve their food. If dogs had this ability, they would be expected to preferably look at the most skilful partner. However, the results of this study did not indicate that the dogs formed a preference for either of the two experimenters, skilful or unskilful.

A explanation could be that dogs might not be able to form an opinion based on skilfulness, and this could be a prerogative of humans and close relatives such as primates (Melis et al., 2006). However, dogs are able to adjust their behaviour based on the skills of a human partner (Horn et al., 2012). This potentially suggests that dogs might have some level of understanding of human's skilfulness.

Another possible explanation is that dogs might form an opinion about humans based on how pleasant is the interaction with them, rather than the level of skilfulness. Dogs have been found to prefer spending time near a human partner that interacted in a friendly way, rather than one ignoring them (Nitzschner et al., 2012). In a recent study, it was also observed that dogs could discriminate between a cooperative human partner, who gave them food, and a competitive partner, who had some food but ate it. The dogs looked more at the cooperative partner than the competitive one; dogs were also more likely to indicate the location of some hidden food when the cooperative partner was in the room (Heberlein et al., 2016). This last study suggests that dogs adjust their communicative behaviour to their experience with humans. In a recent review of the literature, Abdai and Miklósi suggest that both concepts, being skilful and being nice, are important to collaborative contexts and it may be difficult to separate them completely one from the other (Abdai & Miklósi, 2016). It is possible that it was difficult for the dogs in the current study to prefer one experimenter over the other, as both acted equally nicely towards the dogs.

It may also be difficult for dogs to choose between the two human partners during the unsolvable task. Dogs were found to be able to discriminate between two people during such test in one study by D'Aniello et al. (2015). However, in that study dogs had to choose between the owner and a stranger. In the case of the current study, in order to succeed, dogs were required to discriminate two strangers based on elaborated sequences of actions. It is possible that the dogs in our sample might have not have fully understood the demonstration. Although this was designed as a direct experience for dogs, they did not have a chance to use the apparatus and potentially gain an understanding of how to use it. Previous findings suggest that dogs may have a limited understanding of how a physical problem can be solved by a human partner (Horn et al., 2012). For this reason, the dogs in the current study might have failed to fully recognise the experimenters' ability to solve a problem.

Finally, it should be taken into consideration that in this kind of studies, the subjects may be affected also by the behaviour of the experimenters during test trials (Abdai & Miklósi, 2016). It is possible that the dogs in this study were influenced by the experimenters' behaviour during the unsolvable task trials, which was to ignore the dogs' help requests. As dogs look back at humans to request help (Miklósi et al., 2003), they may anticipate a reaction (e.g. help, or at least social interaction) from the humans, due to their past experience in similar situations, which might have contributed to reward their behaviour with time. When an anticipated reward is unexpectedly reduced, many dogs either show a successive *negative contrast*, i.e. a reduction in their responses (Bentosela et al., 2009), or a paradox increase in their behavioural response (Reimer et al., 2016). While the lack of reaction on the side of the experimenter is required by the type of tests as the one described in this study, the effect of affective contrast should be taken into account in the analysis and interpretation of results. For example, it is important to ensure that the first response of the animal is analysed and that the different trials are analysed separately. Moreover, since the behaviour of the experimenters during the test may largely influence dogs' subsequent response, it may be more useful to have only one test trial.

Therefore, it was necessary to design a second study where only one experimenter was present in the unsolvable task and dogs had a chance to directly experience the use of the apparatus in the demonstration. Moreover, the study assessed whether other elements possibly more relevant to dogs, such as the quality of the interaction, would influence dogs' looking back behaviour in the unsolvable task.

Study 2

The aim of this study was to investigate whether dogs form an opinion about humans based on their direct experience with a human partner. Conditions were administered in a two-by-two design, so that dogs had a direct experience with a human partner who was either nice or ignored the dog, and either skilful or not willing to help during a problem-solving task. The test was between subjects and examined whether dogs' in the four groups (*Nice-Skilful, Nice-No-help, Ignoring-Skilful,* and *Ignoring-No-help*) varied in their tendency to request help from the experimenter when they faced an unsolvable problem. In order to avoid carryover effects, in this study each dog will be exposed to only one demonstration and one unsolvable trial.

Dogs discriminate positive and negative emotions in humans (Albuquerque et al., 2016) and recognise a praising tone of voice (Andics et al., 2016), they can form a positive or negative opinion about humans based on their direct experience (Nitzschner et al., 2012), and dogs' gazing behaviour toward humans is influenced by previous collaborative experiences (Marshall-Pescini et al. 2009; D'Aniello et al. 2015). Therefore it was expected that the dogs would be more likely to look back at a nice and/or skilful experimenter.

Methods

Apparatuses and testing areas

Testing took place in the same rooms of the Dog Cognition Centre of the University of Portsmouth as in study 1, arranged in a similar way (Figure 4.4).

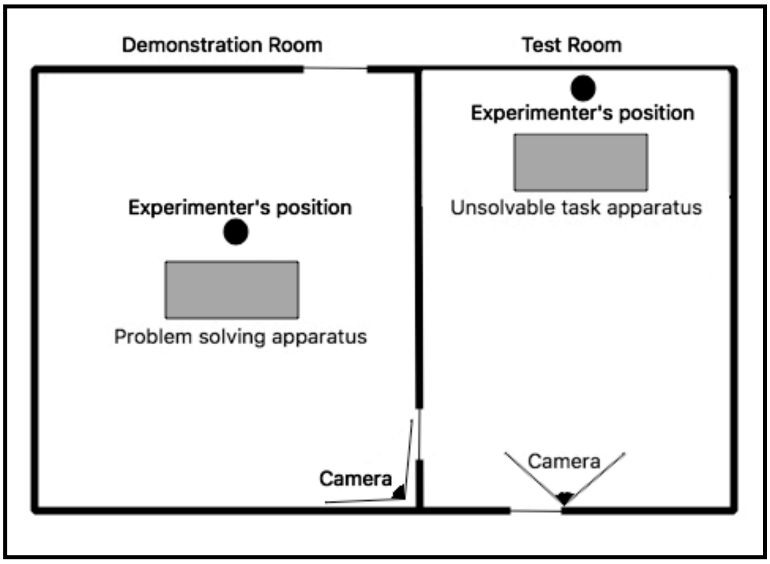

Figure 4.4. Testing rooms

The same rooms as in Study 1 were used. The dark grey squares in each room represent the apparatuses. The black circle near the square represents the position of the experimenter during the demonstration and during the test respectively.

The apparatus for the demonstration was a *Nina Ottoson® Dog Fighter* dog puzzle-toy (Figure 4.5). The apparatus had a number of hollow slides that could be filled with food and wood blocks. The blocks had to be removed in a specific order and using certain movements in order to retrieve the food. Only 4 slides were used. The apparatus for the unsolvable task was the same used in Study 1.

Figure 4.5. Problem solving apparatus

The *Dog Fighter* puzzle-toy had 6 hollow slides with a large opening. Only 4 of the central slides were used. A small piece of hot-dog was placed under the small hollow block (with a red dot), which was placed at the opening and then slid across to the other end. A larger block was placed at the opening, which prevented the small block from being removed. In order to retrieve the food, it was necessary to pull out the large block first, then slide the small block across and remove it from the opening by pulling the string attached to the small block.

Participants

A sample of 48 pet dogs was used, of which 21 dogs were male (56%) and 27 female (M_{age} = 4.17 years, Min_{age} = 1.00 year, Max_{age} = 11.00 years). Overall, 31 dogs were pure breeds (65%). A breakdown of the dogs' information by condition is presented in Appendix F: Subjects' demographic information for Chapter 4. The inclusion and exclusion criteria, and recruitment method were the same as for Study 2. Another two dogs were tested but data were removed before further analysis because of procedural mistakes (1 dog) or because the dog had used the puzzle-toy before (1 dog).

Procedure

The study was comprised of: a habituation phase, in which dogs were given some time to get used to the testing area; a warm-up, in which dogs were given time to familiarise with and try to use the puzzle-toy that was later used in the demonstration, and the baseline level of looking back at a stranger (experimenter) was measured; a demonstration, in which the experimenter attempted to operate the puzzle-toy, acting either skilful or unskilful and nicely or ignoring the dog, according to the condition; and a test phase, in which the dog was tested with the unsolvable task.

Habituation phase: The handler played with the dog for a few minutes, letting it explore both the Demonstration and the Test Rooms, while offering from her hands some of the food used in the test (pieces of hot-dog). Both apparatuses were out of view at this stage, and the experimenter was waiting outside; once the dog was relaxed and interested in the food, the handler called the dog into the Demonstration room, she closed the door between the two rooms and presented the problem-solving toy. At the same time, the experimenter entered the Test Room, unseen by the dog.

Warm-up: In this phase the dog was given time to try and familiarise with the puzzle-toy that was used in the demonstration. The handler put the dog on a 80 cm long lead and secured it to a wall hook. The handler placed the puzzle-toy on the floor, about 1 meter away and out of the dog's reach; then, making sure the dog was watching, she filled the toy with the treats. She then unleashed the dog and walked it to the toy encouraging it to play. The dog was given 40 seconds to try and obtaining the food and solve the puzzle, while the handler stood nearby pretending to be busy and ignoring the dog. After the time elapsed, the warm-up was over.

Demonstrations: After the warm up, the handler attached the dog to the lead that fixed to the wall again. The handler then opened the door between the two rooms and invited the experimenter inside, saying "Hello" in a neutral tone. This was done to ensure that the experimenter entering would not startle the dogs. The experimenter walked up to the dog and stood by its side, facing the wall and avoiding any eye contact. Meanwhile, the handler set up and refilled the puzzle-toy, then as she walked to the opposite side of the room. The experimenter turned around to face the toy simultaneously. The handler stood facing the wall with her back turned to the dog and the experimenter. She quickly left four pieces of food on a small shelf beside her and monitored the dog's behaviour through a mobile screen connected to a video camera. As soon as the handler saw the dog looking back at the experimenter (or after a maximum time of 2 minutes), she walked back to the dog while the experimenter walked to the shelf to pick up the food and sat down in front the puzzle-toy to begin then demonstration according to the conditions:

- *Nice & Skilful demonstration:* the experimenter spoke with an high pitched voice while effectively removing the blocks from the toy and revealing the pieces of food one by one; she established eye contact with the dog each time she spoke.
- *Nice & No-help demonstration* the experimenter spoke with an high pitched voice, but did not attempt to use the toy; instead she leaned over on the toy and then helplessly shrugged her shoulders while establishing eye contact with the dog. These movements were repeated four times to counterbalance the activity level of the skilful demonstration.
- *Ignoring & Skilful demonstration:* the experimenter avoided eye contact and talked to herself in a neutral voice as if bored by the task, while effectively removing the blocks from the toy and revealing the pieces of food one by one.
- *Ignoring & No-help demonstration:* the experimenter avoided eye contact and talked to herself in a neutral voice as if bored by the task, and did not attempt to use the toy; she leaned over the toy

and helplessly shrugged her shoulders while looking at the toy. These movements were repeated four times.

At the end of the demonstration, the experimenter walked away from the toy saying: “All done” in the two Skilful demonstrations, and “I don’t get it” in the No-help demonstrations. As in Study 1, it was necessary to ensure that dogs received the same amount of food during both demonstrations so to avoid any food related bias. Therefore, at the end of No-help demonstrations, the experimenter inconspicuously dropped the food she had in her hand placing it as close as possible the toy. Then, she turned around and sat on a chair, facing the toy but staring at her lap to avoid eye contact. The handler then walked the dog to the apparatus, letting it eat the food, and then walked it to the Test Room.

Test (unsolvable task): Now that dogs had had a chance to gather information about the experimenter and whether she was skilful in solving a problem or rather would not help them, and whether she was nice to them or rather ignored them, dogs were given a chance to request help from the experimenter in the unsolvable task. Upon entering the Test Room, the handler secured the lead to a wall hook. At the same time the experimenter entered and stood with her back against the wall, so that she was 1 meter away from the apparatus. The handler showed the dog one piece of hot-dog and placed it on the wooden board in front of the metal basket; she then centred the dog in the room and let it go get the food; she repeated this twice more. On the second repetition, she took a larger chunk of hot-dog and dropped it inside the basket, making sure the dog was watching. After centring the dog, she quickly left the room and waited next door for 2 minutes. During this time, the experimenter stood still as in Study 1. After the 2 minutes elapsed, the handler returned to the room and the test was over.

Behaviour analysis

Digital video footage was taken for all trials and the Solomon Coder software (beta 091110, copyright 2006–2008 by András Péter, developed at ELTE TTK Department of Ethology, Budapest, Hungary) was used to record dogs' behaviour during the unsolvable task. The coder (RMS) was unaware of the conditions at the time of coding.

Looks towards the experimenter and towards the food were recorded in the same way as in Study 1. However, this time all looks towards the experimenter were recorded, in order to measure whether being nice rather than ignoring the dog had an effect on their interest in the experimenter. The frequency of gaze alternations between the experimenter and the food was recorded with the aim to assess the effect of the conditions on the dogs' help requests.

A random selection of the video material (20%) was coded by a second coder, naïve to the role of each experimenter. The correlation between the two coders was calculated using Spearman r, and inter-coder reliability was assessed according to the limits given by Landis & Koch (1977). Inter-observer reliability was excellent for the frequency of gazes to the experimenter (r_s = .82, N = 11, p = .002), their duration (r_s = .94, N = 11, p = .001); it was substantial for the latencies of looks (r_s = .77, N = 11, p = .005).

Statistical analysis

Data were analysed using IBM SPSS Statistics version 22. The Kolmogorov-Smirnov test for normality revealed that the data were not normally distributed, thus non-parametric tests (two tailed) were used.

Results

Overall, the independent samples Kruskal-Wallis test indicated no significant difference between groups in the baseline latency to look at the experimenter, i.e. before the demonstration ($Mdn_{NiceSkilful}$ = 6.00, interquartile range 1.60 - 120.00, $Mdn_{NiceNoHelp}$ = 7.68, interquartile range 5.58 - 17.23, $Mdn_{IgnoreSkilful}$ = 21.69, interquartile range 11.13 - 33.25; $Mdn_{IgnoreNoHelp}$ = 20.10, interquartile range 13.52 - 30.33; $H_{(3)} = 1.75$, $p = .627$), with a small effect size $\varepsilon^2 = .06$).

The independent samples Kruskal-Wallis test also indicated no difference between the four conditions in the latency and duration of looking back behaviours at the experimenter. Similarly, the frequency of gaze alternations between experimenter and food did not vary significantly across conditions (Table 4.3).

Table 4.3 Looks towards the experimenter and gaze alternations. Medians and interquartile ranges (IQR) are indicated.

	Nice Skilful		Nice No help		Ignore Skilful		Ignore No help				
	Mdn	[IQR]	Mdn	[IQR]	Mdn	[IQR]	Mdn	[IQR]	$H_{(3)}$	p	ε^2
Looking back latency (s)	18.30	[.00, 1.78]	21.90	[.00, 4.15]	32.25	[.00, .00]	30.45	[.00, 1.25]	4.54	.209	.09
Looking back duration (s)	10.70	[3.55, 23.80]	4.85	[2.28, 9.98]	8.85	[5.88, 19.30]	5.00	[1.35, 7.10]	3.73	.293	.08
Gaze alternations frequency	3.00	[1.00, 6.25]	3.00	[22.8, 49.25]	5.00	[1.00, 7.25]	3.00	[1.75, 6.00]	.71	.871	.01

Note: Results of independent samples Kruskal-Wallis test (N = 48).
For all test the effect size (ε^2) was small.

As in study 1, the duration of the first look in the first trial was analysed separately. Kruskal-Wallis test indicated no differences in the looking behaviour between conditions ($Mdn_{NiceSkilful}$ = 1.05, interquartile range .38 - 1.72, $Mdn_{NiceNoHelp}$ = .65, interquartile range .30 - 1.00, $Mdn_{IgnoreSkilful}$ = .55, interquartile range .30 - 1.80; $Mdn_{IgnoreNoHelp}$ = .40, interquartile range .30 - .62; $H_{(3)} = 1.83$, $p = .61$), with a small effect size $\varepsilon^2 = .04$).

We were also interested in the effect that helpfulness alone (Skilful help vs No-help) had on dogs' communication. Therefore the data were merged into two groups based on the helpfulness of the demonstration: Skilful demonstrations (N = 24), and No-help demonstrations (N = 24). A Mann-Whitney U test indicated that there was a trend to significance, where the looks were longer in the Skilful group compared to the No-help group (p = .054) (Table 4.3). None of the other measures (latency of looking back and frequency of gaze alternations) was affected (Table 4.4).

Table 4.4. Effect of the type of help on looks back and gaze alternations. Medians and interquartile ranges (IQR) are indicated.

	Skilful		No-help				
	Mdn	[IQR]	*Mdn*	[IQR]	*z*	*p*	*r*
Duration first look (s)	.85	[.30, 1.72]	.50	[.30, .70]	1.17	.246	.24
Looking back latency (s)	.00	[.00, .95]	.00	[.00, 2.22]	-.23	.818	-.05
Looking back duration (s)	9.20	[3.98, 20.65]	4.90	[1.35, 8.58]	1.93	.054	-.39
Gaze alternations frequency	6.00	[4.75, 8.50]	6.00	[3.00, 8.00]	.65	.521	. 13

Note: Results of the independent sample Mann-Whitney U test (N = 24).
The effect sizes (r) were small or moderate.

Our last question was whether the dogs that experienced the nice demonstration would try to interact more with the experimenter. We regrouped the data based on the quality of the interaction during the demonstration into two groups: nice demonstrations (N = 24), and ignoring demonstrations (N = 24). A Mann-Whitney U test found that none of the measures was affected (Table 4.5).

Table 4.5. Effect of the quality of interaction on looking back and gaze alternations. Medians and interquartile ranges (IQR) are indicated.

	Nice		Ignoring				
	Mdn	[IQR]	Mdn	[IQR]	z	p	r
Duration first look (s)	.70	[.30, 1.52]	.40	[.30, 1.15]	-.67	.507	-.13
Looking back latency (s)	.00	[.00, 2.67]	.00	[.00, .00]	-1.60	.113	-.33
Looking back duration (s)	5.90	[2.65, 16.50]	6.60	[2.55, 15.75]	.08	.939	.02
Gaze alternations frequency	3.00	[1.00, 6.00]	3.50	[1.00, 7.25]	.73	.474	.15

Note: Results of independent sample Mann-Whitney U test (*N* = 24).
The effect sizes (*r*) were small or moderate.

Discussion

In the current study we were interested in whether the quality of the interaction with a human partner and human skilfulness, combined or alone, would affect dogs' looking back behaviour. We found that the dogs did not vary in their tendency to request help from the experimenter depending on whether she was nice and skilful, nice and unwilling to help, ignoring and skilful or ignoring and unwilling to help when faced with an unsolvable problem. However, the duration of looking back behaviour was longer, with a trend towards significance, for the dogs that received a skilful demonstration compared to dogs that received a demonstration that was no help at all. These results indicate that it should not be excluded that dogs, to a certain degree, may possibly take into account a human partner's helpfulness when facing an unsolvable task. The effect sizes in this study were also relatively small, which would suggest that the findings could be affected by the small sample size. However, the results should be interpreted cautiously, because they represent only a trend, which was not replicated by the other measures of the study. Nevertheless, they may suggest that the possibility that dogs can take into account a human partner's helpfulness should not be excluded.

Another possibility is that the dogs associated the experimenter with food during the skilful demonstration (Nitzschner et al., 2014). However, this is unlikely because in this demonstration, dogs did not see the experimenter handle the food directly. Additionally, the amount of food held by the experimenter was identical for the skilful and the no-help demonstrations.

Finally, the frequency of gaze alternations was not affected by the helpfulness of the experimenter or the quality of the demonstration. Similar findings were obtained by Horn and colleagues (2012), who observed that dogs' proximity to the experimenter, rather than gazes, was affected by the human partner's behaviour. Smith and Litchfield (2013) also indicate that gaze alternations in the unsolvable task might be less frequent than overall looking behaviour towards the experimenter. It is possible that while the dogs' help requests did not vary across conditions in the current study, the dogs that experienced a skilful demonstration were overall more attentive to the experimenter and therefore looked at her more, which would explain why the duration of looks varied, while the frequency of gaze alternations did not.

General discussion

The results of Study 1 indicate that dogs did not form a preference between two experimenters based on a demonstration when requesting human help. It is possible that the dogs could not discriminate between the two experimenters or that they did not understand the demonstration. To exclude this possibility, the dogs observed only one experimenter and were allowed to use the puzzle-toy before the demonstration in Study 2. Although the results showed that the dogs did not form a preference based on the helpfulness of the demonstration or the quality of the interaction, the dogs that received a skilful demonstration tended to look at the experimenter more than those who received a No-help demonstration (i.e. the experimenter did not attempt to help solving the problem). However, the dogs did not perform gaze alternations more often in any of the conditions.

One possible explanation for these results could be that dogs might not be able to take into account their opinion about humans when requesting human help. This explanation would be in line with the hypothesis that only humans and evolutionarily close species, i.e. the chimpanzee, have the ability to understand when they require help, discriminate partners based on their skills, and then choose the best collaborator (Melis et al., 2006; Melis & Semmann, 2010). Such explanation is in agreement with recent evidence in the literature on dogs, suggesting that, although they might be able to choose the appropriate collaborative partner, they likely do so by associating the specific location of the partner with food (Petró et al., 2016). Since we were interested in investigating dogs' ability to recognise and use specific characteristics of a partner, such as skilfulness, when help is required, we purposely controlled for other confounders: we performed the demonstration and the test phase in separate rooms and, when more than one partner was present, we counterbalanced their position across different trials. Therefore, our results, should not be biased by factors such as food or location associations, and possibly indicate that dogs might not be able to discriminate humans based on their skills.

Unexpectedly, the dogs in Study 2 did not take into account even the quality of the interaction, i.e. nice versus ignoring, when requesting human help. Dogs appear to be able to recognise such characteristics in humans (Nitzschner et al., 2012), and it could be expected that dogs would decide to interact more with a nice partner rather than one who had ignored them. According to the current findings, it seems to appear that while dogs can form an opinion about humans based on whether they are nice to them, such an opinion does not affect partner choices in dogs when they are facing a problem. There could be two possible explanations for this result. One possibility is that requesting help is not a flexible behaviour in dogs. As previous findings suggest, this may be affected by past experience (D'Aniello & Scandurra, 2016; D'Aniello et al., 2015; Marshall-Pescini et al., 2009; Topál et al., 1997), but possibly not by short term contingencies. According to the domestication hypothesis (Hare et al., 2002; Miklósi et al., 2004), dogs adapted to life with humans and formed a specialization for communication with humans, especially in cooperative contexts (Bräuer et al., 2006; Reid, 2009). In this scenario dogs possibly evolved specialised skills to receive human communication and follow it as a directive (Kaminski et al., 2011a) but in other domains, such as reputation forming, dogs' social skills possibly might not have the same level of flexibility observed in other non-human species, such as chimpanzees (Melis et al., 2006). It is possible, for example, that dogs evolved a strong drive to request human help, regardless of the abilities of the human partner involved. This would explain the limited level of flexibility observed in the current study, as well as previous findings suggesting that more parsimonious mechanisms, such as food enhancement, may explain dogs' behaviour (Nitzschner, et al., 2014; Petró et al., 2016).

Another possibility is that our results were affected by the measure we chose. It has been hypothesised that dogs have evolved the predisposition to look for humans when facing an unsolvable problem (Miklósi et al., 2003) and there are individual differences in dogs' tendency to look at humans (D'Aniello & Scandurra, 2016; D'Aniello et al., 2015; Marshall-Pescini et al., 2009; Topál et al., 1997). Recent findings also show that a dog's breed and age affect their tendency to look at humans during an unsolvable task (Konno, Romero, Inoue-Murayama, Saito, & Hasegawa, 2016). Although we had a good age distribution and a relatively wide representation of breeds, our sample did not allow for comparisons between breeds or age groups. These new findings should be taken into account for future research; however, the results of the current study do not allow us to draw definitive conclusions about whether dogs have the cognitive ability to form an opinion based on skilfulness. It is possible that the low prevalence of eye contacts in certain breeds might be affecting the results. Therefore, a future study could investigate only breeds, and age groups most keen to form eye contact, i.e. hounds, retrievers, and working dogs, and older dogs (Konno et al., 2016). If the results of this future study showed that this type of communication is particularly evident in this subgroup, it would provide supporting evidence for the trend that we found in this study.

Our findings could not confirm whether dogs can take skilfulness into account when requesting human help. Previous research provides controversial evidence. Dogs can coordinate their actions to that of a human partner in order to solve a cooperative problem, although the level of skilfulness of the partner was not manipulated (Ostojić & Clayton, 2013). In a problem solving situation, dogs were observed to flexibly adjust their behaviour to problem-specific actions of a human partner, although this did not affect dogs' tendency to request help, i.e. to look back at the human (Horn et al., 2012).

However, a replication of the same study and the use of inanimate objects as partners, suggested that more parsimonious explanations, such as the association of a specific location with food, may explain the behaviour (Petró et al., 2016). Finally, dogs can form an opinion about humans based on the quality of an interaction they have with the human (Nitzschner et al., 2012). They also coordinate with other dogs in a cooperative task, but they do not appear to monitor each other's behaviour while cooperating (Bräuer et al., 2013a). Our findings add information to this body of research, but could not confirm this possibility, though they do not exclude it. Due to dogs' ability to cooperate with humans (Ostojić & Clayton, 2013), such ability might be expected and should be further investigated. The unsolvable task is a very simple test, based on a behaviour that dogs are evolutionarily predisposed to perform, i.e. looking back (Miklósi et al., 2003). However, previous evidence, together with our findings, highlights some limitations of the test. The looking back behaviour is largely affected by long-term direct experiences in the life of dogs (e.g. specific training, housing conditions) (D'Aniello et al., 2015; Scandurra, Prato-Previde, Valsecchi, Aria, & D'Aniello, 2015) and genetics (Konno et al., 2016). Therefore studies employing the unsolvable task in a group comparison design should adjust for this, for example measuring a baseline level of looking behaviour or counterbalancing potential confounders. Dogs appear to find it difficult to grasp elaborate demonstrations (Horn et al., 2012; Petró et al., 2016), especially if they do not have a chance to directly use the apparatus used for the demonstration. The results of Study 1 in the current work and Horn et al. (2012) suggest that it may be difficult for dogs to recognise subtle differences in the skills of two human partners. Therefore it seems important for manipulations to be simple and very salient when investigating the understanding of skilfulness in dogs.

Finally, Adbai and Miklósi (2016) recently suggested that different procedures might measure different aspects of reputation forming. It may therefore be possible that the skill, even if present, might not be evident in certain contexts but only in others. Therefore, another possibility is to investigate reputation forming through different paradigms. For example cooperative activities, e.g. based on hunting-like behaviours (Bräuer et al., 2013a; Ostojić & Clayton, 2013), could be adopted to further investigate reputation forming in dogs and their ability to select the best cooperative partner.

Chapter 5. Relationship and human-regarding preferences in dogs [4]

Chapter overview

In the previous chapter I suggested that cooperative interactions might be useful for the study of direct and indirect reciprocation in dogs. One of the most common paradigms for the study of various collaborative behaviours, such other-regarding preferences, is the bar-pulling paradigm. Before being able to investigate collaboration or reciprocity, it is necessary to develop a species-specific apparatus, test whether the animal is able to understand its contingencies, and if other-regarding preferences are present in the species. Versions of this paradigm have been used in several species; however, the apparatuses and designs currently available for dogs heavily rely on training and could be used only to test pro-social behaviour.

In this chapter I describe a novel apparatus, which does not require training the dogs to understand the testing conditions. Dogs learned to pull a

[4] Manuscript based on the paper in preparation:
Piotti, P., Spooner, R.M., Shelley, I., Micheletta, J., Kaminski, J. (in preparation) Other-regarding preferences in the domestic dog.

cord in order to open a trap door on a shelf, where two automatic feeders had been placed. The feeders were remotely controlled by the experimenters, who could release food on the shelf before the dog pulled the cord. Based on the testing condition, food could be released near the dog, and/or at the other side of the shelf, so that it would drop in an area inaccessible to the dog, in both places or none of the two. Dogs experienced the consequences of their action only after pulling and opening the trap door and decided whether to pull the cord again or not. Therefore, it was not necessary to formally train them to let them understand the contingencies of each testing conditions. During the test, a human receiver (a stranger or the dog's owner) could be present in the area inaccessible to the dog and pretended to eat the food. Due to the apparatus design, the same animal could be tested on a wide range of conditions based on the outcome of pulling: selfish (only the dog obtained the food), pro-social (both the dog and the receiver obtained the food), altruistic (only the receiver obtained the food), no-food (neither of them obtained the food); there were also two additional control conditions, one for the pro-social and the other for the altruistic condition, where the food was delivered accordingly but the receiver had no access to it. The results indicated that the dogs understood the tests, in that they operated the apparatus when they received the food and did not operate it when they were not rewarded. Dogs also operated the apparatus more in the altruistic condition than in the non-rewarded conditions. This result however, could not be explained by altruistic motives because further analysis indicated no difference between the altruistic condition and the social controls. This finding confirmed that the most parsimonious explanation is that dogs' operated the apparatus in the altruistic and social controls conditions with expectation to receive the food.

Introduction

It is debated to what extent other-regarding preferences are present across non-human species. According to some authors, the level of complexity and flexibility of human altruism is unique among other species (Melis & Semmann, 2010). There are two main lines of thought in this regard. One suggests that pro-sociality, i.e. voluntary behaviour that benefits others (Jensen et al., 2014), and altruism, i.e. behaviour that benefits others at a cost for the actor (Fehr & Fischbacher, 2003), are shared by humans and their closest relative, the chimpanzee, because they have their evolutionary origin in the primate lineage (Bullinger et al., 2013; de Waal, Leimgruber, & Greenberg, 2008; Jensen et al., 2006; Melis et al., 2011; Silk et al., 2005; Vonk et al., 2008; Warneken et al., 2006). A second view suggests that collaborative abilities may rather be closely linked to a species' ecological need, such as foraging strategies (Vail et al., 2014) or cooperative breeding (Burkart, Hrdy, & Van Schaik, 2009). For example, the coral trout (*Plectropomus leopardus*) forms collaborative hunting relationships with moray eels and is able to recruit the best collaborative partner (Vail et al., 2014), in a way that is comparable to the skills observed in chimpanzees (Melis et al., 2006). Vail et al. (2014) conclude that these results suggest that ecological needs, rather than relatedness to humans or brain size, may explain these collaborative abilities.

Other-regarding preferences comparable to those observed in humans may therefore be present in species phylogenetically distant from humans as a result of convergent selection pressures (Marshall-Pescini et al., 2016a; Vail et al., 2014). Pro-sociality is intended as voluntary behaviour performed with the general intent to benefit others (Jensen et al., 2014), which differs from altruism, i.e. behaviour that benefits others at a cost for the actor (Fehr & Fischbacher, 2003).

The investigation of the underlying mechanisms and cognitive requirements of pro-sociality and altruism in species evolutionarily distant from humans, and with an element of convergence with our social structure and niche, would help shed a light on whether this is a trait unique to humans, it is a homologous trait that we share with other primates, it has it main roots in the species' ecological niche, or its origin is a combination of the different factors (Marshall-Pescini et al., 2016a). Dogs are a particularly interesting model for comparisons due to their unique evolutionary history (Cooper et al., 2003; Hare & Tomasello, 2005; Miklósi et al., 2004). One hypothesis is that during domestication dogs have been specifically selected for cooperation and communication with humans, which has led to a genetic predisposition to develop social skills functionally equivalent to humans' (Hare et al., 2002; Hare & Tomasello, 2005; Miklósi et al., 2003; Miklósi & Topál, 2013). For example, dogs show some predispositions to benefit others, although findings vary depending on the task investigated (Bräuer et al., 2013b). Recent research suggest that if faced with a problem that cannot be solved individually, dogs are capable to coordinate their behaviour with either another dog (Bräuer et al., 2013a) or a human partner (Ostojić & Clayton, 2013). However, dogs did not spontaneously help a human partner achieving a goal and need additional prompting in order to do so; moreover, the relationship with the partner, i.e. the owner or a stranger, did not affect the dogs' behaviour (Bräuer et al., 2013b).

Another hypothesis suggests that wolves, dogs' closest living relative, are characterized with high social attentiveness and tolerance and are highly cooperative, and these characteristics of wolves likely provided a good basis for the evolution of dog-human cooperation (Range & Virányi, 2015). For example, Range and Viranyi (2013) investigated dogs and wolves' ability to follow a demonstration from a dog or a human to hidden food. The authors found that both dogs and wolves benefitted equally from the demonstration, regardless of the species of the demonstrator. However, if the demonstrator only pretended to hide the food, then the dogs recognised the fake demonstration, regardless the demonstrator species, while the wolves only did so in case of human demonstrators. The authors interpreted this finding suggesting that wolves are more attentive toward behavioural details of the canine models than the dogs and could recognize that the demonstrator dogs disliked the food reward, which might have decreased the interest of the wolves following that demonstration (Range & Virányi, 2013). Recent studies looked at dogs' altruistic behaviour towards other dogs and towards humans. The findings suggest that dogs might be capable of altruistic acts, choosing to donate food to a conspecific partner, but only if this is familiar (Quervel-Chaumette et al., 2015); however, they do not donate food to a human partner (Quervel-Chaumette et al., 2016). The authors suggested that this discrepancy might depend on the fact that they asked the human partners to not communicate with the dogs during the test, thus inhibiting dogs' responses (Quervel-Chaumette et al., 2016). The authors also found that the task used to investigate other-regarding preferences has a great impact on the dogs' response (Dale et al., 2016)

One of the most common paradigms for the investigation of other-regarding preferences in non-human animals is the *pro-social choice test* (Colman et al., 1969). The subject, or donor, is initially trained to operate a food delivery system, such as the bar-pulling apparatus, which allows it to obtain a reward (e.g. food) by pulling bars or ropes, depending on the species investigated. The donor's actions lead to various possible outcomes: a selfish option, where only the donor is rewarded (Cronin et al., 2009; Jensen et al., 2006; Massen et al., 2011; Schwab et al., 2012; Silk et al., 2005; Vonk et al., 2008), a pro-social option, where the food is delivered to the donor and a partner or receiver (Burkart et al., 2007; Colman et al., 1969; Cronin et al., 2009; Jensen et al., 2006; Lakshminarayanan & Santos, 2008; Massen et al., 2011; Quervel-Chaumette et al., 2015; Silk et al., 2005; Stevens, 2010; Takimoto et al., 2010; Vonk et al., 2008), an altruistic option, where the food is delivered only to the receiver (Dale et al., 2016; Jensen et al., 2006; Melis et al., 2011; Schwab et al., 2012; Silk et al., 2005; Stevens, 2010), and a no-reward option (Brosnan, 2010; Dale et al., 2016; Jensen et al., 2006; Quervel-Chaumette et al., 2015). The effect of the social relationship between donor and receiver is also tested in several studies (Burkart et al., 2007; Cronin et al., 2009; Dale et al., 2016; Massen et al., 2011; Quervel-Chaumette et al., 2015; Schwab et al., 2012; Stevens, 2010; Takimoto et al., 2010). Although the applicability of the test in a variety of species makes it ideal for comparative research, results of pro-social choice tests are often controversial and not unanimous. Authors argue that the reason may rely on a number of task-related aspects that might affect the outcomes: the cognitive demands of the tasks and the subjects' understanding of the mechanics involved, the risk of over-training of the animals (which may result in an inflated estimation of the pro-social choice during the test), the subjects' limited awareness of the consequences of their actions for the partner, the effect of food visibility, the social relationships between the donor and the receiver and their interaction during the task (Burkart & Rueth, 2013; Dale et al., 2016; Marshall-Pescini et al., 2016a). All these aspects should therefore be taken into consideration when adapting the test to a new species.

There are currently three works using the pro-social choice test in dogs: two based on the bar-pulling paradigm (Quervel-Chaumette et al., 2015, 2016) and one based on the use of tokens (Dale et al., 2016). One known issue is the task's complexity (Bräuer, 2015). Dale et al. (2016) suggest that the dogs in their study might not have been able to keep track of where the food was delivered. In all three studies, task complexity meant, for example, that a pro-social condition, where both the donor and receiver obtained a reward, was not included (Dale et al., 2016; Quervel-Chaumette et al., 2015, 2016). However, pro-social behaviour is less costly for the donor than altruistic behaviour, and could potentially lead to different choices towards the receiver. A *knowledge probe* used in the three studies gave some indication of donor's choices in a selfish setting, but the test was not set up to allow this comparison, which was therefore not possible (Dale et al., 2016; Quervel-Chaumette et al., 2015, 2016). Therefore, the authors could only compare altruistic choices towards different receivers, but could not compare clearly dogs' behaviour in an altruistic or pro-social context, compared to a selfish one. Another relevant difficulty for both paradigms is that it is possible that the extensive training required increased the risk of false-positive results (Marshall-Pescini et al., 2016a; Quervel-Chaumette et al., 2015). Such issue calls for the use of test designs and apparatuses that rely on behaviours that are easily understood by dogs without the need of extensive training.

The aim of the current study was to investigate other-regarding preferences in dogs with the use of a novel pro-social choice paradigm, which allowed addressing both of these issues. The apparatus adopted relies on an ecologically relevant behaviour for a canine species, such as pulling down an object dangling from above. The basic task consisted of tugging on a rope vertically suspended from elevated platform to deliver food rewards placed on the platform. Pulling hard on the rope would move a pulley mechanism, causing a trap door to swing downward, and dropping food to the floor. Such design was based on an apparatus previously used with another social canid, spotted hyenas (*Crocuta crocuta*), that quickly learnt to use it with no need to train them (Drea & Carter, 2009).

The current study also aimed at a comprehensive analysis of other-regarding preferences in dogs, including selfish, pro-social and altruistic conditions, as well as a no-reward control and partner absent controls. To achieve this without increasing the cognitive load of the task, dogs were presented with each condition in blocks. The apparatus design included two food dispensers, which could be operated remotely, placed on top of the elevated platform at two opposite sides. By dispensing food from one or the other dispenser, the experimenters could deliver the food either directly to the donor or beyond a fence, where the receiver was waiting. For each condition, dogs experienced the location where food was dispensed, after they had pulled at least once. They were given an extensive amount of time to figure that the outcome for pulling had changed, and choose whether to continue pulling or not.

Finally, the study investigated the effect of the social relationship between the donor and the receiver. Because dogs favour humans as social partners and were probably originally selected to behave collaboratively with humans (Hare et al., 2002, 2005; Miklósi et al., 2003), it has been suggested that dogs could be expected to provide humans with food (Bräuer, 2015). Therefore in our study receivers were human partners, who were either the owner of the dog or a stranger person that the dog never met before.

If pro-social and altruistic behaviour are unique of humans and closest primates, then the dogs in the current study should choose to operate the apparatus only when they obtain a reward, and the partner's absence should not affect their pulling behaviour in the pro-social and altruistic control conditions. On the contrary, if pro-sociality and altruism are the result of an adaptation to ecological needs, then it is possible to expect that a species highly adapted for collaborative interaction with humans would present altruistic or at least pro-social tendencies towards humans. The effect of the donor-receiver relationship would then reflect the level of flexibility that could be expected in dogs' preferences. Specifically, taking into account the identity of the receiver would indicate a highly flexible trait. On the contrary, being equally beneficial to strangers or familiar humans would indicate a more fixed trait, which might potentially be the result of human selection for collaborative behaviour towards humans in general that could have occurred during dogs' domestication process.

Methods

Ethical statement

The study was carried out in strict accordance with the recommendations in the ASAB/ABS guidelines for the use of animals in research and was approved by the Animal Welfare and Ethical Review Board (n. 1114G) in accordance with the UK Home Office guidelines on the Animals (Scientific Procedures) Act 1986 and the regulations of the European Directive 2010/63/EU (Appendix G: Ethical approval for the study in Chapter 5). Dog owners were informed about the procedure involved and gave their permission for their dog to participate in the study.

Participants

A sample of 19 adult dogs were trained and invited to the test. One dog had to be excluded from testing because he did not settle in the testing condition; two dogs were withdrawn by the owners due to health (1 dog) or personal reasons (1 dog). Dogs were recruited through the Dog Cognition Centre Portsmouth Register and through contacts with local dog training groups. The inclusion criteria for the study were that dogs had to be between 1 and 10 years old, were medium or large sized, were comfortable around new people and new places, and were not aggressive over food. In addition, the dogs had to be food and toy motivated. All dogs were normal family dogs that lived with their owners and had the training background typical for a pet dog. Some of the dogs had participated in other studies before, but not studies using an experimental paradigm similar to the one used here.

Sixteen dogs, 10 males and 6 females, represented the final sample (Appendix H: Subjects' information for Chapter 5). In the Owner Receiver group were 6 males (M_{age} = 4.33 years, *SD* = 3.10) and 2 female (M_{age} = 6 years, *SD* = 4.04). In the Stranger Receiver group were 5 males (M_{age} = 4.40 years, *SD* = 2.99) and 3 females (M_{age} = 3.33 years, *SD* = 3.26).

Apparatus and testing room

Testing took place in one of the rooms (4.60 m x 4.20 m) of the Dog Cognition Centre Portsmouth (DOCS). The room was divided in two halves by a gated fence made with mesh, so that dogs could not cross the gate but they could see what happened behind it. Two chairs were placed against the wall opposite the apparatus and on the donor's side (Figure 5.1)

The testing apparatus was designed based on a similar one that a group of spotted hyenas had been able to learn rapidly and without training (Drea & Carter, 2009). The current apparatus consisted of a vertically suspended rope attached to an elevated platform. When the rope was pulled down, a trap door opened downward, letting drop a few dog treats on the floor. A pulley system ensured that the drop down door would close when the rope was not held down. Automatic food dispensers (Trick and Train food dispensers) were placed on top of the platform, at each side of the trap door. The dispensers were operated with remote controls that allowed the experimenters to be able to control whether the food would drop directly where the donor was, or behind a gated fence, where the receiver would be during the testing conditions (receiver's side of the room). During training and testing, the experimenters refilled the trap door through the dispenser as soon as the dog let go of the rope and the door closed (Figure 5.1)

Figure 5.1. Testing room and apparatus during the "absent" condition. The figure on the left shows the set up of the experiment in the "absent" condition. The receiver (owner or stranger) would sit on the chair closer to the gate and a trainer would sit near him/her. The other two experimenters stood at their side. All humans ignored the dog during the test trial. The figure on the right shows the position of the dog while pulling the cord. The feeders are visible on the shelf (the pulley system is hidden in the wood box at the centre of the shelf).

Procedure

Dogs were trained to use the apparatus autonomously. In order to ensure that dogs understood the dynamics of the test, during the training dogs also experienced that the food could be delivered either directly below the rope, or on the receiver's side. After dogs had learnt to operate the apparatus for themselves and had accessed the food both below the rope and behind the fence, dogs were introduced to the test.

Testing consisted of 4 experimental conditions and 2 controls. The experimental conditions varied based on where food was delivered: only to the dog (selfish condition), only to the human receiver (altruistic condition), to both the dog and the receiver (pro-social condition), or none of the two (no-reward condition). In order to test whether the donors acted with the intention to benefit the receiver, in line with previous research (Bullinger et al., 2013; Burkart et al., 2007; Cronin et al., 2009, 2010; Lakshminarayanan & Santos, 2008; Massen et al., 2011; Melis et al., 2011; Silk et al., 2005; Stevens, 2010; Takimoto et al., 2010; Vonk et al., 2008), the altruistic and pro-social conditions were also repeated as social controls, in the absence of the receiver. In the two controls, the receiver was on the same side of the room as the dog, he/she was sitting at the back of the room (i.e. had no access to the food and was distant from the apparatus), pretended to be busy writing or reading and ignored the dog.

Two groups of dogs were tested, varying in the level of familiarity with the human partner: for half of the dogs the human partner was their owner, for the other half the human partner was a stranger.

The owner of the dog could stay in the room during the training, should the dog be uncomfortable in their absence. If this was the case, the owners were sitting at the back of the room pretending to be distracted reading or writing, and they never interfered with the test or training in any way.

Training: Dogs were trained to use the apparatus by rewarding them with food for tugging the rope, attached to a tug-toy, in alternation with an experimenter using the apparatus while the dog was watching (Appendix I: Training method for Chapter 5). The first stage of training was considered concluded when the dog was able to operate the apparatus on its own 5 out of 6 consecutive times, without being given any cue, while the two experimenters stood at the back of the room pretending to be distracted and ignoring the dog. Once the dog reached this stage of training, the experimenters opened the gate in the fence and released the food from the dispenser placed on the other side of the fence, so that the dog could experience that food could be delivered on that side – if the dog did not find the food, the trainer would indicate it or direct the dog. The dog was let practice with this setting until it reached the same learning threshold as in stage 1.

Testing: The owner of the dog and 3 experimenters were present during testing. Two experimenters handled the dog and controlled the food dispensers with a remote and from a distance. For the dogs in the Stranger group the owner sat at back of the room, reading or writing, during all conditions; for the dogs in the Owner group, the same seat was occupied by one of the experimenters who had trained it. The receiver human was on the receiver's side of the room. In the Owner group, upon entering the room, the owner was instructed to cross the gate, which was then locked with a hatch by the experimenters. In the Stranger group the receiver was already in the room, she sat on one of the chairs, ignoring the humans and the dog, and pretending to be busy with her phone. For all dogs a female experimenter that they had not met before acted as stranger; different dogs had different experimenters, but each dog had only one experimenter throughout the experiment. After everyone had settled and seated, one of the experimenters lead the stranger to the receiver's side of the room; this gave some time to the dog to sniff the stranger before starting the test.

Each condition was presented to the dogs in blocks of 12 trials, lasting 1 minute each. Overall, each dogs was tested in 4 experimental conditions (selfish, pro-social, altruistic, and no-reward), and two controls (pro-social control and altruistic control), which were identical to the experimental counterpart but the receiver had no access to the food because she was seating on one of the chairs and ignoring the dog.

To maintain dogs' motivation throughout the test, before each testing block there was a *filler* block, where dogs received the food on their side when they pulled the rope and were let use the apparatus 5 times before being called to the back of the room.

To ensure that food would not accumulate on the tray or drop in un-rewarded trials, after the filler (and between trials), one experimenter emptied the trap door from any leftover food into a tray, and brought the food out of the room. Then the trials started

Between trials, one experimenter would hold the dog with a leash or by the collar. At the beginning of each trial, she would release the dog and start a stopwatch. At the same time the other experimenter would operate the food dispensers to release the food according to the condition, while the receiver would walk up to the apparatus.

During the trial, the receiver would wait looking up at the apparatus and ignoring the dog. If food was released to the receiver, he/she picked it up saying "Oh, food!" and pretended to eat it; s/he then hid it in her pocket and looked back at the apparatus.

After 60 seconds one experimenter would go near the dog and walk it to the back of the room; the receiver also walked to the back of the room. If the dog was still pulling, she let it finish and eat the food, then the trial was over.

After 12 trials the block was over, the dog was taken out of the room and given a break. Dogs were tested on 2 to 6 different days, completing 1 to 3 blocks per day based on the owner's availability (Appendix I: Training method for Chapter 5).

The order with which the conditions were presented to the dogs was counterbalanced and the same counterbalancing order was used for the owner and the stranger group. For each group, half of the dogs were trained and tested on left side of the room, and the other half was on the right side. For both groups there were two dogs (one tested on the left, one tested on right) starting for each of the testing conditions (selfish, pro-social, altruistic, no-reward). The following conditions were presented in a predetermined semi-randomised order, with the stipulation that a condition where the donor was not rewarded was always followed by a condition where the donor was rewarded. Once a dog was invited for being trained, they were randomly allocated to the left or right side, albeit ensuring that half of the dogs were being trained on one side and the other half on the other side. As soon as one dog finished the training it was allocated to a counterbalancing group based on a double *latin-square* randomisation.

Behaviour analysis

Digital video footage was taken for all trials and the Kinovea software (www.kinovea.org) was used to record dogs' behaviour during testing.

The number of times dogs operated the apparatus during a trial (i.e. they pulled the rope and opened the flap). It was also recorded whether the dog did look at the receiver side of the fence (as this reflected whether the dog understood the testing condition).

Statistical analysis

Data were analysed using the statistical software R (R core team, 2015), with the packages *lme4* (Bates, Maechler, Bolker & Walker, 2015) and *lsmeans* (Lenth, 2015). A generalised linear mixed model (GLMM), fit by maximum likelihood (Laplace Approximation), with *log* function was calculated with the response variable "frequency of pulling" (N = 1152, number of subjects = 16), and including the random factor "dog", and the nested random factors "trial" (1 to 12) and "interruption" (whether the dog did or did not have a break before the trial). The fixed factors "condition" (selfish, altruistic, pro-social, no-food, pro-social-control, altruistic-control) and “receiver” (owner, stranger) were added both as main factors and with an interaction. Laplace estimated *p*-values were calculated for the fixed effects (Baayen, 2008). Pairwise post-hoc comparisons were obtained using the least-squares of means method for the interaction (Appendix J: Model fitting additional information for Chapter 5).

Results

Overall, all dogs (100%) looked at the receiver side in the 100% of the blocks, i.e. at least once per condition.

The global model was significantly different from the null model ($GLMM_{condition*receiver}$, $AIC_{NullModel} = 6561.1$, $AIC_{FullModel} = 5051.8$, $N = 16$, $\chi^2_{20} = 2275.3$, $p < .0001$). Post-hoc Tukey results are given on the *log* scale. Pairwise analysis of the main effect of conditions (averaged over the levels of “receiver”) revealed that dogs pulled more in the experimental conditions (selfish, altruistic, pro-social) compared to the main control condition (no-food). There was no difference between the selfish and the pro-social condition ($estimate_{selfish-prosocial} \pm SE = .0871 \pm .0410$, $p = .2753$). On the contrary, dogs pulled more in the selfish condition compared to the altruistic condition ($estimate_{selfish-altruistic} \pm SE = 1.1207 \pm .0570$, $p < .0001$). Finally, there was no difference in dogs’ pulling frequency between the altruistic condition and the altruistic control ($estimate_{altruistic-altrcontrol} \pm SE = .1270 \pm .0722$, $p = .4930$) or between the pro-social condition and the pro-social control ($estimate_{prosocial-proscontrol} \pm SE = -.0701 \pm .0409$, $p = .5231$) (Figure 5.2).

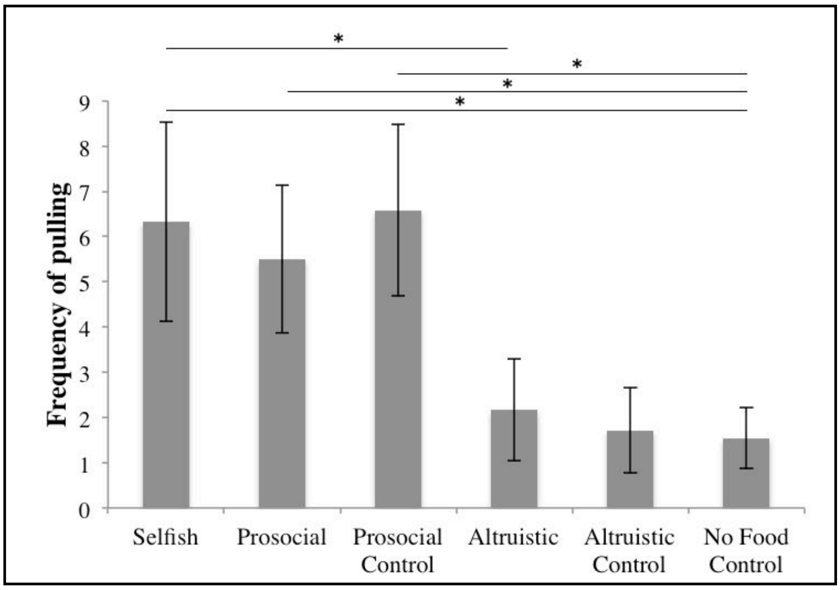

Figure 5.2. Main effect of the condition on the pulling frequency.

The median frequencies of pulling ± SD (N = 16) are represented in the graph. Significant differences resulted from the post-hoc Tukey test (* $p < .0001$), corrected for multiple comparisons, are also indicated.

Pairwise analysis of the main effect of the receiver (averaged over the levels of "condition") revealed no difference between owner and stranger receiver ($estimate_{owner-stranger}$ ± SE = -.1238 ± .1542, p = .4219). Likewise, pairwise analysis of the interaction effect of condition and receiver revealed no difference between owner and stranger for any of the condition. The results of post-hoc Tukey test, corrected for multiple comparisons, indicated no effect of familiarity: for the selfish condition, $estimate_{owner-stranger}$ ± SE = -.1066 ± .1604, p = 1.0000; for the pro-social condition, $estimate_{owner-stranger}$ ± SE = -.1693 ± .1614, p = .9965; for the pro-social control, $estimate_{owner-stranger}$ ±

SE = -.1342 ± .1606, p = .9996; for the altruistic condition, $\text{estimate}_{\text{owner-stranger}}$ ± SE = .1254 ± .1797, p = .9999; for the altruistic control, $\text{estimate}_{\text{owner-stranger}}$ ± SE = . -.0874 ± .1833, p = 1.0000; for the no-food control, $\text{estimate}_{\text{owner-stranger}}$ ± SE = -.3708 ± .1918, p = .7388 (Figure 5.3).

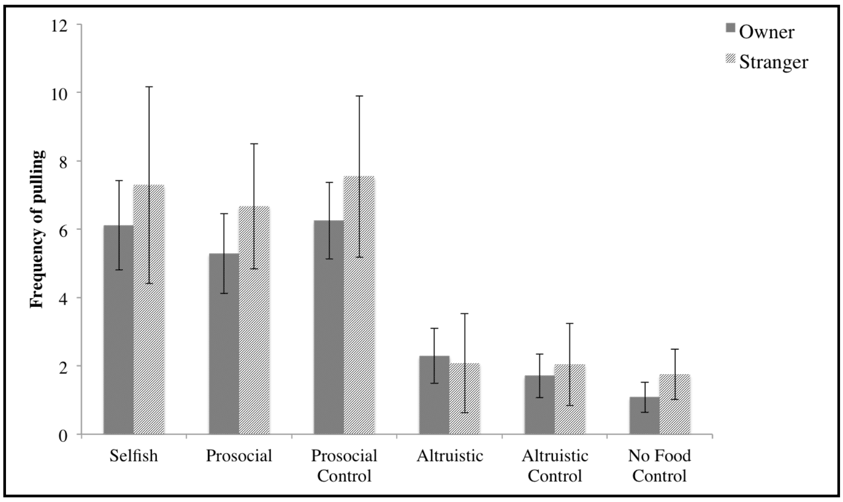

Figure 5.3. Interaction effect of condition and receiver of pulling frequency.

The median frequencies of pulling ± SD (N = 8) are represented in the bar chart. As it can be seen in the graph and as confirmed by the statistical analysis, there was no significant difference in the frequency of pulling between the owner group and in the stranger group for any of the conditions.

Discussion

The main finding of our work is that the dogs did not show any pro-social or altruistic tendency towards their partner. As originally indicated by research involving chimpanzees (Jensen et al., 2006), such conclusion is supported in the first instance by the finding that not only they were more likely to use the apparatus when they received a reward (selfish and pro-social conditions) rather than when they did not (no-reward and altruistic conditions). The conclusion is further confirmed by the fact that, in both of the social control conditions, the absence of the partner did not affect dogs' tendency to use the apparatus. According to previous research (Bullinger et al., 2013; Burkart et al., 2007; Cronin et al., 2009, 2010; Dale et al., 2016; Lakshminarayanan & Santos, 2008; Massen et al., 2011; Melis et al., 2011; Silk et al., 2005; Stevens, 2010; Takimoto et al., 2010; Vonk et al., 2008) such results indicate that the dogs were interested in obtaining the reward for themselves rather than for the benefit of the human partner. Another, non-exclusive, explanation is that dogs were expecting to receive the food from the human partner, as this is the most common experience for dogs when humans have food around them. It is unlikely that dogs had understood that the receiver was keeping the food rather than eating it: we ensured that the dog did not see the receiver hiding the food during the test, the dog was always in a different room when the receiver gave the food back to the experimenters, and in previous studies humans have pretended to eat food in front of dogs which appeared to interpret the action as truthful (Marshall-Pescini, Passalacqua, Miletto Petrazzini, Valsecchi, & Prato-Previde, 2012). It is therefore more likely that dogs initially expected the receiver to give them the food when they picked it up, and finally stopped pulling the apparatus after they did not receive any food. Similar results were obtained in the token-based study by Dale and colleagues (2016), who did not find differences in the frequency of pulling between the altruistic condition and the social control. However, in their study the dogs did not differentiate between conditions and a control where no receiver was in the room, which, according to the authors implies that the dogs did not understand the differences between these three conditions.

It can be excluded that the dogs in our study did not understand the contingency of the task because they had been able to experience that food could be dropped on the receiver side during training, they had visual access to what happened in the receiver's area (and all the dogs looked at least once in each condition), and finally clearly used the apparatus more when they received food compared to when they did not.

The current results differs from the findings obtained by Quervel-Chaumette and colleagues where dogs acted altruistically towards a conspecific partner and did more so in the presence of the partner rather than when it was absent (Quervel-Chaumette et al., 2015). However, they are confirmed by their follow up study where dogs did not give food to a human partner (Quervel-Chaumette et al., 2016).

It is possible that signalling from the receiver has played a role in the study with conspecific receiver. Quervel-Chaumette and colleagues (2015, 20016) do not provide information about the behaviour of the receiver dog before each trial commenced, while in our study the receiver was relatively distant from the source of food and was instructed to ignore the dog. Dogs are sensitive to conspecifics (Cracknell, Mills, & Kaulfuß, 2008) and humans' (Marshall-Pescini et al., 2012) social enhancement effects, therefore differences in the receiver's behaviour across the two studies might possibly explain the discrepant result. The social enhancement explanation is further supported by the fact that in the current study dogs did use the apparatus even in the absence of food, although significantly less than in other conditions, suggesting that even in the absence of any food they did try for a certain time to perform an action that had been previously proved to be successful. Such observation would be possible only with the current study design, where dogs experienced the outcome of their behaviour and had the time to make a decision on whether to repeat it or not during each testing block.

Another possible explanation for the difference between studies relies on the level of training that dogs received. In the previous studies, dogs were highly trained to perform the test task (Dale et al., 2016; Quervel-Chaumette et al., 2015, 2016), during training and in filler trials the donor dogs received the food for the performance of the pro-social task (Quervel-Chaumette et al., 2015, 2016), and finally in the bar-pulling paradigms the reward was visible to the donor and closer to the receiver in the pro-social condition compared to the absent partner control (Quervel-Chaumette et al., 2015, 2016). It is therefore possible that the dogs were repeating the behaviour that they had been trained for, and that the familiar receiver acted as a local or social enhancement and therefore increasing the dogs' level of activity, as seen in other species (Schwab et al., 2012; Zentall, 1996).

Finally, a possible explanation for the difference in dogs' behaviour towards humans and other dogs is that dogs are more likely to share food with a conspecific and receive food from humans, both as a consequence of their life experience, and their evolutionary history. However, given the limitations of the Quervel-Chaumette et al.'s studies (2015, 2016), there is no convincing evidence of this difference. A follow up of the current study design with a conspecific receiver could investigate this possibility.

Our second question regarded whether the identity of the receiver would affect dogs' behaviour and our finding is that dogs did not take into account the identity of the receiver in any of the conditions. This is contradicting again some of the previous findings, where the dogs preferred to use the apparatus in the presence of the familiar partner (Dale et al., 2016; Quervel-Chaumette et al., 2015). However, again social enhancement might explain the previous finding, possibly being more pronounced in the case of the familiar conspecific partner. The fact that in the Dale et al.'s study (2016) the dogs appeared to prefer using the apparatus in the presence of a familiar partner even when they did not fully understood the task's contingencies, further supports this possibility.

In conclusion, our results do not confirm other-regarding preferences in the domestic dogs in food sharing situations and with a human receiver. Such findings do not exclude completely the possibility of altruistic or pro-social tendencies in dogs in other contexts. It might be possible that dogs' own interest in the reward might have masked other helpful tendencies, as found in other studies (Dale et al., 2016; Kaminski et al., 2011a; Piotti & Kaminski, 2016). To tease out this possibility, dogs' altruistic and pro-social behaviour should be investigated also with the use of different paradigms, which do not require the use of food.

Our findings also highlight the potential variation given by different testing designs, especially in regards of the potential effect of extensive training and the advantage of untrained testing conditions.

Chapter 6. General discussion

This PhD thesis investigates collaborative interactions in the domestic dog with a particular focus on dog-human interaction. The approach adopted is that of empirical experiments focused on three building blocks considered particularly relevant for successful collaboration: informative communication, reputation, and other-regarding preferences (Kaplan & Hill, 1985; Tomasello, 2007; Trivers, 1971). The main question regarded what behaviours dogs show in these domains and how flexibly they can use these behaviours (**Table** 6.1).

At the time this PhD has begun, very little was known on the subject. Evidence in the literature indicated that dogs are particularly good at understanding human communicative cues in cooperative contexts (Miklósi et al., 1998; Hare et al., 1998) and they can perform communicative gestures to direct humans toward a target (Miklósi et al., 2000). It was still unknown whether they could use such gesture in a helpful way, which was of interest because informative communication is thought to be unique of humans (Liszkowski et al., 2006; see **Table** 6.1.). Some evidence in the literature indicated that they would rather communicate to 'request' instead of 'inform' a human partner about something that the dog had no interest in (Kaminski et al., 2011). The question was however still open, and lead to two follow-up studies (Chapter 2 and 3). The dogs' increased persistency in indicating the relevant object (Chapter 3) suggests that, although there is no evidence that dogs communicate to inform, they may use communication with helpful motives and may take into account an object's relevance to a human partner in a communicative context, which is one of the prerequisite for informative communication to occur (**Table** 6.1). Such flexibility supports the recent ideas in the literature suggesting that dogs might have specialised particularly to receive human communication and it is likely they interpret it as a directive, i.e. an indication of where to go and what to do (Kaminski et al., 2011a; Tauzin et al., 2015a; Tauzin et al., 2015b; Téglás et al., 2012). The idea that dogs interpret human communication as a directive is consistent with the findings on informative communication described in the first two chapters of this thesis, i.e. that dogs may take into account the relevance of an object for a human partner (see **Table** 6.1). Specifically, in the first experiment (Chapter 2), I explored the possibility of replicating a paradigm for the comparative study of informative communication (Liszkowski et al., 2006), developed for children and chimpanzees (Bullinger et al., 2011). The paradigm required teaching the dogs to discriminate between a useful object, i.e. a tool that could be used to retrieve food, and a random distractor. The useful object could then be used some times for the benefit of the dog and some times for the benefit of the dog's owner. Once the dogs experienced this, an experimenter would hide the two objects while the dog's owner was outside of the room. Upon the owner's return, he/she would clearly show that he/she was looking for something, eliciting a communicative response in the dogs. Although the dogs did indicate the location of the hidden objects, it was clear that they could not discriminate between the useful object and the distractor at the time of testing. It was therefore decided to change the paradigm so that it would not require any training or the use of food but still required dogs to indicate an object for the benefit of a human partner. This led to the paradigm designed in Chapter 3. Again, dogs were asked to indicate the location of a hidden object that a human partner (a stranger) had an interest in (relevant object), rather than a random distractor. In the first study dogs had to ignore something that they wanted (a dog toy), in order to communicate helpfully. The results of this study suggested that the dogs could not overcome their own interest in the toy or the random distractor, i.e. a novel object that the dogs may have wanted to investigate (Kaulfuß & Mills, 2008). However, paying attention while the human partner was using the relevant object, increased dogs' indications towards the relevant object and decreased indications towards the distractor. The second study followed up these findings, simplifying the procedure. A mixed design was used, whereby dogs only saw the relevant object or the distractor being hidden; moreover, the toy was not used, as it appeared to be excessively distracting. In order to control for dogs' *neophilia* (Kaulfuß & Mills, 2008), both objects, relevant and distractor, were available to the dogs prior to testing. An additional variable was introduced and the test was repeated with the experimenter communicating using ostensive vocal cue (high pitch voice) in half of the trials, and being silent in the other half. It was confirmed that the dogs' communication was more persistent when indicating the relevant object and that this result was mediated by the human's communication strategy. It should be noted that at that time neither human nor canine literature had focused on persistence of communicative behaviour, but rather on its frequency (e.g. Liszkowski et al., 2006). Recent studies, however, indicate that the persistence of looking behaviour may provide information on the cognitive mechanisms underlying dog-human communication (Marshall-Pescini, Rao, Viranyi, & Range, 2016). In study 2 of chapter 3, the frequency of dogs' *showing* did not change between conditions; however, dogs that had seen a relevant object being hidden, were more persistent in their behaviour, thus reflecting their ability to take into account of the context where the object was used. It appears therefore clear that the duration of looking bouts has a certain value when interpreting dogs' behaviour. I also suggest that the ostensive cues in this situation may have created a communicative context for dogs, which is consistent with the literature (Topál et al., 2009a). Dogs are particularly good at using human ostensive cues, including high pitch voice, to discriminate when communication is intended for them (Kaminski et al., 2012), they are able to recognize the intonation of a human's voice that is typically associated with praise (Andics et al., 2016) and can discriminate between positive and negative emotional valence of human vocalisations (Albuquerque et al., 2016). Such flexibility in receiving and interpreting congruently human communication is further facilitated by the facts that humans tend to speak to non-verbal listeners in a higher pitch (Ben-aderet, Gallego-abenza, Reby, & Mathevon, 2017). There is some indication that dogs have some helpful motives in communicative contexts and have an expectation for humans to act helpfully towards them (Bräuer et al., 2013a; Hare & Tomasello, 1999; Kaminski et al., 2011a; Kirchhofer et al., 2012; Miklósi et al., 2003). However, there is currently no convincing evidence that dogs understand humans' mental states (Heberlein et al., 2017; Kaminski et al., 2009; Maclean et al., 2014; Viranyi et al., 2006) and their understanding of referentiality is also unclear (Tauzin et al., 2015a; Tauzin et al., 2015b; Téglás et al., 2012). This body of evidence, together with dogs' ability to take into account objects' relevance to humans during communicative contexts (as described in Chapter 3), suggest that dogs' human-like social skills, such as their flexibly use of human pointing (Hare et al., 1998; Miklósi et al., 1998) and sensitivity to ostensive cues (Andics et al., 2016; Kaminski et al., 2012; Tauzin et al., 2015a; Topál et al., 2014) reflect in fact a specialisation for receiving human communication (**Table 6.1**) which dogs evolved during their domestication process (Hare & Tomasello, 2005; Miklósi et al., 2003).

At the time the studies in chapters 2 and 3 were concluded, the evidence in the literature appeared to support the idea that the human-like social skills that can be observed in dogs interested predominantly communication (e.g. Kaminski & Nitzschner, 2013). One way of using communication a collaborative context is help requests. Interestingly, early findings indicated that dogs use a specific communicative gesture the *looking back* behaviour to request human help (Milkósi et al., 2003). It was therefore of interest to know whether dogs able to flexibly use such gesture to ask help from the most appropriate partner, as this as well was considered an human prerequisite (**Table** 6**.**1). At the time, it was debated whether such ability is unique of humans and their closest relatives (Melis et al., 2006), or it may emerge in more distance species as a consequence of convergent evolution (Vail et al., 2014). Evidence indicated that dogs could form an opinion about humans based on their direct experience (Nitzschner et al., 2012), while previous findings on dogs' ability to use indirect experience appeared to be biased by mechanisms such as local enhancement (Nitzschner et al., 2014). There were also some indications that dogs could take into account a partner's role when attempting to solve a problem, although this did not reflect on the *looking back* behaviour (Horn et al., 2012). The findings of this thesis indicate that dogs' use of reputation judgements in collaborative contexts does not appear to be as flexible as that observed in primates (Chapter 4). Similarly, in relation to other-regarding preferences (Chapter 5), dogs do not appear to be moved by altruistic intentions when given the choice to share food with a human partner.

Dogs are thought to have evolved a predisposition to request human help, as a consequence of their unique domestication process, when facing a problem (Miklósi et al., 2003). Reputation is particularly relevant because it may explain the evolution of collaboration, through mechanisms of indirect reciprocity (Nowak & Sigmund, 1998b), especially toward unrelated individuals (Nowak, 2006). Given that dogs' request human help, the question of interest was whether they can also take into account their previous experience with humans (i.e. reputation judgments) when choosing a collaborative partner. Specifically I was interested in whether dogs have the ability to recognise and take into account skilfulness when they request human help. In the first study of Chapter 4, dogs witnessed two experimenters who provided skilful and unskilful demonstrations while attempting to solve a problem. Four blocks of demonstrations were each followed by an unsolvable task trial (Miklósi et al., 2003) and the help requests (looking back behaviours) toward each experimenter were recorded. Results indicated that the dogs did not prefer either experimenter. I concluded that possibly it was too difficult for the dogs to choose between the two humans based on the prior demonstration, or the dogs might not take into account skilfulness in this context. For example, it is possible that dogs only take into account the quality of the interaction with a human partner (Nitzschner et al., 2012). In order to test these possibilities, in the follow up study, a between subject design was adopted and two variables were tested according to a *latin square* design: helpfulness (skilful demonstration vs no help) and quality of interaction (nice vs ignoring). Again dogs did not request more help from the experimenter in any of the conditions. I concluded that one possibility is that dogs do not take into account skilfulness or the quality of the interaction with humans when requesting human help (**Table** 6.1). The results are consistent with recent findings suggesting that while dogs adjust their behaviour based on previous experience regarding a partner's abilities in a somewhat flexible manner (Horn et al., 2012). This flexibility may depend on more parsimonious mechanisms such as, food association, rather than taking into account the *role* of the partner (Petró et al., 2016). The results of this chapter should not exclude completely the possibility of reputation judgements in dogs (**Table** 6.1). It was recently suggested that negativity and/or positivity bias (i.e. preferring or avoiding another individual) are observed in non-human animals, although the literature does not offer yet clear empirical evidence for it in certain contexts (Abdai & Miklósi, 2016). However, it is possible that the test paradigm affect dogs' judgement in unexpected ways. For example, it has been suggested that the passive behaviour of an experimenter has a negative effect on the dogs' judgement (Abdai & Miklósi, 2016). This may have happened as well in the dogs tested in the first study of chapter 4, where each dog was exposed to 4 testing trials, during which the experimenters ignored the dog. Paradigms based on cooperation to reach a common goal (Melis et al., 2006; Plotnik et al., 2011) might be more adequate, as it might be easier for the dogs to identify the goal of the task as well as its relationship with the behaviour of the human partner.

As mentioned above, chapters 3 and 4 also highlight a discrepancy in the analysis of communicative behaviour. Recent findings suggest that the persistency of looking behaviour (duration) might be a relevant measure for the understanding of the underlying mechanisms and motivation for the communicative behaviour of canids (dogs and wolves) (Marshall-Pescini et al., 2016). In the literature of informative communication, the persistency of the behaviour is usually not reported and conclusions are based on the frequency of behaviours (Bourdais, Danis, Bacle, Santolini, & Tijus, 2013; Bullinger et al., 2011; Kaminski et al., 2011; Liszkowski et al., 2006, 2008; Tomasello et al., 2007). However, the findings reported in Chapter 3 highlight that, especially in the case of showing behaviour and other referential behaviours, the frequency might not necessarily vary based on the relevance of the target, but the persistency of the behaviour does. Future studies both involving canines and other species should look into this aspect, which is currently understudied.

Finally, one area that had been largely understudied at the beginning of this PhD was that of other-regarding preferences. At the time there was evidence that dogs can coordinate with a human partner (Bräuer et al., 2013a) or a conspecific (Ostojić & Clayton, 2013) in order to perform a task and obtain food. There was also some evidence that dogs would help a human reaching a certain goal (Bräuer et al., 2013b), although dogs needed to be prompted by the human and therefore the mechanism underlying the behaviour was not clear. It was of interest to understand whether dogs would act altruistically or pro-socially and there were no studies in the canine literature. However, other-regarding preferences had been investigated in several species, recently including the domestic dog (Marshall-Pescini et al., 2016a). This highlighted a number of issues linked to the existing paradigms: overtraining, high cognitive demands and few testing conditions might have limited the results, including those in the canine literature. These issues were addressed in Chapter 5, where I investigated other-regarding preferences in dogs, with the use of a novel version of the bar-pulling paradigm (Colman et al., 1969). In this study I looked at dogs' other-regarding preferences towards humans and the effect of familiarity (i.e. the owner vs a stranger). The dogs in this study did not act altruistically towards the human partner, which is confirmed by the one study in the literature with human receivers (Quervel-Chaumette et al., 2016). As suggested in the literature it is possible that the lack of requests from humans reduced the dogs' responses. Another, non-exclusive, possibility is that dogs might not expect to give food to humans. This may depend on a combination of their life experience and their domestication history, where family dogs have come to depend on humans for the provision of food. In agreement with the issues pointed out in the literature (Marshall-Pescini et al., 2016a), the results in Chapter 5 also confirm the importance of including a control condition for social enhancement in this type of paradigm: while I found some evidence of apparent pro-social behaviour, the control conditions revealed that in fact the dogs were motivated by the expectation to receive the food rewards used in the test. In the light of the existing evidence, the findings of Chapter 5 confirm that: 1) the testing paradigm may affect the donor's behaviour (Dale et al., 2016; Quervel-Chaumette et al., 2015); 2) food visibility may lead the overestimation of pro-social tendencies (Dale et al., 2016); 3) a social control condition is essential to exclude the possibility that "giving" behaviour is motivated by the expectation of receiving the food reward (Dale et al., 2016); 4) overtraining may lead to inflated pro-social behaviours (Marshall-Pescini et al., 2016a). Overall, Chapter 5 also broadens the knowledge on other-regarding preferences in the domestic dogs, specifically providing a novel and stronger paradigm. The results are confirmed by the evidence in the literature (Quervel-Chaumette et al., 2016), however, excluding the possibility inflated altruistic behaviour due to overtraining (Marshall-Pescini et al., 2016a). Given the discrepancy found in the literature between altruistic choices towards humans and towards other dogs, it should be necessary to test the design described in Chapter 5 with a population of dogs as receivers.

Overall, the findings of this PhD indicate that dogs' collaborative behaviour may be different when dogs are receiving human communication compared to other contexts. Existing frameworks suggests that, in humans, collaboration is not a single trait, but is rather expressed through different behaviours, modulated by several cognitive abilities and motivations, which interact with the environment—e.g. they are affected by individual differences, context, etc. (Warneken & Tomasello, 2009a). The focus of this thesis on three building blocks of collaboration, i.e. informing, reputation, other-regarding preferences (Kaplan & Hill, 1985; Tomasello, 2007; Trivers, 1971), allowed to observe different levels of flexibility in dogs' behaviour within these three contexts (see **Table 6.1**). It might be possible that certain abilities are present only in humans and their close relatives (Melis & Semmann, 2010). Dogs do not appear to have some of the building blocks relevant to collaboration as they have been seen in humans and chimpanzees. Dogs are, however, particularly attentive to human communication: they outperform chimpanzees when it comes to following human pointing used as a directive (Kirchhofer et al., 2012), they are sensitive to human's attentional states (Virányi et al., 2004), they use human ostensive cues to discriminate when communication is intended for them (Ben-aderet et al., 2017; Scheider et al., 2011; Tauzin et al., 2015b; Téglás et al., 2012) and may take into account the relevance of the target of human communication (Chapter 3). Taken together this body of evidence suggests that dogs' human like-social skills may in fact represent a specialisation to receive human communication (as described in Chapter 2), which they may have evolved during their domestication process (Kaminski & Nitzschner, 2013; Topál et al., 2009a).

Findings such as dogs' ability to take into account objects' relevance in a communicative context also reinforce the existing trend in comparative research, which highlights the importance of broadening the species of comparison as well as experimental designs, and confirms the relevance of the domestic dogs as a species of interest for the study of social behaviour (Cooper et al., 2003; Hare & Tomasello, 2005; Marshall-Pescini et al., 2016a; Miklósi et al., 2004). Studies involving a wide range of species, which have different phylogenetic and ecological backgrounds, provide information about the origin and development of social evaluation (Abdai & Miklósi, 2016; Marshall-Pescini et al., 2016a). Dogs are a species of extreme interest for the comparative study of collaborative behaviour, due to reasons such as their unique domestication process, possibly heavily influenced by communication and cooperation with humans (Clutton-Brock, 1995; Ruusila & Pesonen, 2002), the possible adaptation to the human environment (Hare et al., 2002; Miklósi et al., 2003), or the inheritance of skills relevant to cooperation, such as social attentiveness and tolerance, from their canine ancestors (Range & Virányi, 2015).

Table 6.1. Summary of the literature and current findings

Collaborative interactions between dogs and humans

Informing

Mechanisms		Evidence: Supportive	Evidence: Contrasting
High level (Tomasello, 2010)	Understanding of communicative intentions	Sensitivity to human ostensive cues (e.g. Téglás et al., 2012; Scheider et al., 2011).	
		Differentiating intentional from unintentional gestures (Kaminski et al., 2012).	
		Perceiving human actions as goal-directed (Marshall-Pescini et al., 2014).	Possibly attending to actions rather than intentions (Gergely et al., 2015).
	Understanding the referential nature of communication	Following human gazes only when preceded by ostensive cues (Téglás et al., 2012).	Pointing is followed as a spatial indication (Tauzin et al., 2015b).
		Sensitivity to the order of human's ostensive and referential signals given during a communicative interaction (Tauzin et al., 2015a).	
		Referential use of communicative gestures, i.e. gaze alternation (Marshall-Pescini et al., 2013).	
	Helpful (informative) motives	Outperforming other species in following pointing limited to cooperative contexts (Hare & Tomasello, 1999; Kirchhofer et al., 2012).	
		Helpful expectations when communicating to humans (Miklósi et al., 2003).	

Reputation

Mechanisms		Evidence: Supportive	Evidence: Contrasting
High level (Melis et al., 2006)	Form an opinion about others based both on direct and indirect experience		Dogs form an opinion about humans based on their direct experience (Nitzschner et al., 2012).
		Some evidence of third-party affective evaluation: dogs appear to avoid people who behave negatively to their owner (Chijiiwa et al., 2015).	Once food and local enhancement are controlled for, evidence for the use of indirect experience is not supported (Nitzschner et al., 2014).
			Evidence that dogs can use third-party interactions in order to evaluate human partners has subsequently been disputed (Nitzschner et al., 2012; 2014).
	Recruit the most effective collaborators when they need help in solving a problem	Dogs seem to be able to discriminate humans based on their role within a problem solving situation (Horn et al., 2012).	However, they most likely associated the action of either agent with the specific location where the food was hidden (Petró et al., 2016).
		Water rescue and agility dogs as well as dogs kept as pets request more help from their owner compared to untrained dogs or outdoor dogs respectively (D'Aniello et al., 2015; Marshall-Pescini et al., 2009; Topal et al., 1997).	It was not possible to demonstrate that dogs can take into account skilfulness when requesting human help (Chapter 4).
Lower level	Difficult to assess in a laboratory setting because it is affected by testing conditions (Abdai & Miklósi, 2016)	Elements affecting reputation, such as being skilful and being nice, are important to collaborative contexts and it may be difficult to separate them completely one from the other (Abdai & Miklósi, 2016).	
		Dogs may be affected also by the behaviour of the experimenters during test trials (e.g. interpret being 'neutral' as 'ignoring' them (Abdai & Miklósi, 2016).	
		When an anticipated reward is unexpectedly reduced (e.g. when ignored during a test), many dogs either show a successive *negative contrast*, i.e. a reduction in their responses (Bentosela et al., 2009), or a paradox increase in their behavioural response (Reimer et al., 2016).	

Other-regarding preferences

gh le ve	Mechanisms	Evidence: Supportive	Evidence: Contrasting
High level	Pro-sociality and altruism have their evolutionary origin in the primate lineage (Bullinger et al., 2013; de Waal, Leimgruber, & Greenberg, 2008; Jensen et al., 2006; Melis et al., 2011; Silk et al., 2005; Vonk et al., 2008; Warneken et al., 2006).	Dogs donated food to a conspecific partner if this is familiar (Quervel-Chaumette et al., 2015).	Results have been contradicted when tested with a different apparatus (Dale et al., 2016).
			Dogs did not spontaneously help a human partner achieving a goal (Bräuer et al., 2013b) nor donated food to a human partner regardless of the familiarity with them (Quervel-Chaumette et al., 2016; Chapter 5).
Lower level	Wolves are characterized with high social attentiveness and tolerance and are highly cooperative, and these characteristics likely provided a good basis for the evolution of dog-human cooperation (Range & Virányi, 2015).	Wolves are more attentive toward behavioural details of the canine models than dogs (Range & Virányi, 2013).	
Low level	Collaborative abilities may rather be closely linked to a species' ecological need, such as foraging strategies (Vail et al., 2014) or cooperative breeding (Burkart, Hrdy, & Van Schaik, 2009)	During domestication dogs have been specifically selected for cooperation and communication with humans (Hare et al., 2002; Hare & Tomasello, 2005; Miklósi et al., 2003; Miklósi & Topál, 2013).	
		Dogs coordinate their behaviour with another dog (Bräuer et al., 2013a) or a human partner (Ostojić & Clayton, 2013).	Dogs did not spontaneously help a human partner achieving a goal and need additional prompting in order to do so; moreover, the relationship with the partner, i.e. the owner or a stranger, did not affect the dogs' behaviour (Bräuer et al., 2013b).
			Dogs did not donate food to a human partner (Quervel-Chaumette et al., 2016) but rather expect the food reward (Chapter 5).
		Dogs donated food to a conspecific partner if this is familiar (Quervel-Chaumette et al., 2015).	The behaviour may be test and training dependent (Dale et al., 2016).

		Communicate helpfully when cued by humans (Bräuer et al., 2013) and indicate objects that only the human has an interest in (Kaminski et al., 2011).	Not taking into account objects' relevance for a human partner (Kaminski et al., 2011).	**Low level**	Help request is a non-flexible behaviour in dogs (possibly driven by selective pressure)	Dogs but not wolves look back at humans to request help when they face an unsolvable situation (Miklosi et al., 2003)		
		Ability to differentiate between objects based on the owner's preference (Turcsán et al., 2015).	Social facilitation may explain the suppressing of the dog's own preferences (Pongrácz et al., 2013).			Cooperative breeds and brachycephalic dogs are more likely to establish eye contact with humans (Gacsi et al., 2009).		
			Human communication is interpreted as directive (Kaminski et al., 2011; Scheider et al., 2013).	**Low level**		Dogs do not take into account skilfulness when they look back to request help (Chapter 4) nor they take into account the role of the human partner (Horn et al., 2012).		
	Understanding of a human's mental state		Lack of evidence for a full understanding of a human's knowledge state (Kaminski et al., 2009; Viranyi et al., 2006; MacLean et al., 2014).			Dogs use associative mechanisms rather than a human partner's role to discriminate between partners when they look back (Petró et al., 2016).		
Balanced	Communicative gestures are connected to targets through joint attention (Gómez, 2007; Gómez et al., 1993; Moore, 2013)	Dogs form joint attention both in relevant and irrelevant conditions, but are more persistent in relevant conditions (i.e. take into account the object's relevance to humans) (Piotti & Kaminski, 2016; Chapter 3).						
Low level	Dogs interpret human communication as directive (Kaminski et al., 2011; Scheider et al., 2013)	Indicate objects that are not relevant to a human partner (Kaminski et al., 2011; Piotti & Kaminski, 2016; Chapter 3).						
		Dogs use pointing as a directive indicating them where to go, rather than what to do, but only if preceded by ostensive cues (Tauzin et al., 2015).						

Limitations	Limitations	Limitations
• Dogs do not seem able to overcome their own interest in a target, when they communicate with humans about something (e.g. Kaminski et al., 2011; Piotti & Kaminski, 2016; Chapter 3): this makes it difficult to directly apply tests designed for humans and should be taken into account when designing the studies. • Dogs' ability to learn to use complex apparatuses is limited by their understanding of the physical properties of objects (Chapter 2): this makes it difficult to directly apply tests designed for humans and should be taken into account when designing. • While in dogs the persistence is being explored as a measure of their cognitive abilities and motivations (e.g. Piotti & Kaminski, 2016; Chapter 3), the measure is rarely reported in the human literature, making it difficult to evaluate inter-species comparisons.	• Reputation forming is affected by testing conditions (Abdai & Miklósi, 2016). • Affective contrast may have an effect on subjects' behaviour during testing (Chapter 4). • Looking back is largely affected by individual differences (e.g. D'Aniello et al., 2015; Gacsi et al., 2009; Marshall-Pescini et al., 2009; Topal et al., 1997), which make between subjects designs difficult to implement (Chapter 4).	• Overtraining might inflate pro-social and altruistic findings (Marshall-Pescining et al., 2016). • Dogs own interest in the reward may mask otherwise helpful behaviour (Chapter 3). • Dogs' may find confusing a task in which they need to donate food to a human, due to their previous experience around food in the presence of humans (Chapter 5).
Conclusion	Conclusion	Conclusion
Variables of interest: frequency as well as persistence of looks. Recommendations: ensure that there are no competing interests, which may mask dogs' helpful behaviour. Future questions: Does helpful communication rely on the establishment of a communicative context (ostensive cues)? Have dogs become predisposed to receive and follow human communication during domestication?	Variables of interest: persistence of looks. Recommendations: take into consideration the negative effect of ignoring the dog during tests; take into consideration the difference between different types of looking behaviour (e.g. referential) Future questions: could a more 'naturalistic' approach aid exploring reputation forming in dogs?	Variables of interest: altruistic behaviour (vs pro-social); behavioural responses following the receiver eating the food and food release. Recommendation: ensure dogs are not cued to perform during the test. Future questions: would dogs cooperate, i.e. work towards a common goal.

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Appendixes

Appendix A: Ethical approval for the studies in Chapters 2 & 3.

From: Matt Guille <matthew.guille@port.ac.uk>

Subject: Re: ethical review animals

Date: 19 April 2013 at 18:46:00 CEST

To: Patrizia Piotti <patrizia.piotti@port.ac.uk>, Madeleine Hildrew <madeleine.hildrew@port.ac.uk>

Dear Patrizia,

I have just this moment opened the final email that allows me to confirm that your project is approved by the ERC. Please keep this email as a confirmation.

best wishes,

Matt

--

Matt Guille

Professor of Developmental Genetics

School of Biological Sciences

University of Portsmouth

King Henry Building

King Henry I Street

Portsmouth PO1 2DT

Tel: 02392 842047

Appendix B: Subjects' demographic information for Chapter 2

Dog Name	Gender	Age (y)	Breed	Lab	Tested	Exclusion Reason	Training Trials	Training Days	Test Group
Benny	M	2	Beagle	MPI	No	Stress	21	3	0
Boscaille	F	5	Malinois	MPI	No	Owner	6	1	0
Catie	F	5	Aussie	MPI	No	Stress	0	1	0
Colin	M	3	Cross	MPI	Yes	n.a.	30	3	2
Daisy	F	8	Boerboel	MPI	Yes	n.a.	12	1	1
Elli	F	3	Belgian Shepherd	MPI	No	Stress	0	1	0
Guenni	M	1	Whippet	MPI	No	Tired	14	3	0
Haily	F	5	Labrador	MPI	Yes	n.a.	18	2	2
Jasper	M	1	Lagotto	MPI	Yes	n.a.	12	1	1
Karou	M	6	Berger des Pyrenees	MPI	No	Time	28	3	0
Kendra	F	3	Labrador	MPI	No	Time	22	3	0
Liam	M	2	Flat Coated R.	MPI	Yes	n.a.	18	2	1
Linux	M	2	Aussie	MPI	No	Stress (warmth)	14	3	0
Luca	F	3	Podenco	MPI	No	Stress (warmth)	9	3	0
Maggie	F	6	Cross	MPI	No	Time	18	3	0
MaggyE	M	1	Aussie	MPI	No	Time	18	3	0
Matilda	M	3	GSD	MPI	No	Stress	22	2	0
Maxl	M	5	Altdeutscher Fuchs	MPI	No	Aggressive	0	1	0
Milou	F	2	Cross	MPI	Yes	n.a.	24	1	2

Ned	M	5	Border Collie	MPI	No	Stress	7	2	0
Schumi	M	8	Schnauzer small	MPI	No	Stress	16	2	0
Souris	F	4	Papillion	MPI	No	Stress (warmth)	12	3	0
Tschaika	F	8	Cross	MPI	No	Stress	0	1	0
Thyson	M	7	JRT	MPI	No	Time	22	3	0
Via	F	3	Doberman	MPI	No	Stress	0	1	0
Yara	F	3	Cross	MPI	No	Stress	30	2	0
Buddy	M	2	Labrador	UOP	Yes	n.a.	12	1	2
Freddie	M	1	Cross	UOP	Yes	n.a.	12	1	1
Missy	F	1	JRT	UOP	No	Stress	0	1	0
Shadow	F	4	Border Collie	UOP	No	Aggressive	3	2	0
Guy	M	5	Cross	UOP	No	Time	6	1	0
EllieR	F	2	Spaniel	UOP	No	Time	12	1	0

Note: MPI = Max Plank Institute, UOP = University of Portsmouth; Groups: 1 = dog started with the selfish condition, 2 = dog started with the helpful condition

Appendix C: Subjects' demographic information for Chapter 3

Study 1

Dog's Name	Gender	Age (years)	Breed Group (BKC)
Ashka	Female	2	Cross
Bailey	Female	4	Cross
Boomer	Female	3.5	Gundog
Charlie	Male	2.5	Cross
Crusoe	Male	4	Working
Dakota	Female	2	Cross
Harry	Male	3.5	Cross
Hudson	Male	4	Terrier
Iggy	Male	5	Gundog
Jeff	Male	7.5	Terrier
Koko	Female	3.5	Hound
Lanson	Male	2	Gundog
Maddie	Female	3.5	Utility
Max	Male	8	Cross
Millie	Female	1.5	Gundog
Moet	Male	4	Gundog
Moses	Female	6	Cross
PoppyP	Female	3	Cross
Rigsby	Male	5	Cross
Rumsey	Male	2.5	Cross
Sailor	Male	1.5	Gundog
Storm	Female	3	Cross
Winston	Male	4	Cross
Woody	Male	6	Pastoral

Note: The dogs' breed groups were defined according to the definitions of the Brit

Club (BKC)

Study 2

Dog	Gender	Breed Group (BKC)	Age (year)	Condition
Alpha	Male	Cross	8	Distractor
Arffer	Male	Cross	6	Distractor
Bear	Male	Cross	1	Distractor
Bella	Female	Gundog	2	Relevant
Ben	Male	Cross	1.5	Relevant
Blue	Male	Gundog	9.5	Distractor
Bob	Male	Cross	3	Relevant
Bollinger	Male	Cross	7.5	Distractor
Bonnie	Male	Cross	2	Distractor
Brian	Male	Gundog	5	Relevant
Brocken	Male	Gundog	3	Distractor
Buzz	Male	Cross	2	Distractor
BuzzG	Male	Cross	3.5	Distractor
Cassidy	Male	Cross	2	Relevant
Daisy	Female	Cross	2.5	Relevant
Hugo	Male	Terrier	2	Relevant
Isabelle	Female	Working	2	Relevant
Jago	Male	Working	5	Distractor
Jango	Male	Working	10	Relevant
Kip	Female	Pastoral	5.5	Relevant
Kite	Female	Pastoral	3.5	Distractor
Krug	Male	Gundog	4	Distractor
Lexi	Female	Working	1.5	Distractor
Lola	Female	Cross	4	Distractor
LolaJ	Female	Cross	1.5	Distractor
Macey	Female	Gundog	6.5	Distractor
Marcus	Male	Gundog	8.5	Relevant
Max	Male	Utility	4	Distractor
Merlin	Male	Gundog	8.5	Distractor
MerlinY	Male	Gundog	3.5	Relevant
Mishka	Female	Working	1.5	Distractor
Misty	Female	Cross	10	Relevant
Monty	Male	Gundog	2	Relevant
MontyS	Male	Utility	5	Distractor
Murphy	Male	Cross	6	Relevant
Nelson	Male	Gundog	9.5	Relevant
Oppo	Male	Gundog	3.5	Distractor
Oscar	Male	Cross	1	Relevant
Ozzie	Male	Pastoral	6	Relevant
Pippa	Female	Terrier	5	Distractor
Quito	Male	Pastoral	6	Distractor

Skye	Female	Cross	2	Relevant
Snoopy	Male	Cross	2	Distractor
Toby	Male	Gundog	4.5	Relevant
Tubby	Male	Toy	3.5	Relevant
Whilma	Female	Hound	3	Relevant
Wilson	Male	Cross	1.5	Relevant
Zippy	Male	Cross	3	Relevant

Note: The dogs' breed groups were defined according to the definitions of the British Kennel Club (BKC)

Appendix D: Model fitting additional information for Chapter 3

Study 1

For the response variable "indication of the target" we were interested in the effect of the experimenter's utterance during the search in each condition. Therefore the global model was calculated adding the fixed factors "utterance" (before utterance and after utterance) and "condition" (*relevant object, useless object, no object*) with an interaction. The fixed factor "attention during the demonstration" (i.e. percentage of time spent looking at the experimenter in the demonstration phase) was added as additional interaction with the previous factors, because it was expected that dogs' attention affected the indications of the target differently based on the condition. The fixed factors "gender" (male and female) and "trial number" (1 to 6) were also added, without interaction, to control for their main effect on the response.

For the response variable "frequency of gaze alternations" we were interested in the effect of the content of the target box on gaze alternations. Therefore the global model was calculated adding the fixed factor "condition" (*relevant object, useless object, no object*) to the null model. To control for the effect of dogs' attention, the fixed factor "attention during the demonstration" (i.e. percentage of time spent looking at the experimenter in the demonstration phase) was added to the model. Because it was expected that the frequency of gaze alternations differed based on their direction and across conditions, and that dogs' attention affected the gaze alternations to the target differently based on the condition, the factors "direction", "condition" and "attention" were included in the model with a 3 level interaction. The fixed factors "gender" (male and female) and "trial number" (1 to 6) were also added, without interaction, to control for their main effect on the response.

For the response variable "duration of gazes (s)" we were again interested in the effect of the content of the target box on dogs' looking behaviour. Therefore we calculated the global model adding the fixed factor "condition" (content of the target, i.e. *relevant object, useless object, no object*) to the null model. To control for the effect of dogs' attention, the fixed factor "attention during the demonstration" (i.e. percentage of time spent looking at the experimenter in the demonstration phase) was added to the model. It was expected that the duration of gazes varied based on their direction, and that dogs' attention affected dog gazes to the target differently based on the condition. Therefore the factors "direction", "condition" and "attention" had a 3 level interaction. The fixed factors "gender" (male and female) and "trial number" (1 to 6) were also added to the model, without interaction, to control for their main effect on the response.

Study 2

For the response variable "gaze alternations" (number of gaze alternations toward the target box) we were interested in the effect of communication style and the object hidden in the target box, therefore a global model was calculated adding the fixed factors "communication" (silent or vocal) and "condition" (*relevant* group or *distractor* group). We expected the "attention" during the demonstration (i.e. percentage of time spent looking at the experimenter) to affect the frequency of gaze alternations therefore we added the fixed factor "attention" to the global model. We expected the communication style and the attention during the demonstration to affect differently the dogs in the relevant group and those in the random group, so a 3 levels interaction between “communication”, “condition” and “attention” was included. The fixed factors “gender” (male and female) and “trial number” (1 to 6) were also added, without interaction, to control for their main effect on the response.

For the response variable “duration of gazes (s)” we calculated a global model by adding the fixed factor “direction” (direction of the gaze alternation, i.e. target box or empty box) to the null model in order to allow assessing the effects of the other factors on different directions of gazes (i.e. empty boxes and target box). We were interested in the effect of communication style and the object hidden in the target box, therefore a global model was calculated adding the fixed factors “communication” (silent or vocal) and “condition” (*relevant* group or *distractor* group). In order investigate the different effects of communication on the duration of gazes in the two conditions and when looking at different boxes, the factors “direction”, “condition”, and “communication” were included in the global model with a 3 level interaction. Following the results of Study 1, we expected the “attention” during the demonstration (i.e. percentage of time spent looking at the experimenter) to have a main effect on the persistency of gazes therefore we added the fixed factor “attention” to the global model. The fixed factors “gender” (male and female) and “trial number” (1 to 6) were also added, without interaction, to control for their main effect on the response

Appendix E: Ethical approval for the studies in Chapter 4

18 May 2015

University of Portsmouth

Professor Matt Guille
School of Biological Sciences
King Henry Building
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Portsmouth PO1 2DY
England

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email: matthew.guile@port.ac.uk

Dear Dr Kaminski,

RE: Ethics submission – Human-dog co-operation

Approval of project by the Animal Welfare and Ethical Review Body (AWERB)

I am very happy to confirm that the AWERB has given its approval for your proposal concerning work within the above project.

The AWERB uses UK Home Office guidelines on the Animals (Scientific Procedures) Act 1986 when assessing proposals and adheres to the regulations of the European Directive 2010/63/EU. Your project does not require a Home Office Project Licence since no pain, suffering or lasting harm will be caused. We are confident that the proposal demonstrates appropriate consideration of the Three Rs and animal welfare. Please use this letter as confirmation of ethical approval from AWERB, University of Portsmouth. Please use the number 515A as confirmation of the successful review.

Yours sincerely,

MJ Guille PhD FSB
Professor of Developmental Genetics
Chair, AWERB

www.port.ac.u

Appendix F: Subjects' demographic information for Chapter 4

Study 1

Dog	Breed	Age (years)	Gender	Helper	First Demonstration	Helper side (unsolvable task)
Dolly	Cross	6.2	F	PP	Unhelpful	LRRL
Buddie	Cross	4.7	M	BS	Unhelpful	LRLR
Dali	Labrador	2.4	M	BS	Helpful	RLRL
Lexi	Rottweiler	2.2	M	PP	Helpful	RLLR
ChesterS	Spaniel	1.9	M	PP	Helpful	LRLR
Lucy	Cross	8.0	F	BS	Unhelpful	RLLR
Bracken	Labrador	7.4	F	PP	Unhelpful	RLRL
MaxL	Labrador	6.3	M	BS	Helpful	LRLR
Bertie	JRT	2.2	M	PP	Unhelpful	LRLR
Wilson	Cross	1.8	M	BS	Unhelpful	LRRL
Roxy	Cross	1.3	F	BS	Helpful	RLLR
Marcel	FrenchBulldog	3.8	M	PP	Helpful	RLLR
Tigger	Cross	8.2	M	PP	Helpful	LRRL
Horace	SpinoneIta	4.2	M	PP	Unhelpful	RLLR
Sammy	BorderCollie	9.5	F	BS	Unhelpful	RLRL
Padme	BorderTerrier	10.2	F	BS	Helpful	LRRL

Alfie	Cross	2.4	M	BS	Helpful	RLRL
ChesterB	Bassetthound	2.6	M	BS	Unhelpful	LRLR
Nugget	Labrador	8.0	M	PP	Helpful	RLRL
Ralph	Cross	5.8	M	BS	Unhelpful	RLLR
Monty	Cross	3.5	M	BS	Helpful	LRRL
Wilf	Cross	7.5	M	PP	Unhelpful	RLRL
Barnsley	Cross	3.8	M	PP	Helpful	LRLR
Fudge	Cross	4.8	M	BS	Unhelpful	LRRL
Oscar	Bichon	2.4	M	PP	Unhelpful	LRRL
Bonnie	Cross	3.1	F	BS	Helpful	RLLR
Poppy	Labrador	1.3	F	PP	Helpful	RLRL
Biscuit	BorderCollie	2.2	M	PP	Helpful	LRRL
Gus	Labrador	8.1	M	PP	Unhelpful	RLLR
Harvey	SchnauzerMini	1.1	M	BS	Helpful	LRLR
Smudge	Spaniel	4.0	M	BS	Unhelpful	RLRL

Study 2

Dog	Breed	Gender	Age (years)	Condition
Arya	GSD	F	1.5	Nice / No-hel
Badger	Newfoundland	M	2	Nice / Skilful
Bailey_B	Labrador	M	3	Ignoring / Skilf
Bailey_G	Cross	M	7	Nice / Skillfu
Bailey_P	Cross	F	3	Nice / Skilful
Belle_D	English Bulldog	F	3	Ignoring / No-h
Budi	GSD	M	1	Nice / Skilful
Buzz_P	Cross	M	6	Nice / Skilful
Charlie_B	Cross	M	10	Nice / No-hel
Clover	Tibetan Terrier	M	1.5	Ignoring / No-h
Copper_M	Border Collie	M	3	Ignoring / No-h
Diesel_E	Cross	M	5	Ignoring / No-h
Dizzy_P	Golden retriever	F	4.5	Nice / Skilful
Dotty_G	Cross	F	3	Ignoring / Skilf
Eddie	Cross	M	1	Ignoring / Skilf
Freddy_L	Cross	M	5.5	Nice / No-hel
Fudge	King Charles Sp.	M	1	Nice / Skilful
Harry	Cross	M	4.5	Nice / No-hel
Harvey_V	Labrador	M	5	Ignoring / No-h
Honey_B	Labrador	F	9	Ignoring / No-h
Kiba_S	Dalmatian	M	3	Nice / Skilful
Lenny_B	Cross	M	2	Nice / No-hel
Lilly_V	Cross	F	2	Ignoring / Skilf
Lucca_E	Labrador	M	3	Ignoring / Skilf
Luna	Border Collie	F	6	Ignoring / No-h
Macey	Labrador	F	8	Nice / Skilful
Mavis_V	Border Terrier	F	2	Ignoring / Skilf
Meeka	Cross	F	3	Ignoring / Skilf
Milo	Cross	M	7	Ignoring / No-h
Molly_B	Bull Terrier	F	7.5	Nice / No-hel
Monty	Labrador	M	1.5	Nice / Skilful
Nessie	Labrador	F	1.5	Nice / No-hel
Ninja	Labrador	F	2	Ignoring / Skilf
Ozzy_D	Pug	M	2	Ignoring / Skilf
Phoebe	Cross	F	1.5	Nice / Skilful
Poppy_M	Cross	F	11	Nice / No-hel
Saphie	Labrador	F	8	Ignoring / No-h
Sasha	Border Collie	F	2	Ignoring / Skilf
Spud_B	JRT	M	2	Ignoring / No-h
Summer_B	Labrador	F	8	Nice / No-hel

Toby_M	Spaniel	M	6	Ignoring / Skilful
Tod_H	Spaniel	M	5	Nice / No-help
Tommy_G	Spaniel	M	2	Nice / No-help
Vialli	Whippet	M	2	Nice / Skilful
Willow_M	Cross	F	8	Ignoring / Skilful
Woody	Cross	M	8	Ignoring / No-help
Woody S	French Bulldog	M	4.5	Nice / No-help
Zayla	GSD	F	2	Ignoring / No-help

Appendix G: Ethical approval for the study in Chapter 5

11 December 2014

University of Portsmouth

Professor Matt Guille
School of Biological Sciences
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Portsmouth PO1 2DY
England

Tel: +44 (0)23 9284 2047
Fax: +44 (0)23 9284 2070
email: matthew.guile@port.ac.uk

Dear Dr Kaminski,

RE: Ethics submission – Do domestic dogs make prosocial choices?

Approval of project by the Animal Welfare and Ethical Review Board (AWERB)

I am very happy to confirm that at the meeting of the board on the 6th November the AWERB gave its approval for your attached proposal concerning work within the above project.

The AWERB uses UK Home Office guidelines on the Animals (Scientific Procedures) Act 1986 when assessing proposals and adheres to the regulations of the European Directive 2010/63/EU. Your project does not require a Home Office Project Licence as the animals are not subjected to procedures that have potential for harm and suffering. We are confident that the attached proposal demonstrates appropriate consideration of the Three Rs and animal welfare. Please use this letter as confirmation of ethical approval from AWERB, University of Portsmouth. Please use the number 1114G as confirmation of the successful review.

Yours sincerely,

MJ Guille PhD FSB
Professor of Developmental Genetics
Chair, AWERB

Appendix H: Subjects' information for Chapter 5

Demographic information

Donor	Receiver	Gender	Age	Breed	Donor's side	No. of training sessions
Jasper	Owner	Male	5	Cross	L	4
Lucca	Owner	Male	2	Labrador	R	4
Gus	Owner	Male	8	Labrador	R	4
Sailor	Owner	Male	2	Irish Water Spaniel	L	6
Sammy	Owner	Female	10	Collie	L	3
Buddie	Owner	Male	5	Cross	L	8
Bella T	Owner	Female	2	Cross	R	6
Benji	Owner	Male	1	Cross	R	3
Jimmy	Stranger	Male	2	Staffordshire Bull Terrier	L	6
Merlin	Stranger	Male	10	Springer spaniel	R	6
Ollie	Stranger	Male	5	Cross	R	
Honour	Stranger	Female	1	Staffordshire Bull Terrier	L	3
Bella D	Stranger	Female	6	Cross	L	2
Bella F	Stranger	Female	3	Labrador	L	8
Groot	Stranger	Male	1	Labrador	R	7
Bronnie	Stranger	Male	4	Cross	R	2

Conditions' order

Donor	Test days	Block 1	Block 2	Block 3	Block 4	Block 5	Block 6
Jasper	3	Selfish	No-food	Pro-social	Altruistic	Pro-social control	Altruistic control
Lucca	2	Altruistic	Pro-social	Altruistic control	Selfish	No-food	Pro-social control
Gus	3	Pro-social	No-food	Selfish	Altruistic control	Pro-social control	Altruistic
Sailor	3	No-food	Selfish	Pro-social	Altruistic	Pro-social control	Altruistic control
Sammy	3	Altruistic	Pro-social	Altruistic control	Selfish	No-food	Pro-social control
Buddie	3	Pro-social	No-food	Pro-social control	Altruistic control	Selfish	Altruistic
Bella T	6	No-food	Selfish	Pro-social	Altruistic control	Pro-social control	Altruistic
Benji	3	Selfish	No-food	Pro-social	Altruistic	Pro-social control	Altruistic control
Jimmy	3	Selfish	No-food	Pro-social	Altruistic	Pro-social control	Altruistic control
Merlin	3	Altruistic	Pro-social	Altruistic control	Selfish	No-food	Pro-social control
Ollie	3	Pro-social	No-food	Selfish	Altruistic control	Pro-social control	Altruistic
Honour	4	No-food	Selfish	Pro-social	Altruistic	Pro-social control	Altruistic control
Bella D	3	Altruistic	Pro-social	Altruistic control	Selfish	No-food	Pro-social control
Bella F	3	Pro-social	No-food	Pro-social control	Altruistic control	Selfish	Altruistic
Groot	3	No-food	Selfish	Pro-social	Altruistic control	Pro-social control	Altruistic
Bronnie	3	Selfish	No-food	Pro-social	Altruistic	Pro-social control	Altruistic control

Appendix I: Training method for Chapter 5

Introduction phase

The dog was brought to the testing room by two experimenters and was initially allowed a few minutes to explore the room, on both sides of the fence. It was then called at the back of the room by one experimenter, who pressed the remote that operated the food dispensers and immediately dropped a few treats on the floor near the dog, so that the dog would familiarise with the dispensers' noise. The other experimenter (the trainer) then walked up to the apparatus while the first experimenter held the dog; the trainer pulled the trap door open, talking with the dog at the same time to make sure it was watching. The dog was then allowed to go and eat the food. This procedure was repeated throughout the training after each break and during the sessions, to give dogs a chance so see how the apparatus worked and learn from the trainer's behaviour.

Training steps

To initially induce the dogs to pull the rope, the trainer also played with them using a tag toy, repeatedly feeding the dog a few treats as soon as it tugged the toy. After the first 2-3 repetitions, the trainer stopped any playful behaviour or verbal praise and only rewarded the dog with treats. This was done to ensure that the dog was tugging the toy to obtain the food, rather than play or rewards.

Once the dog was tugging the toy consistently for food, this was attached to the rope on the apparatus, and dogs were given time to practice with it. Initially the trainer held the rope and helped them pulling if necessary, then she gradually intervened less and moved away from the apparatus. Dogs were also regularly lead by one of the experimenter at the back of the room and then released, to familiarise them with this part of the testing procedure later on.

Dogs were give breaks whenever necessary and each training session lasted 1 hour maximum.

Exclusion criteria

Dogs that did not improve during training for more than 2 consecutive sessions were excluded from the training. Dogs that reached the second threshold were then invited for testing. Dogs were trained on average in 4 training sessions.

Appendix J: Model fitting additional information for Chapter 5

Two generalised linear mixed models (GLMMs), fit by maximum likelihood (Laplace Approximation), were calculated for the variable measured. A GLMM (null model) with log function was calculated with the response variable “frequency of pulling”. The random intercept factor “dog” and the nested random intercept factors “trial” and “interruption” (whether the dog did or did not have a break before the trial) were included in the null model (N = 1152, number of subjects = 16). We were interested in the effect of the condition and the receiver on dogs’ pulling. Therefore another GLMM (global model) was calculated adding the fixed factors “condition” (selfish, altruistic, pro-social, no-food, pro-social-control, altruistic-control), “receiver” (owner, stranger) to the null model. Because we were also interested in whether the frequency of pulling in each condition varied based on the receiver, the factors “condition” and “receiver” were included in the model both as main factors and with an interaction. The global model’s Second-order Akaike Information Criterion (AIC) was evaluated with a likelihood ratio test against the corresponding null model (i.e. which included only random factors).

FORM UPR16

Research Ethics Review Checklist

Please include this completed form as an appendix to your thesis (see the Postgraduate Research Student Handbook for more information

Postgraduate Research Student (PGRS) Information			**Student ID:**	676721
PGRS Name:	Patrizia Piotti			
Department:	Psychology	**First Supervisor:**	Dr Juliane Kaminski	
Start Date: (or progression date for Prof Doc students)		**1st January 2013**		
Study Mode and Route:	Part-time ☒ Full-time ☐	MPhil ☐ PhD ☒	MD ☐ Professional Doctorate ☐	

Title of Thesis:	Collaborative interactions between humans and domestic dogs (Canis familiaris)
Thesis Word Count: (excluding ancillary data)	50898

If you are unsure about any of the following, please contact the local representative on your Faculty Ethics Committee for advice. Please note that it is your responsibility to follow the University's Ethics Policy and any relevant University, academic or professional guidelines in the conduct of your study

Although the Ethics Committee may have given your study a favourable opinion, the final responsibility for the ethical conduct of this work lies with the researcher(s).

UKRIO Finished Research Checklist:
(If you would like to know more about the checklist, please see your Faculty or Departmental Ethics Committee rep or see the online version of the full checklist at: http://www.ukrio.org/what-we-do/code-of-practice-for-research/)

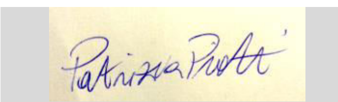
a)	Have all of your research and findings been reported accurately, honestly and within a reasonable time frame?	YES ☒ NO ☐
b)	Have all contributions to knowledge been acknowledged?	YES ☒ NO ☐
c)	Have you complied with all agreements relating to intellectual property, publication and authorship?	YES ☒ NO ☐
d)	Has your research data been retained in a secure and accessible form and will it remain so for the required duration?	YES ☒ NO ☐
e)	Does your research comply with all legal, ethical, and contractual requirements?	YES ☒ NO ☐

Candidate Statement:

I have considered the ethical dimensions of the above named research project, and have successfully obtained the necessary ethical approval(s)

Ethical review number(s) from Faculty Ethics Committee (or from NRES/SCREC):	ERC (email); AWERB 515a; AWERB 1114g

If you have *not* submitted your work for ethical review, and/or you have answered 'No' to one or more of questions a) to e), please explain below why this is so:



Signed *(PGRS)*:		Date: 20/01/2017

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I, ***Patrizia Piotti, Via Tintoretto, 10, Cologno Monzese, ITALY***, "the Depositor", would like to deposit

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Signature: Patrizia Piotti

Date: 24/05/2017…………………………………..

Return to: Faculty Advisor (Research), Research Section, Quality Management Division, Academic Registry, University of Portsmouth, University House, Winston Churchill Avenue, Portsmouth, Hampshire PO1 2UP