Chapter 5
Social Looking in the Domestic Dog

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Abstract The study of dog social cognition is relatively recent and is rapidly developing, providing an interesting and multi-faceted picture of our "best friend's" sociocognitive abilities. In particular, since Miklósi et al.'s (2003) seminal work "A simple reason for a big difference: wolves do not look back at humans, but dogs do", there has been a surge of interest in the area of dog–human communication. In the current chapter we focus on dogs' comprehension of the human gaze and their ability to use human-directed-gazing as a communicative tool. We first review studies on the social significance of human eye contact for dogs, their understanding of eyes as indicators of attention, and their ability to take another's visual perspective into account. We also consider dogs' understanding of human eye-gaze as a communicative act, in terms of its potentially referential nature and as an ostensive cue signalling the communicative intent of the actor. We then move on to review studies on dogs' human-directed gazing behaviour, discussing whether it may be considered part of an intentional and referential communicative act, what the underlying motivations and contexts in which this behaviour is exhibited may be, and what variables affect its occurrence. Where open questions remains, we outline current debates and highlight potential directions for future research.

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A. Horowitz (ed.), *Domestic Dog Cognition and Behavior*,
DOI: 10.1007/978-3-642-53994-7_5, © Springer-Verlag Berlin Heidelberg 2014

5.1 Introduction: Dogs' Scientific Renaissance

Dogs were likely the first animals to be domesticated and they have shared a common environment with humans for longer than any other species (Vilà et al. 1997; Bokyo et al. 2009; Pang et al. 2009; vonHoldt et al. 2010; Ding et al. 2012; Larson et al. 2012; Druzhkova et al. 2013; Wang et al. 2013). At present, they are almost omnipresent in human lives and undoubtedly have a unique relationship with humans, which has been described since ancient times by poets, writers, and artists. Interestingly, the long history of proximity and closeness between dogs and humans has been one of the main reasons why dogs have been widely snubbed and regarded as an ethologically 'uninteresting' species and have only recently become subjects of scientific inquiry in the field of comparative cognition (Miklósi et al. 2004; Miklósi 2007).

In the last 20 years dogs have seen a 'scientific renaissance', with a sudden rise in the number of published studies on canine cognition (Cooper et al. 2003; Miklósi et al. 2004; Bensky et al. 2013). This new wave of canine cognition research has transformed the initially 'uninteresting' dog into a fascinating model for evolutionary cognition research and for the investigation of the building blocks underlying mental abilities in animals, particularly those involving social cognition (Miklósi et al. 2004). From these studies it emerges that dogs' success as domestic animals and their capacity to become "man's best friend" are rooted in a wide range of social skills and competencies that allow them to engage in complex communicative, relational, and cooperative interactions with humans (Miklósi and Topál in press).

Recently, Bensky et al. (2013) reviewed the literature on dog cognition, identifying a number of different areas in which there has been active empirical research. Following the taxonomy proposed by Tomasello and Call (1997), these authors grouped studies on dogs' cognitive abilities into two broad categories, defined mainly in terms of the function of the cognitive processes involved: physical cognition and social cognition. According to this classification, studies on dog physical cognition investigate how dogs perceive and interpret non-social stimuli to make sense of their physical environment, thus focusing on different topics such as discrimination learning, object permanence, object learning, categorization and inferential reasoning, object manipulation, problem-solving, quantitative understanding, spatial cognition, and memory (see Bensky et al. 2013 for a review). On the other hand, studies on social cognition have focused on understanding the dog's social world and social knowledge, investigating what dogs know about others (whether conspecific or human) and how they acquire such knowledge. Therefore, research on dog social cognition covers a wide range of topics dealing with social phenomena ranging from recognition and categorization of conspecifics and humans (Faragó et al. 2010; Huber et al. 2013), perception of their emotions (Nagasawa et al. 2011; Buttleman and Tomasello 2013; Merola et al. 2013b), the development and management of social relationships with humans (e.g. Topál et al. 1998; Prato-Previde et al. 2003; Custance and Mayer 2012; Riemer

et al. 2013) and conspecifics (see Bonanni and Cafazzo in press, Smuts in press for recent reviews), the acquisition of new abilities through observation and interaction with others (e.g. Poncrágz et al. 2003, 2004; Range et al. 2007, 2011; Kubinyi et al. 2009; Tennie et al. 2009), and all the different aspects of intraspecific and interspecific communication (e.g. Bradshaw and Nott 1995; Miklósi et al. 2000; Rossi and Ades 2008; Horowitz 2009; Kaminski et al. 2011; Marshall-Pescini et al. 2012; see also Bensky et al. 2013 and Kaminski and Nitzschner 2013 for recent reviews).

Although there is growing evidence that dogs' social skills are in some respects unique and probably contributed to turning dogs into "man's best friend" (Miklósi and Topál in press), how these abilities evolved (Hare et al. 2002, 2010; Miklósi et al. 2003; Udell et al. 2010; Viranyi and Range in press) and develop (Udell and Wynne 2008, 2010; Wynne et al. 2008; Reid 2009; Hare et al. 2010), which are the cognitive mechanisms underlying them (Elgier et al. 2012; Kaminski and Nitzschner 2013), and the relevance of such issues for the understanding of human evolution (Hare and Tomasello 2005; Kubinyi et al. 2007; Topál et al. 2009; Hare et al. 2012) are all matters of lively debate in the field of comparative cognition, with a number of intriguing questions driving current research activities and different hypotheses being put forward.

In the current chapter, we present findings on dog–human communication, with a focus on dogs' ability to *understand* and respond to human gaze and to *use* human-directed-gazing as a communicative tool during interactions; we discuss the potential origins and factors affecting these abilities; and we discuss the evidence regarding the complexity of such behaviour.

5.2 What's in a Gaze? Dogs' Understanding of Gazing

5.2.1 Social Significance of Eye Contact

For most non-human species direct (especially prolonged) eye contact is considered by the receiver as an aggressive threat (Emery 2000), although recent research has suggested that the significance of direct eye contact may change during development: for example, macaque mothers spend time gazing into their infants' face/eyes in the first few weeks of their life (Ferrari et al. 2009; Simpson et al. in press), despite the fact that as adults direct eye contact is mostly used as a threat in this species.

A number of authors have suggested that one of the fundamental changes in human evolution is the different functional role of direct eye-gaze, in that humans may stare in someone's eyes to threaten them, but also to show love and affection. Indeed such a dual function of eye-gazing appears to be somewhat limited to humans and a few other great ape species (Emery 2000), although in fact studies directly investigating the function of eye-gazing in non-primate species are rare.

According to Schenkel, wolves often use gaze to force others into subordination and maintain their position in the group (Schenkel 1967; Fox 1971). Also in dogs, prolonged and direct eye-gazing has been considered a threatening behaviour, associated with agonisitic interactions (Bradshaw and Nott 1995). Hence in both species, extended duration of gazing is often regarded as a form of ritualized aggression, whereas averting the gaze indicates subordination (Scott and Fuller 1965; Fox 1971).

Although no studies have directly investigated if and how dogs (or wolves) use direct eye-gaze in different contexts (i.e. agonisitic and affiliative), there is at least one situation in which prolonged eye-gaze may be interpreted in an affiliative manner i.e. whilst exhibiting a play bow. In this situation the actor normally looks directly in the face of the individual being invited to play and the eye contact may last a few seconds. Hence it would seem that dogs (and potentially wolves) may in fact modulate the significance of a conspecific's prolonged and direct eye-gaze by varying the accompanying postures, and that it can hence be exhibited both in an agonistic and affiliative context.

One potentially important question, therefore, is how dogs perceive a direct and prolonged gaze, not by a conspecific but by a human being. Similarly to the conspecific context, it would seem that a stare can be read as a threat in some cases, since for example, gazing by the owner can trigger aggression in dogs who have dominance-related problems with their owner (Line and Voith 1986). Indeed, in a forced eye-contact test, in which dogs were gently held and a human looked in their eyes attempting to maintain eye contact with them, it was found that they would tolerate their owner's direct eye contact significantly more than a stranger's (Hernádi et al. 2012). The fact that direct eye contact is tolerated more when performed by a person with whom dogs have a strong bond suggests that, with few or no other accopmanying signals, a direct gaze puts dogs in an uncomfortable situation. Indeed, interestingly, it appears that a number of behaviours can affect how a direct gaze is perceived. Vas et al. (2005; see also Vas et al. 2008; Gácsi et al. 2013a, b) were interested in understanding how dogs would modify their own behaviours in response to a human partner changing their behaviour from exhibiting a threatening to a friendly approach towards them (or vice versa). In both cases, the experimenter approached the dog whilst maintaining full eye contact with it as much as possible, but what varied were the accompanying behaviours: in the 'friendly' approach the experimenter walked at a normal speed and talked to the dog in a friendly tone of voice; whereas in the 'threatening' situation she approached haltingly with the upper body bent forward, and in complete silence. The dogs responded differently, with a more fearful (and in some cases aggressive) response to the experimenter and increased heart rate (Gácsi et al. 2013a, b) when she approached in a threatening way, but rapidly switching to a more relaxed stance once the experimenter exhibited the friendlier behaviours.

Hence, it seems that dogs like many other species, may indeed consider direct eye-gaze to be a threatening social stimulus, also when exhibited by humans, however the interpretation of this cue appears to be dependent on which other behaviours occur together with it.

Considering the above, the next important issue is whether dogs' flexibility in understanding human eye-gaze is a specific adaptation to life with humans, selected for during the course of domestication. In multiple studies involving different tasks, young hand-reared wolf pups were significantly slower or more reluctant to establish eye contact with a human than similarly-raised dog pups (Gácsi et al. 2005, 2009a; Virányi et al. 2008; see also Sect. 5.3.4 below). However, a wolf-dog comparison as regards the *understanding* of human eye-gaze is at present difficult to evaluate since it is based on only one study. Adult wolves presented with a stranger approaching either in a friendly or threatening manner whilst maintaining eye contact (the same procedure adopted by Vas et al. 2005) looked away from the approaching threatening stranger significantly faster than dogs. However, unlike dogs they showed no signs of fearfulness or aggression (Gácsi et al. 2013a, b), making any interpretation of the avoidance of eye contact difficult. In the friendly approach, wolves and dogs behaved in largely similar ways and both species behaved differently in the two contexts, which would suggest that at the very least wolves were also capable of perceiving direct eye contact differently in the two context. However, a more systematic comparison of how direct eye-gaze is understood and used in different context both with conspecifics and humans would help to tell us more about the potential changes brought about by the domestication process to this basic, but important behaviour.

Aside from the emotional and social valence, eye-gazing can also deliver important information as regards the gazer's attentional state, the focus of their attention, and, potentially, their communicative intent.

5.2.2 *Do Dogs Understand that Eye-gazing Can Reveal Something of the Gazer's State of Attention? Do They Know we can 'See' Them and Are They Sensitive to Others' Visual Perspective?*

Only one study, to our knowledge, has investigated dogs' understanding of their conspecific's attentional stance. Horowitz (2009) looked at whether dogs would exhibit and modulate potential attention-getting behaviours such as paw, bump, or bark in accordance with their partners' attentional state in the context of play. Indeed, the author found that play signals were sent nearly exclusively to forward-facing conspecifics, whereas attention-getting behaviors were used most often when a playmate was facing away. Furthermore, the forcefulness of the attention-getter varied in accordance with the degree of disattention in the audience: stronger attention-getters were used when a playmate was looking away or distracted, less forceful ones when the partner was facing forward or laterally. So from this study it appears that dogs perceive something of the attentional state of their conspecifics, although whether eye contact is used as a cue to attention has not so far been investigated.

In contrast to the paucity of studies with conspecifics, a number of studies have been carried out investigating dogs' understanding of human attention. In an experimental paradigm borrowed from the primate literature (Povinelli and Eddy 1996; Kaminski et al. 2004), researchers investigated whether dogs would beg food more from a person who is looking at them or one who is distracted in different ways (e.g. back-turned, reading a book, etc.). In most cases dogs, efficiently chose the 'attending' experimenter (Gácsi et al. 2004; Virányi et al. 2004). A second approach to investigating dogs' understanding of human attention relied on dogs' obedience to human commands. In two studies, dogs were told not to take food from the floor; following the command, the human either kept looking at the dogs, or she was distracted, turned her back, or closed her eyes. Dogs obeyed the commands more when the human was attentive and, impressively, they were also capable of distinguishing between the eyes open versus eyes closed condition (Call et al. 2003; Schwab and Huber 2006). Similarly, Virányi et al. (2004) asked dogs to perform a set of training exercises—however, they imparted the commands whilst directing the attention either to the dog, to another person in the room, to neither, or whilst actually being on the other side of a barrier. Again the likelihood of obedience was directly related to the attentiveness of the owner towards the dog.

In a twist to the 'commands' test, Bräuer et al. (2004) required dogs to refrain from taking food from the floor. However, in this case the food was placed behind three different barriers: a small, a large, or a transparent one. If dogs are sensitive to the human's visual access to the food they should choose to approach the food behind the large barrier (which would be effective in avoiding detection), and, indeed, this is what dogs did. This study suggests that dogs are not only sensitive to whether humans are attending to them or not, but potentially also to the direction of their attention—that is, to their visual perspective.

To investigate the latter issue in more detail Kaminski et al. (2009) set up a familiar toy-retrieval game with dogs who normally engaged in these games at home. However, in the experimental room in which the game took place, there were always two toys placed in different locations behind barriers so that although both toys were visible to the dogs, only one toy was visible to the experimenter. When asking the dog to 'fetch', the experimenter gave no behavioural cues as to which toy she was referring to. Results suggest that dogs appreciated the experimenter's visual perspective despite the fact that it was different from their own, since they mostly retrieved the toy which was visible to her.

In a final recent study dogs' understanding of human eye-gaze was investigated by attempting to address whether dogs actually understand what 'seeing' means. Kaminski et al. (2013) presented a forbidden-food-on-the-floor test but with another twist, since in this case what varied was the direction of the illumination: in some cases the lamp illuminating the person was switched on, in other cases the light was focused on the food, in yet further situations either both or none were in the light. Control conditions were also carried out to check what dogs would do in the different illumination conditions if the experimenter was not in the room. Dogs hesitated longer before taking the food when the food was illuminated than when it was not—irrespective of seeing the human. This result suggests that dogs may

have some understanding that when the food and the area around it is illuminated humans can see them, providing some evidence that dogs take into account the human's visual access to the desired food while making their decision to steal it.

As has been suggested by some authors (Bräuer et al. 2004; Bräuer in press), dogs may 'solve' a number of these tasks by simply inhibiting their behaviour when they see their human partner's eyes. Indeed, considering that eye gaze in a social context may be read as a 'threat', in a 'command test' such as the food-on-the-floor situation, such an avoidance strategy may come quite naturally to dogs. However, what is interesting to note here is that in 'begging' paradigms, by contrast, dogs choose the human partner whose eyes are in fact *visible*, suggesting that they are indeed capable of reading the social message of human eye gaze in different ways, depending on the contextual information. Furthermore, this particular criticism is not applicable to the Kaminski et al. (2013) study in which dogs stole food if the food was in the dark irrespective of whether they could see the person or not.

Another criticism raised against a number of these studies is that in most cases results can be explained by dogs' having learned from daily experience with humans how to best obtain what they want in a specific context (Udell et al. 2011). For example, in the begging paradigm the scenarios which were more likely to be familiar to dogs (e.g. the experimenter reading a book) were easier for them to solve correctly than those which were likely to have been less familiar (e.g. a person with a bucket over their head) (Udell et al. 2011). Although little is as yet known of the mechanisms or the ontogeny of dogs' comprehension of human attention, a learned component is likely to play at least a part in its acquisition. Notably, however, while this criticism is valid for experimental paradigms such as the begging and obedience tests, it is less likely to explain the studies carried out by Kaminski et al. (2009) involving the familiar 'retrieval' context but with multiple barriers or the Kaminski et al. (2013) study, since it is unlikely that dogs would have extensive experience of the different illumination or barrier combinations presented in those studies.

Indeed what appears striking when putting all the evidence together is the multitude of contexts and hence the flexibility that dogs seem to exhibit in their understanding of human attention (Virányi and Range 2011); perhaps this suggests that rather than simply responding to single cues or triggering stimuli which may have been reinforced in the past, dogs have the capacity to extract knowledge from their experiences and use this knowledge to solve novel social problems (Call 2001).

5.2.3 Can Dogs Follow Eye-gazing and Read this Behaviour as a Referential Gesture?

As well as its use as indicator of whether another is attending or not to a given situation, eye-gazing may also be used to infer the *direction* of another's attention. The functional relevance of this ability may be particularly important for social

species, since it would allow an individual to gain valuable information about both its social and physical environment (Emery 2000).

Multiple studies have been carried out on the abilities of various non-human species to follow eye-gaze, and the list of species that appear to be capable of such gaze following is constantly growing. At least three different types of gaze-following contexts can be identified: (1) gaze following into distant space; (2) gaze-following around barriers (which has been shown only in the great apes—Bräuer et al. 2005—and in two corvid species—Bugnyar et al. 2004 and Schloegl et al. 2008); (3) gaze-following to a specific target object, which appears to be the hardest to master by non-human species (Call and Tomasello 2005). Considering that the ability to gaze-follow in one context does not necessarily carry over to others, there is growing evidence that these abilities actual tap into different underlying mechanisms (Povinelli and Eddy 1996; Tomasello et al. 1999; Triesch et al. 2007).

Unfortunately, gaze-following in dogs has been investigated almost exclusively with a human as a demonstrator. The only report of conspecific gaze-following is a conference abstract describing a comparative study carried out in dogs and wolves living in packs where it was found that both species followed their partner's gaze into distant space (Werhahn et al. 2013). With human-reared wolves, gaze-following into distant space has been shown to occur both with conspecifics and familiar humans from 14 weeks of age (Range and Viranyi 2011), although this has not as yet been tested with dogs.

As regards gaze-following into distant space with humans as demonstrators, a few more studies have been carried out with dogs, with mixed results. Agnetta et al. (2000) tested dogs in a gaze-following task where a human experimenter turned her head and looked at one of three predetermined locations (straight up, directly to the left, or directly to the right of the dog) for approximately five seconds. The results found that dogs did not reliably follow human gaze into distant space. However, in the same study authors also used a two choice task—i.e. food was hidden under one of two bowls equidistant from the human signal—and in one of the conditions the demonstrator turned his head and looked at the correct bowl for 5 s. Interestingly, in this case the dogs' performance was above chance at the group level, with 7 of the total 16 dogs also performing above chance at the individual level.

In a similar study, Soproni et al. (2002) also adopted a two-way choice task with the demonstrator either turning her head and gazing toward the correct bowl, turning her head and gazing above the baited bowl to the upper corner of the room, or orienting her head and body to the midline facing the dog and turning only her eye-gaze toward the correct bowl. Results showed that whereas dogs followed the referential head- and eye-gaze directed to the bowl above chance, they did not do so in the other two conditions.

Overall, it appears that whereas dogs have difficulty in following eye-gaze into distant space, in the two-way choice task, they appear to be able to use eye-gaze to infer where the hidden food is located. Indeed, even puppies of between 9 and 24 weeks of age appear to be able to use gazing as a referential cue in a two-way choice task, even if they find this cue much more difficult to follow than, for example, pointing, or a combination of pointing and gazing (Hare et al. 2002). In

fact, although it seems that dogs can use gazing as a referential cue, it appears that the ease with which they do so is contingent on how it is presented, since Bräuer et al. (2006) found that a continuous, prolonged gaze directed at the bowl was easier for dogs to follow than more rapid alternating glances between the object and the subject.

The importance of contingent cues is confirmed by a more recent study, using an innovative eye-tracking methodology, in which researchers showed that dogs could reliably follow human eye-gazing in a two-way object choice task (see also Rossi et al., this volume). Importantly, dogs did so significantly more if the referential gesture was preceded by direct eye contact between the demonstrator and the dog, and accompanied by the use of the dog's name in a high-pitched tone of voice (Teglas et al. 2012). According to these authors, the direct eye contact exhibited by the demonstrator prior to the referential gestures set the communicative context between the human and dog, hence alerting the latter that the subsequent actions were intended for them. In other words the eye contact acted as an ostensive cue (see Sect. 5.2.4).

Taken together, dogs' gaze-following abilities in a referential context, coupled with the preliminary report that dogs can follow conspecific eye gaze into distant space, suggests that, this ability is present in dogs. It is more likely that methodological issues in the experimental setup of the two studies finding no human gaze-following affected the results. Future studies on this topic will be necessary to draw final conclusions on this issue. Still, results suggest that dogs' understanding of eye-gaze includes a perception of its directionality and potentially an understanding that eye-gazing can be referential.

5.2.4 *Do Dogs Understand that Eye-gazing May be Used as an 'Ostensive Cue' to Signal a Communicative Context?*

One of the most interesting aspects emerging from recent research on dog–human communication is the possibility that like human infants, dogs may be sensitive to 'ostensive cues'. Ostensive cues in adult-child dyads are communicative signals such as direct eye contact and body orientation as well as the use of motherese and the child's name, which have the function of alerting infants that a 'learning context' is being set up, and hence assisting them in the social learning process (Nielsen 2006; Brugger et al. 2007; Southgate et al. 2009; Csibra and Gergely 2011). Indeed, the use of ostensive cues by a demonstrator has been shown to overide childrens' own perceptions and lead them into making inefficient choices by, for example, 'over-imitating': i.e., copying redundant actions (Nielsen 2006; Brugger et al. 2007; Lyons et al. 2007, 2011) or carrying out 'obvious' errors in their decision making process (Topál et al. 2008).

It has been proposed that dogs, potentially uniquely amongst non-human species, also respond to human ostensive cues in similar contexts—although the

functional relevance of these behaviours may be different (see Topál et al. in press for a review). Support for this idea has been growing, as results have found that dogs: show more search errors in A-not-B task when the demonstrator exhibits ostenisve cues rather than other non-social attention getters (Topál et al. 2009a, 2010; Marshall-Pescini et al. 2010; Kis et al. 2012; Sümegi et al. in press); make more counterproductive choices in a food quantity discrimination task when a combination of communicative cues are used (Marshall-Pescini et al. 2012); and follow pointing in a two-way choice task more accurately when they are preceded by communicative cues (Kaminski et al. 2012).

What is striking is that in some cases dogs appear to rely more on the communicative cues delivered by a complete stranger (the experimenter) than their own experience (Szetei et al. 2003; Erdőhegyi et al. 2007; Topál et al. 2009a; Kupán et al. 2011). For example, in a food-quantity discrimination task, although the different size food plates are continuously visible during the demonstration, dogs tend to choose the smaller one when their owner or the experimenter communicate a preference for it (Prato-Previde et al. 2008; Marshall-Pescini et al. 2011; Horowitz et al. 2013).

Exactly what mechanisms are responsible for the powerful social influence effect shown by humans' communicative cues on dogs' choices is still a matter of debate (Topál et al. 2009a, 2010; Marshall-Pescini et al. 2010; Kis et al. 2012), however what is perhaps more interesting for the purpose of this chapter is to note that various studies converge in suggesting that direct eye contact appears to be one of the most potent communicative cues that dogs rely on (Kaminski et al. 2012; Marshall-Pescini et al. 2012; Teglas et al. 2012).

Overall, it would seem that dogs have a rather sophisticated understanding of eye-gazing. Although there are relatively few studies focusing on dogs' understanding of conspecific eye-gazing—this area needs more attention in the future—their understanding of human eye-gazing is rather impressive. Dogs appear to perceive that eye contact may be used to convey emotional and socially relevant information in the dyadic context, and that its valence as a threatening or affiliative signal may change depending on the behaviours that accompany it. Furthermore, dogs also seem to be able to use human eye-gaze referentially (although with more difficulty than pointing), suggesting that they may understand that eye-gaze can be used to direct attention to a target. Finally, a few studies suggest that human eye-gazing is also an important attention-getter in dog–human communication and that it may serve to alert dogs when human communication is intended for and directed at them.

5.3 Looking at Humans: How, When, and Why Dogs Engage in Looking Behaviour

In humans and other animal species intraspecific communication occurs in a variety of different situations, involves the use of a range of observable behaviours, and in general takes place between conspecifics. However, dogs' natural habitat

has particular features which requires members of this species to communicate with human beings regularly and effectively. During everyday social interactions with humans, in addition to responding to human communication, dogs also spontaneously and actively communicate with humans through a variety of signals, including gazing, different types of vocalizations, and other behavioural actions (e.g., running back and forth, touching, and assuming specific body postures). These behaviours, besides expressing internal emotional and motivational states, seem to be aimed at achieving specific goals, such as initiating play, going for a walk, or obtaining a person's attention, help, or comfort.

In the past dog–human communication received little scientific attention (e.g. Warden and Warner 1928; McConnell and Baylis 1985; Mitchell and Thompson 1993), but recently this issue has been more systematically investigated. Research has considered different topics including: which signals dogs use and in which contexts (e.g. Hare et al. 1998; Miklósi et al. 2000; Gaunet 2008, 2010; Kaminski et al. 2011; Merola et al. 2012a, b, 2013a); to what extent evolutionary factors, lifetime developmental experiences, and current living conditions affect dogs' communicative skills (Miklósi et al. 2003, 2005; Marshall-Pescini et al. 2009; Barrera et al. 2011; Gaunet and Deputte 2011; Passalacqua et al. 2011, 2013); and how complex the mechanisms underpinning dogs' human-directed communication may be (Bentosela et al. 2008, 2009; Elgier et al. 2009a, b). Concerning the latter, specific attention has been given to the issue of whether dogs' communication towards humans might be considered referential (i.e. about an event, an agent, or a place) and intentional (i.e. in line with the social or spatial context) (Miklósi et al. 2000; Gaunet and Deputte 2011; Marshall-Pescini et al. 2013).

5.3.1 *Looking Behaviour: Is it Part of a Referential Communicative Act?*

During communication, *looking at others* and *alternating gaze* between an observer (whether conspecific or not) and a specific target are considered ways to initiate communication by attracting and directing the audience's attention towards a specific object or location (Gómez 1990, 1996). There is agreement that in apes, gazing and even more so gaze alternation, in combination with oriented vocalizations and different forms of "pointing" behaviours (gestures with whole hand and arm, body orientation, and positioning), represent functionally referential and intentional communicative behaviours (Call and Tomasello 1994; Leavens et al. 1996, 1998, 2004, 2005a, b; Gómez 2007). Similarly, the capacity to adjust gaze and other communicative signals towards the recipient is interpreted as an indication that the subject understands the partner's role and importance in the communication process (Cheney and Seyfarth 1990; Call and Tomasello 1994; Tomasello et al. 1994).

It has been proposed that for a communicative act to be 'referential' and 'intentional' a number of operational criteria should be satisfied (e.g. Leavens et al. 2004, 2005a, b). In particular, there is agreement that the communicating subject

should (1) exhibit gaze alternation between its social partner(s) and distant or inaccessible objects; (2) engage in behaviours clearly aimed at obtaining the partner's attention (e.g. vocalisations, body movements); (3) exhibit communicative signals only if in the presence of an audience; (4) adapt communicative behaviours to the attentional state of the audience; (5) show persistence in, and (6) elaboration of, communicative behaviour when the partner is not attending or responding.

So far, the above-mentioned criteria have been established in human infants (Tomasello 2008) and in apes (Leavens et al. 2004, 2005a, b; Cartmill and Byrne 2007, 2010; Roberts et al. 2013), but, as outlined below, a number of recent studies suggest that at least some of these may also be fulfilled in dogs' communicative interactions with humans.

Most evidence relative to human-directed looking behaviour and gaze alternation has been reported in two different situations: when dogs are unable to obtain a reward located in an out-of-reach position (e.g. Hare et al. 1998; Miklósi et al. 2000; Gaunet 2008, 2010; Gaunet and Deputte 2011), and when they are presented with a difficult or unsolvable problem (e.g. Miklósi et al. 2003; Marshall-Pescini et al. 2009, 2013; Passalacqua et al. 2011, 2013).

For instance, Miklósi et al. (2000) addressed the issue of whether and how dogs use gaze and gaze alternation to communicate. They grouped dogs' indicative behaviours (e.g. looking at an external referent, gaze alternation, jumping, running back and forth, etc.) and introduced the term "showing behaviour" as a communicative act with a directional component related to an external target and an attention-getting component aimed at attracting the social partner's attention. The authors tested dogs in three different conditions in which the presence of the human and/or the hidden object was manipulated to assess under what conditions 'showing' behaviour emerged and to differentiate between motivational and referential components of dogs' signals (Marler et al. 1992). It emerged that when both the food and a naive owner were present, 'looking' behaviour towards the owner and the location of food were more frequent, and gaze alternation between them emerged. Vocalisations were also observed to be an integral part of gazing behaviour, since they were always associated with gazing (at the owner or at the location of the hidden food).

Similar results have been recently reported by Gaunet and Deputte (2011) who found that besides using gaze and gaze alternation dogs can provide information about the location of a desired object by using the position of their body: namely, by standing in close proximity to it while signalling to the human. Interestingly, this shows that apart from using an individual (human or dog)'s body location as a local enhancement cue (Udell et al. 2008a), dogs may be able to use their own body position and orientation as an intentionally communicative cue. How flexibly dogs can use this behaviour, and in what contexts, remains to be tested.

Another situation in which dogs have been observed to use gaze alternation also accompanied by different attention-getters, is the 'unsolvable task' paradigm, in which an initially accessible apparatus containing food becomes impossible to access (Miklósi et al. 2003; Gaunet 2008; Marshall-Pescini et al. 2009). Taken

together, these studies provide coherent evidence that dogs use gaze and gaze alternation to communicate with their human partners when confronted with a distant or inaccessible object or food source they desire; it also emerges that dogs can combine looking behaviour with other 'indicative' cues, and that these cues can be preceded by apparent attention-getting signals, fulfilling at least the first two criteria for intentional referential communication (Leavens 2005a).

Recently Gaunet (2010) also tested whether dogs would show elaboration and persistence in their communication (criteria 5 and 6). As with other studies, dogs were given the possibility of 'showing' where their favourite toy had been hidden. However, on some occasions the receiver of their communicative act would retrieve and give the dog an unfamiliar and uninteresting object instead of their favourite toy. Hence in the latter case the dogs' communication was unsuccessful, since it did not result in the desired outcome. In this study, dogs exhibited persistence in (although not elaboration of) their "showing" behaviour when their attempts to 'manipulate' the human partner failed (therefore fulfilling criterion 5). To our knowledge this is the only study investigating the possibility of elaboration and persistence of these behaviours in a communicative settings; hence, results can only be considered preliminary.

Significantly more attention has been given to whether dogs can also modulate their communicative behaviours in accordance with the presence or absence of an audience and perhaps more importantly taking into account the audience's attentional state.

5.3.2 *Do Dogs Adjust Gazing (and Showing) in Accordance with Their Human Audience?*

A key issue in social cognition research is the relationship between communication and cognitive skills, and in particular the extent to which communication is influenced by the presence of an audience and varies according to its characteristics (Marler et al. 1986; Cheney and Seyfarth 1990; Evans 1997; Tomasello and Call 1997; see operational criteria 3 and 4, Sect. 5.3.1). In particular, the 'audience effect' provides evidence that an individual has some understanding that others play a role in the communication process, by recognizing for example that: (1) there must be an audience to which the behaviours can be directed; (2) the audience must be attending to the message; and (3) information provided should take into account the state of knowledge of the audience, which may vary according to circumstances (Cheney and Seyfarth 1990; Call and Tomasello 1994; Tomasello et al. 1994).

So far a number of studies have evaluated whether and to what extent dogs' gazing and communicative behaviour is influenced by a human partner's presence, their attentional state, and their state of knowledge (Hare et al. 1998; Miklósi et al. 2000; Gaunet 2010; Topál et al. 2006; Virányi et al. 2006; Gaunet and Deputte 2011; Marshall-Pescini et al. 2013), providing mixed results.

The first study looking at this question (Hare et al. 1998), with only two dogs, showed that these dogs exhibited more communicative acts as regards the location of the hidden food in the presence than in the absence of an audience, but found no evidence that they would adapt their communicative behaviour to the audience's attentional state (i.e. facing the dog, back turned, eyes covered). With a slightly larger sample (n = 10), Miklósi et al. (2000) found that, in a food hiding situation, dogs used gaze and gaze alternation significantly more when in the presence of both a human partner and the hidden food than when left alone in the presence of the food. However, the authors did not test whether dogs could modify their behaviour in accordance with the audience's attentional state.

Gaunet (2010) adopted another approach to investigate the same issue, comparing the communicative behaviour of guide dogs for the blind and pet dogs when tested with their blind or sighted owners in a play session based on a 'fetch' task. The authors suggested that if guide dogs appreciated something of the visual status and abilities of their human partners, they would behave differently from pet dogs and adapt their behaviour in accordance with the visual abilities of their audience (e.g. reducing gazing behaviour to attract attention and increasing the emission of sounds and contacts). They found no group differences in communicative behaviour between guide dogs and pet dogs towards their respective owners, thus concluding that in their experimental setting guide dogs did not show sensitivity to the blind owner's visual attentional state (criterion 4, Sect. 5.3.1). Though this finding is in line with previous ones in showing a very limited sensitivity of guide dogs to their human partner visual status (Gaunet 2008; Ittyerah and Gaunet 2009), a number of explanations are possible (Ittyerah and Gaunet 2009; Gásci et al. 2004) and, among these, the fact that guide dogs are raised and in general continue to be surrounded by sighted people may have affected their performance.

In a later study the same author and colleagues (Gaunet and Deputte 2011) tested pet dogs in a hidden object paradigm, varying the location of the audience by placing barriers in the room in which the object was hidden. Results showed that besides signalling the presence of the out-of-reach object, dogs also adjusted their position so as to adopt the optimal location which allowed them to alternate their gaze between the hidden object and the owner, and insured that the owner would be in a position to direct their gaze to the hidden object. In sum, dogs adjusted their behaviour to the human recipient's point of view.

The possibility that dogs adapt their behaviour according to the state of attention of a human partner was also investigated recently by Marshall-Pescini et al. (2013). In particular, these authors evaluated whether dogs and toddlers adjusted their human-directed gazing behaviour and gaze-alternation depending on the attentional state of the audience using an unsolvable task paradigm and varying, in the crucial unsolvable trial, the attentional stance of the audience (facing versus back turned). Both dogs and toddlers increased their gaze alternation between the apparatus and the caregiver when the task became unsolvable. Both also preferentially directed their gazing behaviour towards the attentive audience, suggesting a basic understanding in both species that, for their

requesting gesture to be effective, the audience needed to be looking towards them and the object of interest.

Only two studies, to our knowledge, have evaluated whether dogs take into account the state of knowledge of the audience (which may vary according to circumstances) when providing information, by testing whether dogs are capable of adapting their behaviour to what their audience knows when looking at humans and exhibiting "showing behaviour" (Topál et al. 2006; Virányi et al. 2006). Both studies used an adapted nonverbal knowledge-attribution paradigm, originally used with nonhuman primates—the "Ignorant–Helper" paradigm (Kaminski et al. 2008)—in which dogs must communicate with a human "helper" to obtain an out-of-reach reward, and the helper's state of knowledge is manipulated. Virányi et al. (2006) presented dogs with conditions in which they had to discriminate between what a person had, or had not, seen being hidden in a specific situation, and compared their performance with that of two-and-one-half-year-old children. Both a toy and a stick (necessary to retrieve the toy) were hidden in various out-of-reach locations in a room; however, depending on the experimental condition, the dog's helper (i.e. the person who retrieved the object for the dog) could witness the hiding of both, none, or only one of the two objects. The question was whether dogs would be sensitive to what the helper had witnessed, and thus adjust their communicative behaviour accordingly (i.e. looking at the location of the toy only when the helper had not witnessed it being baited).

Results showed that infants were capable of discriminating between situations, indicating the appropriate object in accordance with what the helper had or had not witnessed. On the other hand, dogs hardly ever indicated the stick location, preferentially indicating the toy location (Virányi et al. 2006). The dogs' behaviour could be explained by the fact that, despite a pre-training phase, dogs failed to appreciate the functional connection between the stick and the toy, thus considering the former barely relevant in the situation (whereas children would by this age have had multiple experience with tools). Species difference in performance could be also attributed to working memory problems in dogs or to a different 'motivational value' of the two goal objects (stick and toy), with dogs being over-motivated to get the toy.

Interestingly, dogs, like children, signalled the place of the toy more frequently if the helper had been absent during toy-hiding compared to those conditions when she had participated in the hiding: thus, dogs apparently discriminated between when the helper had or had not witnessed the toy being hidden and adapted somewhat to the helper's knowledge state, but there was less sophistication in communication compared to infants. Again, though, as outlined by Virányi et al. (2006), this performance could be explained at different levels, and a number of more parsimonious explanations need to be ruled out before concluding that dogs are able to attribute knowledge and ignorance to their human partners.

Overall, these findings indicate that dogs are sensitive to the presence or absence of an audience when communicating, but provide mixed results on their ability to take into account human attentional states. In particular, more studies are

needed before it can be concluded that dogs are capable (or incapable) of attributing knowledge and ignorance to their human partners.

Taken together, the experimental evidence suggests the existence of some behavioural flexibility in communication between dogs and humans, supporting the idea that gaze alternation and showing behaviour may be considered intentional and referential communicative acts. However, the relative paucity of studies on dogs' ability to adapt to their audience's state of attention and knowledge, and the mixed results emerging from this literature, mandates a note of caution as to the depth of dogs' underlying comprehension of their communicative actions.

5.3.3 What Do Dogs Want When They Look at us?

Given all the studies mentioned above, perhaps the most intriguing outstanding question is what dogs want, or in other words, what dogs might be 'saying' through looking at us? There are number of possible answers to this question, although there has been little systematic research trying to tease them apart.

The simplest explanation is that dogs use 'looking' as a way to obtain attention from their human partners. Indeed, in a questionnaire asking what kind of behaviours dogs used to get their attention, owners reported that 'looking' was one of the more prominent ones (Mills et al. in press). However, the available evidence, based on different experimental procedures, indicates that dogs also engage in active communication with humans and look at them to request their intervention when unable to obtain a desired goal. Interestingly, in these cases, dogs seem to use gaze alternation (and not just direct gazing) to direct humans to the object of their desire, suggesting there is both intentionality and referentiality in the exhibition of this behaviour (see Sect. 5.3.1).

Another important function of looking is that of monitoring one's own environment to gain information prior to making a decision. Studies on free-ranging dogs show that when a pack encounters another pack, a number of individuals will confront the strangers by barking and moving forward, but they will look back often to check the status of their companions (i.e. whether they are following or not), and their decision to engage in a confrontation will be based on their partners' movements as well as the size of the two packs (Bonanni and Cafazzo in press; Bonanni et al. 2011). Thus, monitoring each other's action is likely an important behaviour for pack animals, since it allows behavioural synchronization, which is necessary for cohesive action to occur. Something similar might also occur during dogs' interaction with humans.

Moreover, dogs are in general strongly dependent on their human partners, establishing close bonds with them (Topál et al. 1998; Prato-Previde et al. 2003) and, like infants and hand reared chimpanzees, dogs appear to use their caregivers as a 'secure base' from which to explore the environment (Bard 1991; Palmer and Custance 2008; Gácsi et al. 2013a; see Prato-Previde and Valsecchi in press for a review). It is possible that dogs may especially look at humans to seek information

about external objects or events in a context of *uncertainty*. There is evidence that human infants at around twelve months of age (Mumme et al. 1966; Vaish and Striano 2004; de Rosnay et al. 2006), and in some cases chimpanzees (Itakura 1995; Russell et al. 1997 but see Tomonaga et al. 2004), look at other individuals more when facing unfamiliar situations that are difficult to interpret, and act in accordance with the informer's positive or negative emotional reactions. This process has been dubbed 'social referencing'. Social referencing, as other social learning processes, is considered to be a useful and safe way to learn about the outside world (Feinman 1982; Roberts et al. 2008). In fact, emotional cues not only provide important information about the emotional states of others and the likelihood of their future behaviour, but also about the nature of the environmental events leading to such states.

To investigate the possibility that dogs may look at humans when facing an ambiguous situation, and take into account the informer's emotional cues and behaviour, we borrowed a social referencing paradigm from the infant literature in developing a series of studies (Merola et al. 2012a, b, 2013a). In the first study, adult dogs were tested with their owner delivering either a positive or negative message from a distance and then either approaching or moving away from a potentially scary object (i.e. a noisy fan with ribbons flying around when activated). We found that the majority of dogs looked back to their human partner when confronted with the strange object and chose to move forward or away from it depending on the person's movements, thus mirroring their owner's behaviour. Hence, dogs looked referentially towards their owner and there was evidence that they synchronized their behaviour with him or her (Merola et al. 2012a).

In a subsequent study, we tested dogs with either their owner or a stranger, acting as the informant and delivering either a positive or negative emotional message using only facial and vocal expressions (rather than also approaching or withdrawing from the object). As is the case with human infants, most dogs looked referentially at the human informant regardless of her identity; however, they based their decision on whether to approach the potentially scary object on their owner's, and not the stranger's, emotional message (Merola et al. 2012b). According to a number of authors (e.g. Stenberg 2003; Walden and Geunyoung 2005; Stenberg and Hagekull 2007), looking at a stranger as much as at a familiar caregiver in a social referencing paradigm indicates that looking behaviour under ambiguous conditions cannot be considered just a form of comfort seeking (due to the activation of the attachment system); rather, it indicates a search for information about the specific context. The recognition of the valence of the owners' message is probably based on dogs' daily experience with the owner. This interpretation is supported by another recent study in which dogs showed recognition of positive but not negative emotions, and did so only when the owner, not a stranger, was expressing it (Merola et al. 2013b).

Overall, these social referencing studies suggest that in a context of uncertainty, most dogs look at their owners (but also a stranger) and monitor what humans do before deciding on their own course of action. However, dogs' reduced synchronization to the stranger's emotional cues remains open to interpretation, since it is

unclear whether it is due to their inability to comprehend the stranger's emotional communication or whether the dog's willingness to modify their own behaviour is tied to their relationship with the person. This will be an interesting avenue for future studies.

Finally, at least in principle dogs might engage in communication with humans to provide information. In fact communication can be initiated also with the aim of informing others—providing them with information when they need it (Tomasello 2008). Human infants, unlike chimpanzees, engage in cooperative communication from a very early age, even when doing so has no direct benefit for themselves (Liszkowski et al. 2006, 2008; Bullinger et al. 2011).

The possibility that dogs might use gaze to provide information to humans even without any direct benefit for themselves has been investigated in a study by Kaminski et al. (2011), who tested the occurrence and the flexibility of "showing" behaviour in situations in which the hidden or out-of-reach object was of interest either only to the dog, only to the human, or both. Based on the dog's showing behaviour, the human partner found the target object more frequently in situations where dogs requested their own preferred object than in situations where the information was relevant only to the human. This confirms that dogs can show communicative behaviour, including gazing and gaze alternation, to request access to a toy they themselves desire, but provides no evidence that dogs are capable of informing a human of the location of the object that only the human desires.

The lack of flexibility exhibited by dogs in this study may support the notion that gaze alternation is a behaviour elicited by specific trigger situations as a way to use humans as social tools to obtain a desired goal, and that dogs have learned to do so during their daily interactions with people. However, further research will be necessary to probe the flexibility of dogs' showing behaviour in different contexts, and hence draw conclusions on whether it is in fact exhibited only in a 'requesting' context.

5.3.4 Nature and Nurture in Dogs' 'Looking' Behaviour

It has been suggested that human-directed gazing represents a foundation on which dog–human communication evolved, and that dogs' propensity to look at humans, or to quickly learn to do so, represents a behavioural feature that distinguishes dogs from wolves, emerging during the course of domestication (Miklósi et al. 2003; Kubinyi et al. 2007; Virányi et al. 2008; Gácsi et al. 2009a, b).

On a number of tasks—for example in two-way choice pointing tasks (Virányi et al. 2008; Gácsi et al. 2009a, b), and a task in which animals were reinforced for looking into a person's face—young hand-raised wolf pups were significantly slower to initiate or maintain eye contact with humans compared to similarly-raised dog pups (Gácsi et al. 2005). This difference was maintained also as juveniles (Gácsi et al. 2009a, b). Furthermore, when young hand-reared wolves and dogs were presented with a task which after being accessible became

unsolvable, wolves tended to work independently and tried out different strategies, whereas dogs looked towards their human partner sooner and for longer than wolves (Miklósi et al. 2003).

Recently, Smith and Litchfield (2013) used the same unsolvable task to test dingoes (*Canis dingo*). Dingoes are interesting subjects within the framework of the 'domestication debate', since they arrived in Australia between 3500 and 500 years ago, are thought to have evolved from very early domestic dogs of East Asiatic origin (Savolainen et al. 2002, 2004), and, since their arrival in Australia, have had no further direct selection pressures from indigenous Australians (Smith and Litchfield 2009). Hence, dingoes may be able to tell us something of the effects of domestication without the subsequent 'interference' of direct selection for specific breed characteristics.

In Smith and Litchfield's (2013) study, based on Miklósi et al. operational definition of "looking back", dingoes looked back at the experimenter earlier compared to both dogs and wolves, though they used fleeting glances more similar to those used by wolves than by dogs. However, when applying a restrictive and more context specific definition of "looking back", no evidence of looking back in dingoes emerged. This finding raises important methodological issues on the measurement of "looking back" behaviours but leaves open the question of whether it was the process of domestication or the subsequent systematic process of breed selection that had a stronger effect on the emergence of looking towards humans for information. Indeed a number of studies have shown significant breed differences in gazing behaviour, suggesting that more recent artificial selection has had a fundamental impact on its emergence (Jakovcevic et al. 2010; Passalacqua et al. 2011).

Jakovcevic et al. (2010) compared three breeds of dogs, retrievers, German shepherds and poodles, in the acquisition and extinction of gazing behaviour in a situation in which food was in sight but out of the dogs' reach. They found that, with or without any previous training, retrievers took longer to extinguish the gazing response compared to the other groups.

Passalacqua et al. (2011) used the 'unsolvable task' paradigm to investigate the effect of breed (and also age and experience) on human-directed gazing behaviour in three different breed groups: 'primitive', 'hunting/herding', and 'molossoid' (i.e. mastiff-types). They found no evidence of breed group differences at 2 months, but breed group differences started to emerge at 4.5 months and were clearly evident in adult dogs, with dogs in the hunting/herding group showing significantly more human-directed gazing behaviour than dogs in the other two breed groups.

Taken together these findings suggest that genetic changes occurred during both domestication and artificial selection which have shaped dog's human-directed gazing behaviour, predisposing this species, and certain breeds selected for close work with people in particular, for effective communication with humans. The role of genes in human-directed gazing behaviour is further supported by a study by Hory et al. (2013), providing evidence for an association between owner-directed gazing behaviour in an unsolvable task and polymorphisms in the dog DRD4 gene.

Looking behaviour in dogs and its occurrence are also influenced by ontogenetic factors and environmental and life experiences (Udell and Wynne 2010; Passalacqua et al. 2011) including learning opportunities and training and living conditions (Marshall-Pescini et al. 2009; Bentosela et al. 2008, 2009; Barrera et al. 2011). For example, Passalacqua et al. (2011) found that, independently from breed group, at two months of age only about 50 % of the pups tested in an unsolvable task showed looking behaviour towards humans. This tendency increased with age, as 4.5-month-old pups used gaze more than two-month-old ones, but less than adults, the latter being the fastest at looking back towards humans for longer periods. These findings, like those that have emerged in the "response-to-human-cues" literature (Gácsi et al. 2009b), indicate that exposure to a household environment and to humans may be a crucial factor for this behaviour to emerge.

Perhaps not surprisingly, learning also plays an important role in the looking behaviour of dogs, with a number of studies clearly showing that gazing is shaped by reinforcement contingencies (Bentosela et al. 2008, 2009; Barrera et al. 2011). For example, Bentosela et al. (2008), using a test situation involving food in sight but out of the dogs' reach, showed that gaze duration toward the experimenter's face significantly increased with just three reinforcement trials, and also quickly diminished when it was no longer reinforced ('extinction'). However, there were differences between dogs living in shelters and pet dogs on this task, with shelter dogs showing a shorter gaze duration and a faster extinction process when reinforcement was no longer provided (Barrera et al. 2011). This suggests that apart from reinforcement schedules, different living conditions and life experiences may affect this behaviour.

The latter point emerges also from a study comparing highly trained and untrained dogs on the unsolvable task. Marshall-Pescini et al. (2009) found that agility-trained dogs gazed longer at humans than dogs trained for search-and-rescue, which in turn gazed longer than untrained dogs. Interestingly, dogs trained for search-and-rescue were more prone to vocalize towards the owner when the task became unsolvable. This pattern of results reveals that, although in neither of the two training contexts dogs were specifically trained to look at their owner, the type of experiences that dogs have whilst in the training context affect this behaviour. Indeed, agility and search-and-rescue dogs differ in the amount of physical closeness and independence and in the decision-making processes required to carry out their respective tasks, as nicely reflected in the results.

Finally, a couple of recent studies have shown a relationship between gazing behaviour towards humans and both sociability levels and anxiety in dogs. More sociable dogs are more prone to use gaze to obtain out of reach food (Jakovcevic et al. 2012), whereas dogs with anxiety-related problems exhibit different patterns of human-directed gazing behaviour and gaze alternation compared to non-anxious dogs when faced with an unsolvable task (Passalacqua et al. 2013). These studies provide preliminary evidence that in dogs, just as is reported in humans (e.g. Iizuka 1994; Schneier et al. 2011; Wieser et al. 2009) gazing behaviour may be related

to personality traits. This intriguing aspect could have practical applications but is in need of further testing.

Taken together, these results clearly show that human-directed gazing is the result of a complex combination of genetic and environmental factors. The predisposition for an increased likelihood of gazing was probably inadvertently selected for during the process of domestication, since looking at humans forms the basis of any communicative act. Breed selection, especially in breeds required to perform a close working or cooperative activity with humans, further shaped this behaviour, resulting in noticeable differences between breeds. However, the genetic predisposition is greatly affected by the social environment dogs are exposed to. Exposure to a human household for just a couple of months significantly increases the occurrence of this behaviour (Passalacqua et al. 2011) and experiences such as specific training regimes can also modulate its frequency (Marshall-Pescini et al. 2009). Future studies combining genetic and environmental variables in systematic ways may reveal much of the flexibility of this behaviour.

5.4 Conclusions

In the last 10 years, since Miklósi et al.'s (2003) seminal work "A simple reason for a big difference: wolves do not look back at humans, but dogs do", there has been an explosion of studies focusing on dogs' communicative abilities. In this chapter we reviewed studies focused on dogs' understanding of the human gaze, and how they themselves use gazing to communicate, especially with humans. As regards dogs' understanding of gazing, gathering evidence suggests that this signal, whether exhibited by conspecifics or humans, has no fixed meaning, and can carry different meanings depending on the context and what other cues accompany it. Dogs appear to be able to use human gazing as a referential cue, although there is mixed evidence as regards their ability to follow human gaze into space and around barriers. There is also evidence that dogs can use human eyes as a cue to their attentional state, and in some (but not all) cases use them to perceive another's perspective. There is also some support for the idea that dogs use human gazing as an ostensive cue, i.e. as a signal that a communicative interaction is about to take place.

Considering the multitude of studies using different paradigms and the mostly consistent results emerging from these, what is striking is the flexibility exhibited by dogs in their understanding of the human gaze. Of course, there are still open questions needing further investigation, especially as regards the origin and development of such understanding: for example, to what extent dogs understand and use their conspecifics' gaze? Is the dog's understanding of the human gaze a recent adaptation or can it be found equally in human-raised wolves?

As regards dogs' use of gazing behaviours towards humans, there is growing evidence that dogs use this behaviour as a form of communication, first and

foremost to gain their human partners' attention. However, dogs' use of gaze alternation in a variety of contexts, showing elements of persistence if the desired outcome is not achieved, exhibiting it whilst taking into account the line of sight and in some cases the attentional state of the audience (and possibly their level of knowledge), suggests that this behaviour can be considered both an intentional and referential communicative act. Exactly in what contexts this is more likely to occur and what the underlying motivations for social looking are, awaits further investigation. Most studies converge on the fact that dogs show gaze alternation in a requesting context when they seek to achieve a desired goal. However, dogs also look to their human partners before approaching a potentially scary object and they take into consideration their partner's emotional and behavioural action in deciding how to act. This suggests that looking towards humans may also function as a way to monitor and synchronize their own response to the environment with that of their partner. Yet dogs do not seem to be able to exhibit gaze alternation to help their partner obtain their goal. Whether this is for a lack of understanding of the other's goal or a lack of motivation remains an open question.

Finally, studies comparing identically-raised wolves and dogs, different dog breeds, using both behavioural and genetic methods and analysing the different experiential factors, which may affect human-directed gazing behaviour, suggest that this behaviour is the product of a combination of genetic and environmental factors. Clearly the investigation of these aspects is still relatively limited and future studies simultaneously analysing both will be needed to better understand the interplay between them.

Acknowledgements We are grateful to all the owners and their dogs that participated as volunteers in our studies. A special thanks to Paola Valsecchi, Isabella Merola, Chiara Passalacqua, Lara Tomaleo, Martina Lazzaroni, and Elisa Colombo for their contribution in many of the studies cited above. Thanks to Alexandra Horowitz for inviting us to contribute to this book. Sarah Marshall-Pescini was supported from grants from the University of Milan and funding from the European Research Council under the European Union's Seventh Framework Programme (FP/2007-2013)/ERC Grant Agreement n. [311870]. Last but not least we thank our dogs Laika, Mago and Tika for participating as pilot subjects in planning our studies at the "*Canis sapiens Lab*".

References

Agnetta, B., Hare B., & Tomasello, M. (2000). Cues to food location that domestic dogs (*Canis familiaris*) of different ages do and do not use. *Animal Cognition, 3,* 107–112.

Barrera, G., Mustaca, A., & Bentosela, M. (2011). Communication between domestic dogs and humans: Effects of shelter housing upon the gaze to the human. *Animal Cognition, 14,* 727–734.

Bard, K. (1991). Distribution of attachment classifications in nursery chimpanzees. *American Journal of Primatology*, 24–88.

Bensky M. K., Gosling, S. D., & Sinn, D. L. (2013). The world from a dog's point of view: A review and synthesis of dog cognition research. *Advances in the Study of Behavior, 45,* 209–406.

Bentosela, M., Barrera, G., Jakovcevic, A., Elgier, A. M., & Mustaca, A. E. (2008). Effect of reinforcement, reinforcer omission and extinction on a communicative response in domestic dogs (*Canis familiaris*). *Behavioural Processes, 78*, 464–469.

Bentosela, M., Jakovcevic, A., Elgier, A. M., Mustaca, A. E., & Papini, M. R. (2009). Incentive contrast in domestic dogs (*Canis familiaris*). *Journal of Comparative Psychology, 123*, 125–130.

Bonanni, R., Natoli, E., Cafazzo, S., & Valsecchi, P. (2011). Free-ranging dogs assess the quantity of opponents in intergroup conflicts. *Animal Cognition, 14*, 103–115.

Bonanni, R., & Cafazzo, S. (in press). The social organization of a population of free-ranging dogs in a suburban area of Rome: A reassessment of the effects of domestication on dogs' behaviour. In J. Kaminski & S. Marshall-Pescini (Eds.), *The social dog: Behaviour and cognition*. San Diego, CA: Elsevier.

Boyko, A. R., Boyko, R. H., Boyko, C. M., Parker, H. G., Castelhano, M., Corey, L., et al. (2009). Complex population structure in African village dogs and its implications for inferring dog domestication history. *Proceedings of the National Academy of Sciences USA, 106*(33), 13903–13908.

Bradshaw, J. W. S., & Nott, H. M. R. (1995). Social and communication behaviour of companion dogs. In J. Serpell (Ed.), *The domestic dog: Its evolution, behaviour and interactions with people* (pp. 115–130). Cambridge: Cambridge University Press.

Bräuer, J., Call, J., & Tomasello, M. (2004). Visual perspective taking in dogs (*Canis familiaris*) in the presence of barriers. *Applied Animal Behaviour Science, 88*, 299–317.

Bräuer, J., Call, J., & Tomasello, M. (2005). All Great Ape species follow gaze to distant locations and around barriers. *Journal of Comparative Psychology, 119*, 145–154.

Bräuer, J., Kaminski, J, Riedel, J, Call, J., & Tomasello, M. (2006). Making inferences about the location of hidden food: Social dog-causal ape. *Journal of Comparative Psychology, 120*, 38–47.

Bräuer, J. (in press). What dogs understand about humans. In J. Kaminski & S. Marshall-Pescini (Eds.), *The social dog: Behaviour and cognition*. San Diego, CA: Elsevier.

Brugger, A., Lariviere LA, Mumme DL, & Bushnell E.W. (2007). Doing the right thing: Infants' selection of actions to imitate from observed event sequences. *Child development, 7*, 806–824.

Bugnyar, T., Stowe, M., & Heinrich, B. (2004). Ravens, Corvus corax, follow gaze direction of humans around obstacles. *Proceedings of the Royal Society B, 271*, 1331–1336.

Bullinger, A., Zimmermann, F., Kaminski, J., & Tomasello, M. (2011). Different social motives in the gestural communication of chimpanzees and human children. *Developmental Science, 14*, 58–68.

Buttelmann, D., & Tomasello M (2013) Can domestic dogs (*Canis familiaris*) use referential emotional expressions to locate hidden food? *Animal Cognition, 16*, 137–145.

Call, J. (2001). Chimpanzee social cognition. *TRENDS in Cognitive Sciences, 5*, 388–393.

Call, J., Braüer, J., Kaminski, J., & Tomasello, M. (2003). Domestic dogs (*Canis familiaris*) are sensitive to the attentional state of humans. *Journal of Comparative Psychology, 117*, 257–263.

Call, J., & Tomasello, M. (1994). Production and comprehension of referential pointing by orangutans (Pongo pygmaeus). *Journal of Comparative Psychology, 108*, 307–317.

Call, J., & Tomasello, M. (2005). What chimpanzees know about seeing, revisited: An explanation of the third kind. In N. Eilan, C. Hoerl, T. McCormack & J. Roessler (Eds.), *Joint attention: Communication and other minds* (pp. 45–64). Oxford: Oxford University Press.

Cartmill, E. A., & Byrne, R. W. (2007). Orangutans modify their gestural signaling according to their audience's comprehension. *Current Biology, 17*, 1345–1348.

Cartmill, E. A., & Byrne R. W. (2010). Semantics of primate gestures: Intentional meanings of orangutan gestures. *Animal Cognition, 13*, 793–804.

Cheney, D. L., & Seyfarth, R. M. (1990). *How monkeys see the world*. Chicago: University of Chicago Press.

Cooper, J. J., Ashton, C., Bishop, S., West, R., Mills D. S., & Young R. J. (2003). Celver hounds: Social cognition in the domestic dog (*Canis familiaris*). *Applied Animal Behaviour Science, 81*, 229–244.

Csibra, G., & Gergely, G. (2011). Natural pedagogy as evolutionary adaptation. *Philosophical Transactions of The Royal Society B, 366*, 1149–1157.

Custance, D., & Mayer, J. (2012). Empathetic-like responding by domestic dogs (*Canis familiaris*) to distress in humans: An exploratory study. *Animal Cognition, 15*, 851–859.

de Rosnay, M., Cooper, P. J., Tsigaras, N., & Murray, L. (2006). Transmission of social anxiety from mother to infant: An experimental study using a social referencing paradigm. *Behaviour Research and Therapy, 44*, 1164–1165.

Ding, Z. L., Oskarsson, M., Ardalan, A., Angleby, H., Dahlgren, L. G., Tepeli, C., et al. (2012). Origins of domestic dog in Southern East Asia is supported by analysis of Y-chromosome DNA. *Heredity, 108*, 507–514.

Druzhkova, A. S., Thalmann, O., Trifonov, V. A., Leonard, J. A., Vorobieva, N. V., Ovodov, N. D., et al. (2013). Ancient DNA analysis affirms the canid from Altai as a primitive dog. *PLoS ONE, 8*, 57754.

Elgier, A. M., Jakovcevic, A., Barrera, G., Mustaca, A. E., & Bentosela, M. (2009a). Communication between domestic dogs (*Canis familiaris*) and humans: Dogs are good learners. *Behavioural Processes, 81*, 402–408.

Elgier, A. M., Jakovcevic, A., Mustaca, A. E., & Bentosela, M. (2009b). Learning and owner–stranger effects on interspecific communication in domestic dogs (*Canis familiaris*). *Behavioural Processes, 81*, 44–49.

Elgier, A. M., Jakovcevic, A., Mustaca, A. E., & Bentosela, M. (2012). Pointing following in dogs: Are simple or complex cognitive mechanisms involved? *Animal Cognition*, *15*, 1111–1119.

Emery, N. J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews, 24*, 581–604.

Erdőhegyi, Á., Topál, J., Virányi, Zs., & Miklósi Á. (2007). Dog-logic: Inferential reasoning in a two-way choice task and its restricted use. *Animal Behaviour, 74*, 725–737.

Faragó, T., Pongrácz, P., Miklósi, Á., Huber, L., Virányi, Z., & Range, F. (2010). Dogs' expectation about signalers' body size by virtue of their growls. *PLoS ONE, 5*, e15175.

Feinman, S. (1982). Social referencing in infancy. *Merrill-Palmer Quarterly, 28*, 445–470.

Ferrari, P. F., Paukner, A., Ionica, C., & Suomi, S. J. (2009). Reciprocal face-to-face communication between rhesus macaque mothers and their newborn infants. *Current Biology, 19*, 1768–1772.

Fox, M. W. (1971). *Behaviour of wolves, dogs and related canids*. London: Jonathan Cape.

Evans, C. S. (1997). Referential signals. In D. Owings, M. Beecher & N. Thompson (Eds.), *Perspectives in ethology* (pp. 99–143). New York: Plenum.

Gásci, M., Miklósi, A., Varga, O., Topál, J., & Csányi, V. (2004). Are readers of our face readers of our minds? Dogs (*Canis familiaris*) show situation-dependent recognition of human's attention. *Animal Cognition, 7*, 144–153.

Gácsi, M., Gyori, B., Miklósi, Á., Virányi, Z., & Kubinyi, E. (2005). Species-Specific Differences and Similarities in the Behavior of Hand-Raised Dog and Wolf Pups in Social Situations with Humans. *Developmental Psychobiology, 47*, 111–122.

Gácsi, M., Györi, B., Virányi, Z., Kubinyi, E., Range, F., Belényi, B., & Miklósi, Á. (2009a). Explaining dog wolf differences in utilizing human pointing gestures: Selection for synergistic shifts in the development of some social skills. *PLoS ONE*, *4*(8), e6584.

Gácsi, M., Kara, E., Belenyi, B., Topál, J., & Miklósi, Á. (2009b). The effect of development and individual differences in pointing comprehension of dogs. *Animal Cognition, 12*, 471–479.

Gácsi, M., Vas, J., Topál, J., & Miklósi, Á. (2013a) Wolves do not join the dance: Sophisticated aggression control by adjusting to human social signals in dogs. *Applied Animal Behaviour Science, 145*, 109–122.

Gácsi, M., Maros, K., Sernkvist, S., Farago, T., & Miklósi, Á. (2013b). Human analogue safe haven effect of the owner: Behavioural and heart rate response to stressful social stimuli in dogs. *PLoS ONE, 8*, e58475.

Gaunet, F. (2008). How do guide dogs of blind owners and pet dogs of sighted owners (*Canis familiaris*) ask their owners for food? *Animal Cognition, 11*, 475–83.

Gaunet, F. (2010). How do guide dogs and pet dogs (*Canis familiaris*) ask their owners for their toy and for playing? *Animal Cognition, 13*, 311–323.

Gaunet, F., & Deputte, B. L. (2011). Functionally referential and intentional communication in the domestic dog: Effects of spatial and social contexts. *Animal Cognition, 14*, 849–860.

Gómez, J. C. (1990). The emergence of intentional communication as a problem-solving strategy in the gorilla. In S. Parker & K. Gibson (Eds.), *"Language" and intelligence in monkeys and apes: Comparative developmental perspectives* (pp. 333–355), Cambridge: Cambridge University Press.

Gómez, J. G. (1996). Non-human primate theories of (non-human primate) minds: Some issues concerning the origins of mindreading. In P. Carruthers & P. K. Smith (Eds.), *Theories of theories of mind* (pp. 330–343). Cambridge: Cambridge University Press.

Gómez, J. G. (2007). Pointing Behaviors in Apes and Human Infants: A Balanced Interpretation. *Child Development, 78*, 729–734.

Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science, 298*, 1634–1636.

Hare, B., Call, J., & Tomasello, M. (1998). Communication of food location between human and dog. *Evolution of Communication, 2*, 137–159.

Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences, 9*, 439–444.

Hare, B., Rosati, A., Kaminski, J., Brauer, J., Call, J., & Tomasello, M. (2010). The domestication hypothesis for dogs' skills with human communication: A response to Udell et al., 2008 and Wynne et al., 2008. *Animal Behaviour, 79*, e1–e6.

Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour, 83*, 573–585.

Hernádi, A., Kis, A., Turcsán, B., & Topál, J. (2012). Man's Underground Best Friend: Domestic Ferrets, Unlike the Wild Forms, Show Evidence of Dog-Like Social-Cognitive Skills. *PLoS ONE, 7*, e43267.

Horowitz, A. (2009). Attention to attention in domestic dog (*Canis Familiaris*) dyadic play. *Animal Cognition, 12*, 107–118.

Horowitz, A., Hecht, J., & Dedrick, A. (2013). Smelling more or less: Investigating the olfactory experience of the domestic dog. *Learning and Motivation, 44*, 207–217.

Hory, Y., Kishi H., Murayama, M. I., Inoue, M., & Fujita, K. (2013). Dopamine receptor D4 gene (DRD4) is associated with gazing toward humans in domestic dogs (*Canis familiaris*). *Open Journal of Animal Sciences, 3*, 54–58.

Huber, L., Racca, A., Scaf, B., Virányi, Z., & Range, F.(2013). Discrimination of familiar human faces in dogs. *Learning and Motivation, 44*, 258–269.

Jakovcevic, A., Elgier, A. M., Mustaca, A. E., & Bentosela, M. (2010). Breed differences in dogs' (*Canis familiaris*) gaze to the human face. *Behavioural Processes, 84*, 602–607.

Jakovcevic, A., Mustaca, A., & Bentosela, M. (2012). Do more sociable dogs gaze longer to the human face than less sociable ones? *Behavioural Processes, 90*, 217–222.

Kaminski, J., Call, J., & Tomasello, M. (2004). Body orientation and face orientation: Two factors controlling apes' begging behavior from humans. *Animal Cognition, 7*, 216–223.

Kaminski, J., Call, J., & Tomasello, M. (2008) Chimpanzees know what others know, but not what they believe. *Cognition, 109*, 224–234.

Kaminski, J., Bräuer, J., Call J., & Tomasello, M. (2009). Domestic dogs are sensitive to a human's perspective. *Behaviour, 146*, 979–988.

Kaminski, J., Neumann M., Bräuer, J., Call J., & Tomasello, M. (2011). Domestic dogs communicate to request and not to inform. *Animal Behaviour, 82*, 651–658.

Kaminski, J., Pitsch, A., & Tomasello, M. (2013). Dogs steal in the dark. *Animal Cognition, 16*, 385–394.

Kaminski, J., & Nitzschner, M. (2013). Do dogs get the point? A review of dog–human communication ability. *Learning and Motivation, 44*, 294–302.

Kaminski, J., Schulz L., & Tomasello, M. (2012). How dogs know when communication is intended for them. *Developmental Science, 15*, 222–232.

Kis, A., Topál, J., Gácsi, M., Range, F., Huber, L., Miklósi, Á., & Virányi, Z. (2012). Does the A-not-B error in adult pet dogs indicate sensitivity to human communication? *Animal Cognition, 15*, 737–743.

Kubinyi, E., Pongrácz, P., & Miklósi, Á. (2009). Dog as a model for studying conspecific and heterospecific social learning. *Journal of Veterinary Behavior: Clinical Applications and Research, 4*, 31–41.

Kubinyi, E., Virányi, Z., & Miklósi, Á., (2007). Comparative social cognition: From wolf to dog to humans. *Comparative Cognition and Behavior Reviews, 2*, 26–46.

Kupán, K., Miklósi, Á., Gergely, G., & Topál, J. (2011). Why do dogs (Canis familiaris) select the empty container in an observational learning task? *Animal Cognition, 14*, 259–268.

Iizuka, Y. (1994). Gaze during speaking as related to shyness. *Perceptual and Motor Skills, 78*, 1259–1264.

Itakura, S. (1995). Snakes as agents of evolutionary change in primate brains. *Journal of Human Evolution, 51*, 44–48.

Ittyerah, M., & Gaunet, F. (2009). The response of guide dogs and pet dogs (*Canis Familiaris*) to cues of human referential communication. *Animal Cognition, 12*, 257–265.

Larson, G., et al. (2012). Rethinking dog domestication by integrating genetics, archeology, and biogeography. *Proceedings of the National Academy of Sciences USA*, *109*(23), 8878–8883.

Leavens, D. A., Hopkins, W. D., & Bard, K. A. (1996). Indexical and referential pointing in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psycholology, 110*, 346–353.

Leavens, D. A., & Hopkins, W. D. (1998.) Intentional communication by chimpanzees (*Pan troglodytes*): A cross-sectional study of the use of referential gestures. *Developmental Psychology, 34*, 813–822.

Leavens, D. A., Hopkins, W. D., & Thomas, R. (2004). Referential communication by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psycholology*, *118*, 48–57.

Leavens, D. A., Hopkins, W. D., & Bard, K. A. (2005a) Understanding the point of chimpanzee pointing: Epigenesis and ecological validity. *Current Directions in Psychological Science, 14*, 185–189.

Leavens, D. A., Russell, J. L., & Hopkins, W. D. (2005b) Intentionality as measured in the persistence and elaboration of communication by chimpanzees (*Pan troglodytes*). *Child Development, 76*, 291–306.

Line, S., Voith, V. L. (1986). Dominance aggression of dogs towards people: Behavior profile and response to treatment. *Applied Animal Behaviour Science, 16*, 77–83.

Liszkowski, U., Carpenter, M., Striano, T., & Tomasello, M. (2006). 12- and 18-month-olds point to provide information for others. *Journal of Cognition and Development, 7*, 173–187.

Liszkowski, U., Carpenter, M., & Tomasello, M. (2008). Twelve-month-olds communicate helpfully and appropriately for knowledgeable and ignorant partners. *Cognition, 108*, 732–739.

Lyons, D. E., Young, A. G., & Keil, F. C. (2007). The hidden structure of overimitation. *PNAS, 104*(19), 1158–1167.

Lyons, D. E., Damrosch, D. H., Lin, J. K., Macris, D. M., & Keil F. C. (2011). The scope and limits of overimitation in the transmission of artifact culture. *Philosophical Transactions of the Royal Society B, 366*, 1158–1167.

Marler, P., Dufty, A., & Pickert, R. (1986). Vocal communication in the domestic chicken: II. Is a sender sensitive to the presence and nature of a receiver? *Animal Behaviour, 34*, 194–198.

Marler, P., Evans, C.H., & Hauser, M. (1992). Animal signals: Motivational, referenial or both? In H. Papousek, U. Jürgens & M. Papousek (Eds.), *Nonverbal vocal communication:*

Comparative and developmental approaches (pp. 66–86). Cambridge: Cambridge University Press.

Marshall-Pescini, S., Passalacqua, C., Barnard, S., Valsecchi, P., & Prato-Previde, E. (2009) Agility and search and rescue training differently affects pet dogs' behaviour in socio-cognitive tasks. *Behavioural Processes, 81*, 416–422.

Marshall-Pescini, S., Passalacqua, C., Valsecchi, P., & Prato-Previde, E. (2010). Comment on "Differential sensitivity to human communication in dogs, wolves and human infants." *Science, 329*, 142-c.

Marshall-Pescini, S., Prato-Previde, E., & Valsecchi, P. (2011). Are dogs (Canis familiaris) misled more by their owners than by strangers in a food choice task? *Animal Cognition, 14*, 137–142.

Marshall-Pescini, S., Passalacqua, C., Miletto Petrazzini, M. E., Valsecchi, P., & Prato-Previde, E. (2012). Do dogs (*Canis lupus familiaris*) make counterproductive choices because they are sensitive to human ostensive cues? *PLoS ONE, 7*, e35437.

Marshall-Pescini, S., Colombo, E., Passalacqua, C., Merola, I., & Prato Previde, E. (2013) Gaze alternation in dogs and toddlers in an unsolvable task: Evidence of an audience effect. *Animal Cognition, 16*, 933–943.

McConnell, P., & Baylis, J. (1985). Interspecific communication in cooperative herding. Acoustic and visual signals from human shepherds and herding dogs. *Z. Tierpsychol*, *67*, 302–328.

Merola, I., Prato-Previde, E., & Marshall-Pescini, S. (2012a). Social referencing in dog-owner dyads? *Animal Cognition, 15*, 175–185.

Merola, I., Prato-Previde, E., & Marshall-Pescini, S. (2012b). Dogs' social referencing towards owners and strangers. *PLoS ONE, 7*, e47653.

Merola, I., Marshall-Pescini, S., D'Aniello, B., & Prato-Previde, E. (2013a). Social referencing: Water rescue trained dogs are less affected than pet dogs by the stranger's message. *Applied Animal Behaviour Science, 147*, 132–138.

Merola, I., Prato-Previde, E., Lazzaroni, M., & Marshall-Pescini, S. (2013b). Dogs' comprehension of referential emotional expressions: Familiar people and familiar emotions are easier. *Animal Cognition, 16*(6), 1–13.

Miklósi, Á. (2007). Dog behaviour, evolution, and cognition. Oxford: Oxford University Press.

Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003). A simple reason for a big difference: Wolves do not look back at humans, but dogs do. *Current Biology, 13*, 763–766.

Miklósi, Á., Polgárdi, Topál, J., & Csányi, V. (2000). Intentional behaviour in dog-human communication: An experimental analysis of "showing" behaviour in the dog. *Animal Cognition, 3*, 159–166.

Miklósi, Á., Pongrácz P., Lakatos G., Topál J., & Csányi, V. (2005). A comparative study of the use of visual communicative signals in interaction between dogs (*Canis familiaris*) and humans and cats (*Felis catus*) and humans. *Journal of Comparative Psychology, 119*, 179–186.

Miklósi, Á., & Topál, J. (in press). What does it take to become 'best friends'? Evolutionary change in canine social competence. *Trends in Cognitive Science*.

Miklósi, Á., Topál, J., & Csányi, V. (2004). Comparative social cognition: What can dogs teach us? *Animal Behaviour, 67*, 995–1004.

Mills, D., van der Zee, E., & Zulch, H. (in press) When the bond goes wrong: Problem behaviours in the social context. In J. Kaminski & S. Marshall-Pescini (Eds.), *The social dog: Behaviour and cognition*. San Diego, CA: Elsevier.

Mitchell, R. W., & Thompson, N. S. (1993). Familiarity and the rarity of deception: Two theories and their relevance to play between dogs (*Canis familiaris*) and humans (*Homo sapiens*). *Journal of Comparative Psychology, 7*, 291–300.

Mumme, D. L., Fernald, A., & Herrera, C. (1966). Infants' responses to facial and vocal emotional signals in a social referencing paradigm. *Child Development, 67*, 3219–3237.

Nagasawa, M., Murai, K., Mogi, K., & Kikusui, T. (2011). Dogs can discriminate smiling faces from blank expression. *Animal Cognition, 14*, 525–533.

Nielsen, M. (2006). Copying actions and copying outcomes: Social learning through the second year. *Developmental Psychology, 42*, 555–565.

Palmer, R., & Custance, D. (2008). A counterbalanced version of Ainsworth's Strange Situation Procedure reveals secure-base effects in dog–human relationships. *Applied Animal Behaviour Science, 109*, 306–319.

Pang, J., et al. (2009). mtDNA Data indicate a single origin for dogs south of Yangtze River, less than 16,300 years ago, from numerous wolves. *Molecular Biological Evolution, 26*, 2849–2864.

Passalacqua, C., Marshall-Pescini, S., Barnard, S., Lakatos, G., Valsecchi, P., & Prato-Previde, E. (2011). Human-directed gazing behaviour in puppies and adult dogs, Canis lupus familiaris. *Animal Behaviour, 82*, 1043–1050.

Passalacqua, C., Marshall-Pescini, S., Merola I., Palestrini C., & Prato-Previde, E. (2013). Different problem-solving strategies in dogs diagnosed with anxiety-related disorders and control dogs in an unsolvabletask paradigm. *Applied Animal Behaviour Science, 147*, 139–148.

Pongrácz, P., Miklósi, Á., Kubinyi, E., Topál, J., & Csányi, V. (2003). Interaction between individual experience and social learning in dogs. *Animal Behaviour, 65*, 595–603.

Pongrácz, P., Miklósi, A., Timár-Geng, K., & Csányi, V. (2004). Verbal attention getting as a key factor in social learning between dog (*Canis familiaris*) and human. *Journal of Comparative Psychology, 118*, 375–383.

Povinelli, D. J., & Eddy, T. J. (1996). What young chimpanzees know about seeing. *Monographs of the Society for Research in Child Development, 61*, 1–152.

Prato-Previde, E., Custance D. M., Spiezio, C., & Sabatini, F. (2003). Is the dog-human relationship an attachment bond? An observational study using Ainsworth's Strange Situation. *Behaviour, 140*, 225–254.

Prato-Previde, E., Marshall-Pescini, S., & Valsecchi, P. (2008). Is your choice my choice? The owners' effect on pet dogs' (Canis familiaris) performance in a food choice task. *Animal Cognition, 11*, 167–174.

Prato-Previde, E., & Valsecchi, P. (in press) The immaterial cord: The dog human attachment bond. In J. Kaminski & S. Marshall-Pescini (Eds.), *The social dog: Behaviour and cognition*. San Diego, CA: Elsevier.

Range, F., Viranyi, Z., & Huber, L. (2007). Selective imitation in domestic dogs. *Current Biology, 17*, 868–872.

Range, F., & Virányi, Z. (2011). Development of gaze following abilities in wolves (*Canis lupus*). *PLoS ONE, 6*, e16888.

Range, F., Huber, L., & Heyes, C. (2011). Automatic imitation in dogs. *Proceedings of the Royal Society B: Biological Sciences, 278*, 211–217.

Reid, P. J. (2009). Adapting to the human world: Dogs responsiveness to our social cues. *Behavioural Processes, 80*, 325–333.

Riemer, S., Müller, C., Virányi, Z., Huber, L., & Range, F. (in press). Choice of conflict resolution strategy is linked to sociability in dog puppies. *Applied Animal Behaviour Science.*

Roberts, S. G., McComb, K., & Ruffman, T. (2008). An experimental investigation of referential looking in free-ranging Barbary macaques (*Macaca sylvanus*). *Journal of Comparative Psychology, 122*, 94–99.

Roberts, A. I., Vick, S. J., & Buchanan-Smith H. M. (2013). Communicative intentions in wild chimpanzees: Persistence and elaboration in gestural signalling. *Animal Cognition, 16*, 187–196.

Rossi, A. P., & Ades, C. (2008). A dog at the keyboard: Using arbitrary signs to communicate requests. *Animal Cognition, 11*, 329–338.

Russell, C. L., Bard, K. A., & Adamson, L. B. (1997). Social referencing by young chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 111*, 185–193.

Savolainen, P., Zhang, Y., Luo, J., Lundeberg, J., & Leitner, T. (2002). Genetic evidence for an east Asian origin of domestic dogs. *Science, 298*, 1610–1613.

Savolainen, P., Leitner, T., Wilton, A., Matisoo-Smith, E., & Lundeberg, J. (2004). A detailed picture of the origin of the Australian dingo, obtained from the study of mitochondrial DNA. *Proceedings of the National Academy of Sciences USA, 101*, 12387–12390.

Schenkel, R. (1967). Submission: Its features and function in the wolf and dog. *American Zoologist, 7*, 319–329.

Schloegl, C., Schmidt, J., Scheid, C., Kotrschal, K., & Bugnyar, T. (2008). Gaze following in non-human animals: The corvid example. In F. Columbus (Ed.), *Animal behaviour: New research* (pp. 73–92). New York: Nova Science Publishers.

Schwab, C., & Huber, L. (2006). Obey or not obey? Dogs (*Canis familiaris*) behave differently in response to attentional states of their owners. *Journal of Comparative Psychology, 120*, 169–175.

Scott, J. P., & Fuller, J. L. (1965). Genetics and the social behavior of the dog. Chicago: University of Chicago Press.

Simpson, E. A., Paukner, A., Suomi, S. J., & Ferrari, P. F. (in press). Visual attention during neonatal imitation in newborn macaque monkeys. *Developmental Psychobiology*.

Schneier, F. R., Rodebaugh, T. L., Blanco, C., Lewin, H., & Liebowitz, M. R. (2011). Fear and avoidance of eye contact in social anxiety disorder. *Comprehensive Psychiatry, 52*, 81–87.

Smith, B. P., & Litchfield, C. A. (2013). Looking back at 'looking back': Operazionalizing referential gaze for dingoes in an unsolvable task. *Animal Cognition, 16*, 961–971.

Soproni, K., Miklósi, A., Topál, J., & Csányi, V. (2002). Dogs' (*Canis familiaris*) responsiveness to human pointing gestures. *Journal of Comparative Psychology, 116*, 27–34.

Southgate, V., Chevallier, C., & Csibra, G. (2009). Sensitivity to communicative relevance tells young children what to imitate. *Developmental Science, 12*,1013–1019.

Smith, B., & Litchfield, C. (2009) Review of the relationship between Indig- enous Australians, dingoes (Canis *dingo),* and domestic dogs (Canis *familiaris). Anthrozoös, 22*, 111–128.

Smuts, B. (in press) Social behavior among companion dogs with an emphasis on play. In J. Kaminski & S. Marshall-Pescini (Eds.), *The social dog: Behaviour and cognition*. San Diego, CA: Elsevier.

Sümegi, Z., Kis, A., Miklósi, Á., & Topál, J. (in press). Why do adult dogs (*Canis familiaris*) commit the A-not-B search error? *Journal of Comparative Psychology*.

Szetei, V., Miklósi, Á., Topál, J., & Csányi, V. (2003). When dogs seem to lose their nose: An investigation on the use of visual and olfactory cues in communicative context between dog and owner. *Applied Animal Behaviour Science, 83*, 141–152.

Stenberg, G. (2003). Effects of maternal inattentiveness on infant social referencing. *Infant Child Development, 12*, 339–41.

Stenberg, G., & Hagekull, B. (2007). Infant looking behavior in ambiguous situation: Social referencing or attachment behavior? *Infancy, 11*, 111–129.

Teglas, E., Gergely, A., Kupan, K., Miklósi, Á., & Topál, J. (2012). Dogs' gaze following is tuned to human communicative signals. *Current Biology, 22*, 209–212.

Tennie, C., Glabsch, E., Tempelmann, S., Bräuer, J., Kaminski, J., & Call, J. (2009). Dogs, *Canis familiaris*, fail to copy intransitive actions in third-party contextual imitation tasks. *Animal Behaviour, 77*, 1491–1499.

Tomasello, M. (2008). *Origins of human communication*. Cambridge, Massachusetts: MIT Press.

Tomasello, M., & Call, J. (1997). *Primate cognition*. New York: Oxford University Press

Tomasello, M., Call, J., Nagell, K., Olguin, R., & Carpenter, M. (1994). The learning and use of gestural signals by young chimpanzees: A trans-generational study. *Primates, 35*, 137–154.

Tomasello, M., Hare, B., & Agnetta, B. (1999). Chimpanzees, *Pan troglodytes*, follow gaze direction geometrically. *Animal Behaviour, 58*, 769–777.

Tomonaga, M., Tanaka, M., Matsuzawa, T., Myowa-Yamakoshi, M., Kosugi, D., & Mizuno, Y., et al. (2004). Development of social cognition in infant chimpanzees (Pan troglodytes): Face recognition, smiling, gaze and the lack of triadic interactions. *Japanese Psychological Research, 46*, 227–235.

Topál, J., Erdohegyi, Á., Mányik, R., & Miklósi, Á. (2006). Mindreading in a dog: An adaptation of a primate "mental attribution" study. *International Journal of Psychology and Psychological Therapy, 6*, 365–379.

Topál, J, Gergely, G, Miklósi Á, Erdohegyi, Á., & Csibra, G. (2008). Infants' perseverative search errors are induced by pragmatic misinterpretation. *Science, 321*, 1831–1834.

Topál, J., Gergely, G., Erdohegy, Á., Csibra G., & Miklósi, Á. (2009a). Differential sensitivity to human communication in dogs, wolves and human infants. *Science, 325*, 1269–1272.

Topál, J., Miklósi, Á., Csanyi, V., & Doka, A. (1998). Attachment behavior in dogs (Canis familiaris): A new application of Ainsworth's (1969) strange situation test. *Journal of Comparative Psychology, 112*, 219–229.

Topál, J., Miklósi, Á., Gácsi, M., Dóka, A., Pongrácz, P., & Kubinyi, E., et al. (2009). The dog as a model for understanding human social behavior. *Advances in the Study of Behavior, 39*, 71–116.

Topál, J., Miklósi, Á., Sumegi, Z., & Kis, A. (2010). Response to comments on ''differential sensitivity to human communication in dogs, wolves and human infants.'' *Science, 329*, 142-d.

Topál, J., Kis, A., & Katalin˙ O. (in press). Dogs' sensitivity to human ostensive cues: A unique adaptation? In J. Kaminski & S. Marshall-Pescini (Eds.), *The social dog: Behaviour and cognition*. San Diego, CA: Elsevier.

Triesch, J., Jasso, H., & Deák, G. O. (2007). Emergence of mirror neurons in a model of gaze following. *Adaptive Behavior, 15*(2), 149–165.

Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2010). What did domestication do to dogs? A new account of dogs' sensitivity to human actions. *Biological Reviews, 85*, 327–345.

Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2011). Can your dog read your mind? Understanding the causes of canine perspective taking. *Learning and Behavior, 39*, 289–302.

Udell, M. A. R., Giglio, R. F., & Wynne, C. D. L. (2008a). Domestic dogs (Canis familiaris) use human gestures but not nonhuman tokens to find hidden food. *Journal of Comparative Psychology, 122*, 84–93.

Udell, M. A. R., & Wynne, C. D. L. (2008b). A review of domestic dogs' (Canis familiaris) human-like behaviors: Or why behavior analysts should stop worrying and love their dogs. *Journal of the Experimental Analysis of Behavior, 89*, 247–261.

Udell, M. A. R., & Wynne, C. D. L. (2010). Ontogeny and phylogeny: Both are essential to human-sensitive behaviour in the genus Canis. *Animal Behaviour, 79*, e9–e14.

Vaish, A., & Striano, T. (2004). Is visual reference necessary? Contributions of facial versus vocal cues in 12-month-olds' social referencing behavior. *Developmental Science, 7*, 261–269.

Vas, J., Topál, J., Gácsi, M., Miklósi, A., & Csányi, V. (2005). A friend or an enemy? Dogs' reaction to an unfamiliar person showing cues of threat and friendliness at different times. *Applied Animal Behaviour Science, 94*, 99–115.

Vas, J., Topál, J., Gyori, B., & Miklósi, A. (2008). Consistency of dogs' reactions to threatening cues of an unfamiliar person *Applied Animal Behaviour Science, 112*(3–4), 331–344.

Vilà, C., Savolainen, P., Maldonado, J. E., Amorin, I. R., Rice, J. E., & Honeycutt, R. L., et al. (1997). Multiple and ancient oigins of the domestic dog. *Science, 276*, 1687–1689.

Virányi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy, D., & Miklósi, Á. (2008). Comprehension of human pointing gestures in young human-reared wolves and dogs. *Animal Cognition, 11*, 373–387.

Virányi, Z., Topál, J., Gácsi, M., Miklósi, A., & Csányi, V. (2004). Dogs respond appropriately to cues of humans' attentional focus. *Behavioural Processes, 31*, 161–172.

Virányi, Z., Topál, J., Gácsi, M., Miklósi, Á., & Csányi, V. (2006). A nonverbal test of knowledge attribution: A comparative study on dogs and children. *Animal Cognition, 9*, 13–26.

Virányi, Z., & Range, F. (2011). Evaluating the logic of perspective-taking experiments. *Learning & Behavior, 39*, 306–309.

Virányi, Z., & Range, F., (in press). On the way to a better understanding of dog domestication: Aggression and cooperativeness in dogs and wolves. In J. Kaminski & S. Marshall-Pescini (Eds.), *The social dog: Behaviour and cognition*. San Diego, CA: Elsevier.

vonHoldt, B. M., et al. (2010). Genome-wide SNP and haplotype analyses reveal a rich history underlying dog domestication. *Nature, 464*, 898–902.

Walden, T. A., & Geunyoung, K. (2005). Infants' social looking toward mother and stranger. *The International Journal of Behavioral Development, 29*, 356–360.

Wang, G., et al. (2013). The genomics of selection in dogs and the parallel evolution between dogs and humans. *Nature Communication*, *4*, 1860.

Warden, C., & Warner, L. (1928). The sensory capacities and intelligence of dogs. *The Quarterly Review of Biology, 3*, 1–28.

Werhahn, G., Barrera, G., Viranyi, Z., & Range, F. (2013). Wolves and dogs follow their conspecifics gaze into distant space. In *Proceedings of the 3rd ToK Conference of Comparative Cognition*, Vienna, Austria, 3–5 July 2013.

Wieser, M. J., Pauli, P., Alpers, G. W., & Mühlberger, A. (2009). Is eye to eye contact really threatening and avoided in social anxiety?–an eye-tracking and psychophysiology study. *Journal of Anxiety Disorders, 23*, 93–103.

Wynne, C. D. L., Udell, M. A. R., & Lord, K. A. (2008). Ontogeny's impacts on human dog communication. *Animal Behaviour, 76*, 1–4.