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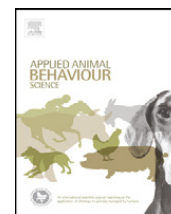
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Friend or foe: Context dependent sensitivity to human behaviour in dogs

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ABSTRACT

During the course of domestication dogs (*Canis familiaris*) have inhabited a social field characterized by inter-specific interactions with humans. The mutually advantageous social contact between dogs and humans is facilitated by effective mechanisms that negotiate ongoing interactions and avoid the escalation of conflicts.

We investigated the reaction of 37 family dogs towards the approaching owner and experimenter who communicated either threat or friendliness both in playful and non-playful situations. Dogs' behavioural responses were in accordance with the conflicting (threatening) and non-conflicting (friendly) manner of the approaching humans both in the non-playful and the playful situations. The familiarity of the interacting human partner (owner or experimenter) affected the behaviour of dogs only in the non-playful situations, where contact-seeking was less typical and gaze-averting tendencies were more pronounced towards the experimenter. The threatening approach elicited tolerant/contact-seeking reactions towards the owner in both situations and also towards the experimenter in the playful situation. But dogs were avoidant/aggressive with the experimenter in the non-playful situation. Play bows were triggered by both human partners' threatening approach, but only in the playful situation. Results suggest that this signal appears when the human partners' behaviour becomes ambiguous in relation to the social context.

We propose that the flexible utilization of various conflict-resolving behaviours depending on the actual partners represent fundamental elements of dogs' social competence. These skills help dogs to manoeuvre efficiently in the course of dog–human interactions in various social contexts.

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1. Introduction

Living in social groups provides obvious benefits to group members. Nevertheless, group-living has also costs because conflicts among group members may occur in many contexts. In stable and individualized groups, members need effective mechanisms to prevent harmful escalation of conflicts (Aureli and de Waal, 2000). Escalation of conflict into potentially harmful aggressive

interaction can occur during serious agonistic interactions when a subject reacts fearfully or aggressively to the threat or physical aggression of a companion (Aureli et al., 2002). Social play provides a context for the escalation of agonistic interactions, because it is characterized by the incorporation of behavioural elements from various interactions such as mating, predation and fighting, which could be misinterpreted by the playing partner (Bekoff, 1995; Bekoff and Allen, 1998).

Play signals are suggested to be play-specific behavioural elements that can be used by participants (and also by human observers) to distinguish playful from non-playful interactions (Fagen, 1981). Communicating the maintenance of ongoing play is particularly important

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when one of the participants performs an ambiguous action (Bekoff, 1995). The highly stereotyped form of the canid play bow and its occurrence before or after certain non-playful actions (e.g. bites) supports its communicational function during intra-specific play in canid species (wolves, coyotes and dogs) (Bekoff, 1977, 1995).

So far research has mainly been focused on the species-specific differences in canid play (e.g. Feddersen-Petersen, 1986, 1991), and developmental changes (Koda, 2001). However, dogs are unique candidates for studying social play also because they engage in social play not only with conspecifics but also with humans throughout their entire life. In two recent papers Rooney and her colleagues have investigated the forms and effects of play signals in inter-specific playful interactions between dogs and humans (Rooney et al., 2001; Rooney and Bradshaw, 2006). They observed that humans utilize various forms of behaviours as play signals in spontaneous playful interactions with their dog. They also tested the effectiveness of some human behaviours in eliciting play behaviour from the dog, and showed that dogs decoded a diverse set of human signals as play invitations. The most effective forms (lunge, human bow) resembled some important features of the dogs' species-typical play signals. These findings are in line with Mitchell and his colleague's earlier study (Mitchell and Thompson, 1991) which pointed out that dogs might have individual preferences for engaging in certain play routines. They observed that dogs were ready to join in compatible play projects with humans and with compatible interactions they could extend and easily initiated mutual play. Most recently, in a study of 68 family dogs, Tóth et al. (2008) found that over time the dogs and their owners developed a routine of games and the dogs did not generalize the observed behaviour routines to other, functionally different situations. They suggested that no direct relationship exists between competitive behaviour in game situations and striving after dominance in non-playful activities, because the human partners' play signals clearly distinguish games from real competitive situations.

It has been assumed that forming stable groups with another species presented new challenges for dogs, and selection during the course of domestication favoured the fine tuning of their ability to read and anticipate the behaviour of humans while interacting with them (Miklósi et al., 2004). Here we investigate the ability of dogs to adjust their behaviour flexibly to different human partners (owner and experimenter) when they communicate friendly or threatening intentions embedded in playful or non-playful situations.

Importantly, it has been reported that dogs show remarkable behavioural flexibility in an inter-specific agonistic situation (Vas et al., 2005, 2008). In these studies the researchers compared the reaction of dogs to an approaching unfamiliar human who sequentially communicated either friendly or threatening intention. They found that dogs were able to switch rapidly between friendly and agonistic motivational states in accordance with the behaviour of the approaching human. The stranger's friendly approach resulted in friendly or passive behaviour responses of the dogs, while a threatening stranger (approaching silently, gazing at the dog) evoked

mainly fear, avoidance or aggression. The main component of the threatening behaviour was direct staring into the dog's eyes. Continuous staring is mainly used in dominance related interactions between canid conspecifics (Schenkel, 1967), but it has also been observed when a human intimidates or aggressively arouses a dog and thus evokes agonistic or active appeasing behaviour (Bradshaw and Nott, 1995; Fox, 1971; Vas et al., 2005). A human's threatening display may present a conflict situation to dogs, that they can best resolve by quickly and flexibly adjusting their responses to the actual changes of their human partner's behaviour.

In our study we applied a modified version of the Vas et al. procedure (2005). The dogs were subjected to a series of interactions with their owner and an experimenter, in playful and non-playful situations, during which they were approached either in a friendly or threatening way by the human partner. Our hypothesis is that the uncertainty about the consequences of a threat can lead to different behavioural strategies in different contexts, and can vary according to the familiarity of the interacting partner. Bekoff and Allen (1998) found that during mutual play activities play-signals are used to maintain playful interactions and prevent misinterpretation of ambiguous situations when out of context actions occur (e.g. threatening during play). Based on their findings we expected that a potentially ambiguous situation evokes play signals only in playful situations, and during conflicts dogs show less tolerating/submissive and more aggressive/avoiding behaviour toward the partners with whom they do not have a close relationship.

2. Methods

2.1. Subjects

All dog owners were volunteer participants; they were recruited from a dog school (Top Mancs, Budapest, Hungary) and from common dog walking areas in Budapest. All dogs were kept as pets, they lived in their owner's flat or garden. Three owners participated with two dogs and one with four dogs; these dogs were assigned to groups with different orders of test situations. Only dogs that could be motivated to play with a rope tug or a wooden stick were selected. Thirty-seven adult family dogs (17 females, 20 males; age range between: 1 and 10 years, mean age: 2.99 years \pm 2.34) participated in the study. The dogs were from 14 different breeds and 15 mongrels (four golden retrievers, three Belgian shepherds, two Cavalier King Charles spaniels, two border collies, two Parson Russell terriers, one boxer, German shepherd, kelpie, Labrador retriever, miniature spitz, pumi, Shetland sheepdog, Staffordshire bull terrier, Welsh terrier). The only selection criterion was that the dogs should not be harmfully aggressive towards the experimenter (BG). As in one of the test situations the unleashed dogs encountered the experimenter (E) in a potentially aggression evoking situation, we had to be sure that our subjects do not have attacking tendencies. Eighteen dogs had former playing experience with E, which suggested that these dogs would not show unexpected aggressive behaviour

Table 1
Episodes of the playful and non-playful situations.

	Playful situation	Non-playful situation
Warm up/starting episode	Dog and human are playing for 1 min	Tethering the dog to a tree and human stands at the start point
First approach	Threatening or friendly	Threatening or friendly
Interval	Playing for half minute	Dog and human return to start point
Second approach	Threatening or friendly	Threatening or friendly
Terminal episode	Playing for 1 min	Human returns to the start point and calls the released dog

during the testing trials. (The possible effect of this difference in the familiarity of E was controlled for during data analyses.) The remaining 19 dogs were pre-tested by another experimenter at least one day before the experiment in order to exclude individuals with high attacking risk. This other experimenter did not participate in the rest of the present study. The pre-test was conducted precisely like the 'threatening approach' test published in Vas et al. (2005). None of the dogs had to be excluded based on the pre-test.

2.2. Procedure

The tests took place at visually separated outdoor locations that were familiar to the dogs. Only the owner, E and a cameraman were present. The cameraman stood 6–7 m from the dog. E was the same woman (B. Gy.) for each dog.

Our testing design was factorial with three dimensions: two situations (playful or non-playful), two partners (owner or E) and two types of approaches (friendly and threatening). All dogs were observed in four test conditions (situation \times partner) and the two different kinds of controlled human approaches (threatening and friendly) were embedded in all four situations (see Table 1).

Some parts of our method (the protocol of the controlled approaches and the design of the non-playful situation) were adopted with slight modifications from a published study (Vas et al., 2005).

The four test conditions took place at the same location and were carried out mostly in two sessions. The sessions consisted of a playful situation with one of the partners (owner or E), and a non-playful situation with the other partner. Mean time (\pm SD) between the sessions was 24 days \pm 37 days. The instructions were identical when the owner's and BG's roles were reversed. The order of the situations was randomized across the dogs as was the order in which BG and the owner interacted with the dogs.

2.3. Playful situation

The human partners played with the dog using a rope tug or a wooden stick depending on the preference of the dog (it was important that the dog and the human could grab the play object simultaneously). The human was told not to discipline the dog during the game but try to play in a relaxed way adjusting the interaction to the dog's playing style. It was crucial to involve the dog in mutual play as much as possible with varying different game types (e.g. tug of war, throwing the object and play-chasing). After playing for 1 min the actual human partner performed one of the controlled approaches (friendly or threatening) (see Table 1).

After finishing the approach she/he immediately restarted the play for another half minute and then performed the other type of approach. Finally she/he continued to play again for another minute. At the very beginning of each of the two approaches the dog had to be stationary and the play object had to be in its mouth or right in front of it. Both controlled approaches had to be conducted according to a detailed protocol (see Section 2.5).

2.4. Non-playful situation

The owner was asked to tether the dog to a tree with a 1.5 m long leash and to make the dog orient at the starting point of the controlled approaches in a standing or sitting position.

During the test situation with E, the owner stood quietly and motionless at a predetermined point near to the leashed dog, approximately 0.5 m behind it. E performed the first approach, then returned to the starting point and waited until the owner managed to get the dog to its initial position. Then she performed the other type of approach. Finally E went back to the start point again, sat on her heels, and called the dog on its name. The owner unleashed the dog and E waited until the dog got in physical contact with her, but not longer than for 1 min. The instructions were identical when the owner's and BG's roles were reversed: the owner performed the two approaches while E stood behind the dog. During these two non-playful situations no play objects were in sight of the dog, or in the hand or pocket of any of the human participants.

2.5. Controlled approaches

The two controlled approaches were labelled as friendly and threatening, based on the terminology used by Vas et al. (2005). Both kinds of approaches were conducted following the same protocol in all four test situations (playful with E, playful with owner, non-playful with E, non-playful with owner). Besides presenting the detailed protocol, E demonstrated both types of controlled approaches to the owners before the test. She also trained the owners how to perform the approaches.

At the beginning of each controlled approach the human stood approximately 5 m away from the dog and waited until the dog oriented towards her. This means that in the non-playful situation the human stood still, 5 m from the leashed dog, while in the playful situation she/he stopped playing and dynamically adjusted her starting point according to the actual position of the dog. At the moment when she/he managed to establish eye-contact with the dog she/he started the approach.

The friendly approach was performed at a normal, steady pace, whilst the human was continuously talking to the dog in a friendly voice (e.g. Hi, you're a nice dog!) and looking into its eyes in a relaxed way. During the threatening approach the human moved toward the dog step by step, slowly, and haltingly. She/he bent her/his torso slightly forward, kept her/his hands behind her/his back, stared steadily into the dog's eyes and did not say a word till the end of the approach. During both kinds of approaches the human tried to maintain continuous eye-contact (relaxed or staring) with the subject, her/his walking pace (usual or slow), position of her/his upper body part (straight up or bend forward) and vocal behaviour (friendly talk or mute) were distinctly different.

The termination of each approach was adjusted to the reaction of the dog. If the dog did not show any visible sign of fear or aggression, the human fully approached the dog and tried to stroke its head. If the dog interrupted the eye-contact with the approaching human, she/he paused for about 2 s and then tried to attract the dog's attention by making some noise (coughing or scratching the ground with her/his feet). If the dog looked back, she/he continued the approach; if it did not, she waited for another 2 s and then made some noise again. For keeping the situation only moderately stressful and for safety reasons the approaches were interrupted if the dog showed signs of pronounced fear or aggression. The test was terminated: after the third unsuccessful attempt to make the dog look at the approaching human, if the dog moved 1.5 m away from the approaching human, if the dog barked or growled for more than 4 s or tried to attack the approaching human (this meant that it moved ahead in the direction of the human while continuously barking and/or growling at her), if the dog performed a play bow.

2.6. Data collection and analysis

All test trials were filmed and the recordings were analysed later by one of the authors (B. Gy.). Since the duration of the approaches depended on the dog's reaction, comparisons were made along nominal and ordinal score variables which described the behaviour of the dogs (for definitions, see Tables 2 and 3). A second person coded a randomly selected sample (30%) of all the recordings in order to assess inter-observer agreement for which we calculated Cohen's Kappa coefficients (Martin and Bateson, 1993). We have got high values for all measured variables (play bow: 0.94, variables of non-playful situation: moving off: 0.81, gaze averting: 0.95, vocalization: 1, contact-seeking: 0.96; variables of playful situation: moving off: 0.88, gaze averting: 0.88, vocalization: 0.90, guarding: 0.84).

Variables describing the dogs' behaviours towards the owner vs. E and also their reactions during the friendly vs. threatening approaches were compared using the Wilcoxon matched pair signed rank test. The differences in the dogs' overall behaviour patterns between the playful and non-playful situations and the frequencies of play bow were analysed by the McNemar test. We calculated corrected significance levels adjusted for multiple comparisons using the False Discovery Rate (FDR) method (Benjamini et al., 2001). We represent our data on stacked

Table 2

Behavioural variables coded in the playful situation with both human partners during both kinds of the controlled approaches.

Variable	Description of scores
Play bow	0: No occurrence of play bow during the human partner's approach 1: Dog performs play bow (crouches on its forelimbs, stands on its hind legs and might bark and/or wags its tail, Bekoff, 1977) during the approach
Gaze averting	0: Dog is continuously looking at the approaching human 1: Dog looks away for more than 2 s, so the human has to make attention-getting noise(s) to re-establish eye-contact 2: Dog looks away and does not look back even after the third attention-getting noise
Vocalization	0: Dog neither barks nor growls 1: Barking or growling does not last for more than 4 s 2: Dog barks or growls for more than 4 s
Moving off	0: Dog does not move away and the human can go within arm's length (approximately 0.5 m) off the dog 1: Dog makes some movements to avoid the human, but finally she can approach it within arm's length 2: Dog moves away repeatedly from the human, who cannot approach it within 0.5 m
Guarding the play object	0: No signs of guarding behaviour are observed during the human's approach 1: The body posture is stiff (the muscles are tense) while the dog is continuously staring at the human, and/or the dog is growling, baring its teeth, curling its lips. These signs do not become more intense, so the human can touch the play object at the end of the approach 2: The body posture is stiff while the dog is staring at the human, and/or the dog growls, bares its teeth, curls up its lips. These signs are gradually getting more intense during the approach or when the human reaches for the play object

bar graphs, because these illustrate the results in a clear and comprehensive form.

3. Results

Prior playing experience with E did not affect the dogs' behaviour (Mann–Whitney tests, all $p > 0.05$), therefore all dogs (distantly familiar or unfamiliar with E) were analysed as a whole sample.

3.1. Playful situations

Differences in the dogs' reaction to the threatening and the friendly approaches showed that in many respects dogs altered their behaviour according to the type of the approach.

In case of E, the threatening approach evoked play bow from significantly more dogs than the friendly approach (McNemar test: $p < 0.001$). Moreover, during the threatening approach dogs vocalized more ($T = 8$, $p = 0.007$), and broke eye-contact fewer times ($T = -20$, $p = 0.006$).

Similar differences were found in respect of the owners. During the threatening approach dogs were more likely to

Table 3
Behavioural variables coded in the non-playful situation with each human partner during both kinds of the controlled approaches.

Variable	Description of scores
Play bow	see Table 2
Gaze averting	see Table 2
Vocalization	see Table 2
Moving off	0: Dog does not move away from the approaching human while keeping persistent eye-contact with her 1: Dog moves away from the approaching human, but does not move behind the human standing near to it and does not jerk on the leash 2: Dog moves behind the human standing near to it and/or jerks on the leash
Contact-seeking	0: The approach is terminated before the human reaches the dog (for rules of termination see 'Controlled approaches' in the text) 1: At the end of the approach the human strokes the dog's head, but the dog neither wags its tail nor tries to lick the hand or face of the human 2: At the end of the approach the human strokes the dog's head, and the dog wags its tail and/or tries to lick the hand or face of the human

perform play bow ($p < 0.001$) and vocalize ($T = 8, p = 0.008$), and gaze-averting was less typical ($T = -23, p < 0.001$).

There was no difference in the tendency for moving away from E or the owner depending on the type of the approach ($T = 5, p = 0.470$ and $T = 6, p = 0.272$). Guarding behaviour appeared to be more intense during both partner's threatening than friendly approaches (E: $T = 5, p = 0.034$; owner: $T = 4, p = 0.046$), but applying the FDR correction these p values exceeded the adjusted significance level.

The comparison of the dogs' reaction to the owner and E revealed no significant differences in any variables (friendly approach: play bow: $p = 1$; vocalization: $T = 3, p = 0.102$; guarding: $T = 2, p = 0.180$; gaze averting: $T = -10, p = 0.599$; moving off: $T = 5, p = 0.351$; threatening approach: play bow: $p = 0.057$; vocalization: $T = 5, p = 0.470$; guarding: $T = 6, p = 0.132$; gaze averting: $T = 14, p = 0.350$; moving off: $T = -6, p = 0.520$). (See Fig. 1. for a summary of the dogs' behaviours.)

3.2. Non-playful situations

The dogs behaved differently in many respects not only depending on the type of the approach (friendly and threatening), but also their partner (owner or E).

In the non-playful situations the dogs performed play bow rarely toward their human partners (four dogs altogether; two during the owner's threatening approach, one during E's threatening approach, and one during the owner's friendly approach).

During the threatening approach dogs tended to vocalize more towards both partners (E: $T = 14, p < 0.001$, owner: $T = 13, p = 0.001$) and avert their gaze more (E: $T = 22, p < 0.001$, owner: $T = 15, p < 0.001$), and showed less contact-seeking (E: $T = -26, p < 0.001$, owner: $T = -16, p < 0.001$). The tendency to move away from the approaching human was not affected by the type of approach (E: $T = 7, p = 0.083$, owner: $T = 2, p = 0.157$). (See Fig. 2 for a summary of the dogs' behaviours.)

Comparing the dogs' reactions toward the two partners during their threatening approach we found that E elicited more gaze averting ($T = 14, p = 0.007$), and less contact-seeking ($T = -15, p = 0.007$) behaviours, than the owner. We did not find differences in this respect in the dogs' tendencies of moving off ($T = 6, p = 0.114$) and vocalizing ($T = 9, p = 0.71$).

During the friendly approach, however, only one behaviour was different; dogs averted their gaze more during E's approach (gaze averting: $T = 9, p = 0.003$; moving off: $T = 2, p = 0.180$; vocalizing: $T = 1, p = 0.317$; contact-seeking: $T = -8, p = 0.109$).

3.3. Comparison of responses for the threatening approaches in the two situations

In order to reveal context specific behavioural differences in the reactions of dogs we used McNemar test to analyse the distribution of dogs among two main response categories and the occurrence of play bows during the playful and the non-playful threatening approaches. Based on the measured behavioural variables (gaze averting, vocalization, moving off, guarding, and contact-seeking) we categorized the dogs into two exclusive groups labelled as 'tolerating/contact-seeking' and 'avoiding/aggressive', based on their overall behavioural reaction during the threatening approaches (Table 4).

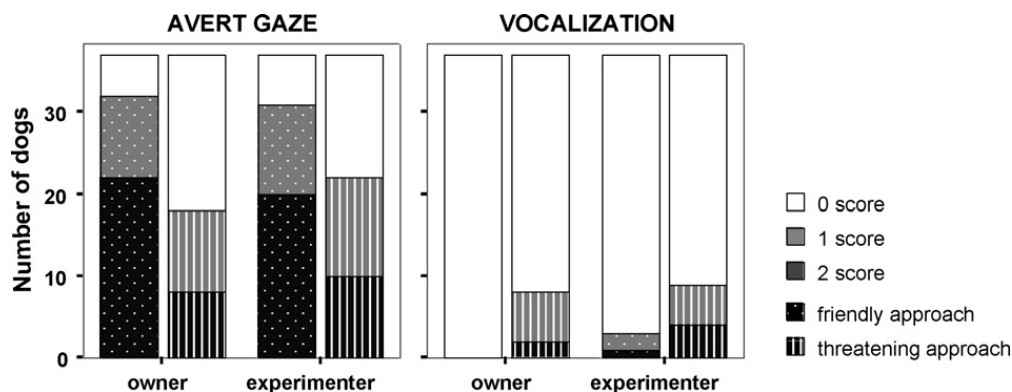


Fig. 1. Behaviours in the playful situations; the different colours show the number of dogs in each score-category. (For scoring details see Tables 2 and 3.)

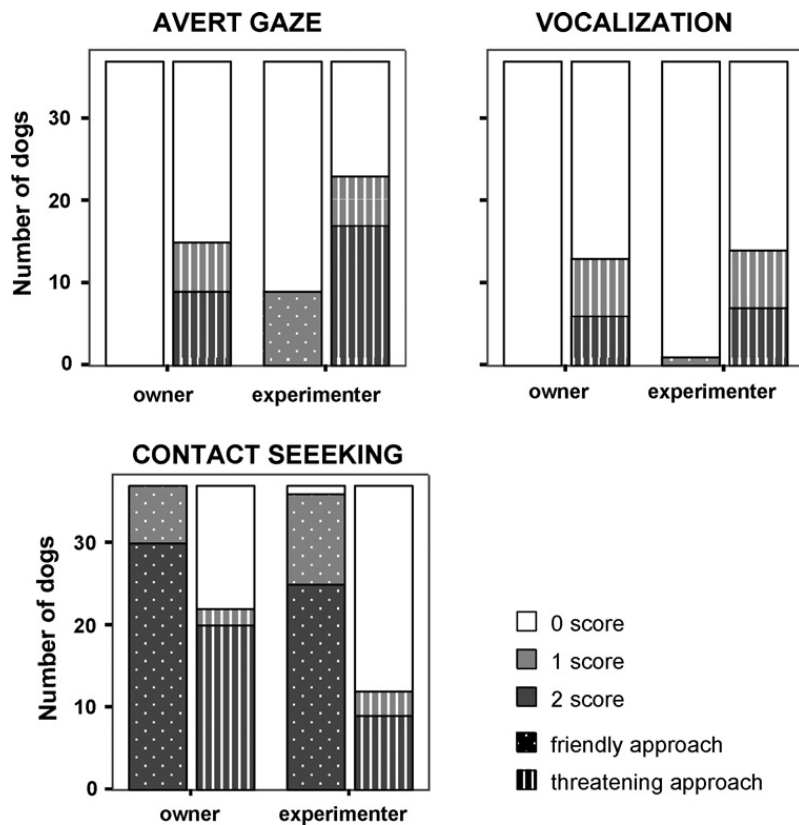


Fig. 2. Behaviours in the non-playful situations; the different colours show the number of dogs in each score-category. (For scoring details see Tables 2 and 3.)

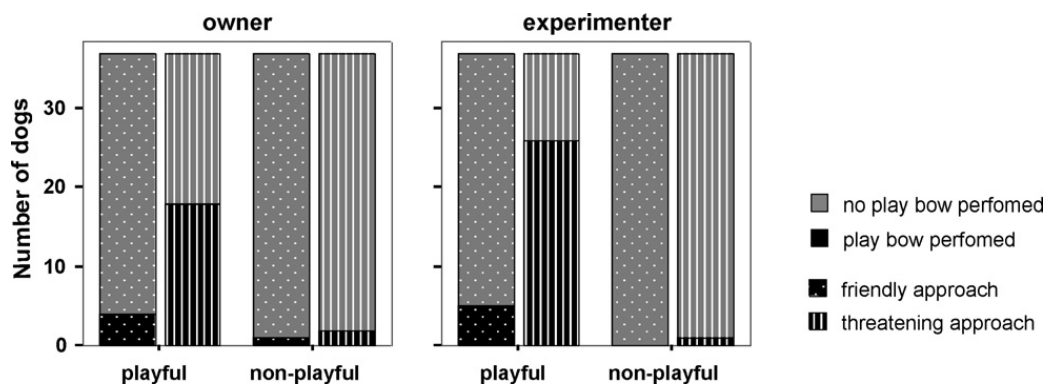


Fig. 3. Number of dogs performing play bow in both situations during the approaches.

The dogs' behavioural response toward the threatening owner did not differ in the two situations, because most of them were tolerating/contact-seeking both in the playful and the non-playful situation ($p = 1$, see Fig. 3). However, dogs reacted differently to the threatening E in the two situations: they were rather avoiding/aggressive in the

non-playful situation and tolerating/contact-seeking in the playful situation ($p = 0.021$, see Table 5).

More dogs performed play bow during both human partners' threatening approach in the playful situation than in the non-playful situation (owner: $p < 0.001$, E: $p < 0.001$, see Fig. 3).

Table 4

Response categorization of dogs based on their overall reaction pattern into two distinct categories in both playful and non-playful situations.

	Aggressive/avoiding	Tolerating/contact-seeking
Playful situation	The human cannot take the play object at the end of the approach because the dog guards it and/or takes it away	The human can take the play object at the end of the approach
Non-playful situation	The human cannot pet the dog at the end of the approach, because the dog averts its gaze continuously or moves away	The human can pet the dog at the end of the approach

Table 5

Comparison of the distribution of behavioural response categories during the playful and the non-playful threatening approaches of the owner and the experimenter.

	Non-playful situation		
	Owner	Avoiding/aggressive	Tolerating/contact-seeking
Playful situation	Avoiding/aggressive	4	10
	Tolerating/contact-seeking	11	12
	Non-playful situation		
	Experimenter	Avoiding/aggressive	Tolerating/contact-seeking
Playful situation	Avoiding/aggressive	11	13
	Tolerating/contact-seeking	3	10

4. Discussion

Recently, our research group has argued that dogs possess some special social skills for responding human communicational cues (Topál et al., 2009; Miklósi et al., 2004 for review). Some aspects or rudimentary forms of these socio-cognitive abilities may have been inherited from the ancestors of the dog (Kubinyi et al., 2007). Moreover, special features of human social behaviour and the environment could represent an adaptational demand that has favoured the evolutionary and developmental emergence of dogs' sensitivity to certain human-specific cues.

We investigated how in playful and non-playful situations dogs decode some human behavioural cues that communicate different modes of social interaction (friendly vs. moderately agonistic or ambivalent). In the present study family dogs did not show significant differences in their behaviour toward the two human partners (E and the owner) in the playful situation. However, during the non-playful situation the same dogs averted their gaze less frequently so eye-contacts were more enduring with the owner, and at the end of the threatening approach they also showed more contact-seeking towards her/him than towards E.

We suppose that the humans' gazing behaviour accompanied by the other cues played a central role in eliciting the observed behavioural reactions from the dogs, which may depend on the familiarity of the signaller person. If the outcome of a situation is perceived to be dangerous for the dog then breaking eye-contact by gaze averting could indicate subordination and avoidance of interaction. But one could also assume that continuous assurance about an appeasing motivational state could have been an alternative conflict-avoiding solution. We think that this latter can be advantageous (and therefore more frequent) between individuals with closer and more affective relationship. This hypothesis gains support from our result that the threatening behaviour of the owner and the E had different effect on dogs' reaction in this predicted way. A possible alternative explanation could be that the owner's behaviour might be different from that of E's, because the owner was inexperienced in our test situations. But other findings showed that inexperienced and experienced women elicited the same behavioural response from an unfamiliar dog (Vas et al., 2008).

We observed that both in the playful and in the non-playful situations dogs' reactions varied according to the

threatening or friendly manner of the approaching human. In the playful situation the threatening approach evoked more vocalization, less interruption of eye-contact and the occurrence of play bow in more dogs. Analysis of the non-playful situation revealed that the threatening behaviour elicited more gaze-averting, more vocalization and less contact-seeking behaviour than the friendly approach did. The two different kinds of approaches affected the same aspects of dogs' behaviour in the case of both human partners.

It has been proposed that dogs' sensitivity to the behaviour of humans is accompanied by an increased flexibility in the organization of their behaviour which could be the result of relaxed selection pressure over domestication (Frank, 1980; Frank and Frank, 1987). Our findings are consistent with this hypothesis because dogs recognized and quickly reacted to the switch in humans' behaviour (friendly or threatening approach) both during playful and non-playful interactions. Their reaction depended on cues communicating different (friendly or threatening) motivational states and they showed a similar pattern of reaction in relation to both kinds of human. We divided the dogs into two distinct categories (namely tolerating/contact-seeking and avoidant/aggressive), based on their overall reaction patterns to a threatening human. Our results support the hypothesis that dogs make strategic behavioural decisions depending on the identity of their human partner. They prefer to show affiliative behaviour toward the owner in potentially conflicting situations, but tend to display an agonistic attitude when facing a not closely familiar human.

The increased vocalization activity during the threatening approaches could reflect the increased level of dogs' arousal. Our result is in line with other studies which showed that dogs (Pongrácz et al., 2010), and also wolves (Cohen and Fox, 1976) vocalize, especially bark mostly in the contexts of defence and threat. Gaze averting tendencies were more frequent during the threatening approaches compared to the friendly ones both in the playful and in the non-playful situations. While gaze averting could be an effective way to avoid conflict in the non-playful situation, it seemed that during play situation performing a play bow could serve the same conflict-resolving function. This might point to the important effect of the context on the response for human behavioural cues.

During social interactions the decoding of the emotional state reflected by the gaze of another individual could

be of great importance (Emery, 2000). Dogs more readily initiate eye-contact with humans than wolves do, as early as the age of five weeks (Gácsi et al., 2005) and in cooperative problem-solving situations they use 'showing' (Miklósi et al., 2000) and gaze altering behaviour (Miklósi et al., 2003). On the other hand the steady extended stare of a conspecific or a human could represent a ritualized signal of dominant status relating to agonistic inner motivational state of the sender (Fox, 1971; Vas et al., 2005). It could be assumed that in our study the dogs showed a tendency to perceive the steady eye-contact as a dominant signal in the non-playful situation. However, the threatening approaches during the play context made the social situation ambiguous for the dogs. Thus they showed lasting eye-contact more frequently with the approaching human, and also increased the display of play bows, presumably so as to change the human's behaviour back to playful.

One of our questions was to investigate whether dogs use play bow toward a human playing partner, when the partner's behaviour is ambiguous. Although out of play context the threatening approach elicited play bow rarely, during play situation when the human partner's playful behaviour suddenly switched to threatening most of the dogs reacted with performing a canid play bow. Moreover, both the owner's and experimenter's threatening approach elicited play bow in the play context.

Interestingly, Rooney et al. (2001) disregarded the possibility of studying play signals displayed by dogs during dog-human play and they preferred to study the effect of human play signals on dogs. They suggested that their approach is advantageous because it controls the emergence of signals which make their observations less time-consuming and less opportunistic, as opposed to the sporadic occurrences of dogs' play signals. However, our study provides a good example that putting dogs in a specific social context can elicit communicative signals and signalling seems to be positively associated with the ambiguity of the social situation. Our findings support the notion that dogs use play bow as a context-specific play signal towards human play-partners, in order to maintain playful mood and restart ongoing play or perhaps to avoid the escalation of conflicts when their partners' behaviour becomes ambiguous. These observations are in line with the notion that play signals should be primarily used in the context of play (Pellis and Pellis, 1996) and in such situations when the consequence of an action is ambiguous (Bekoff, 1995).

It is often assumed that evolution of sociality leads to effective mechanisms to predict the behaviour of group mates during coordinated interactions (Call, 2001; Krebs and Dawkins, 1984). In a broader sense the complete set of social skills, which characterize a species, is referred to as 'social competence' (Topál et al., 2006). Based on our observations we propose that sensitivity to human behavioural cues; the ability to adjust reactions according to the context of the interaction and the flexible utilization of various conflict-resolving behaviours depending on the actual partners represent fundamental elements of dogs' social competence. These abilities enable the dogs to fit in with human societies and to form peaceful mixed-species groups with them.

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