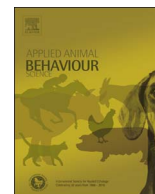




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Understanding of human referential gestures is not correlated to human-directed social behaviour in Labrador retrievers and German shepherd dogs

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ABSTRACT

Dogs are known to excel in interspecific communication with humans and both communicate with humans and follow human communicative cues. Two tests commonly used to test these skills are, firstly, the problem-solving paradigm, and, secondly, following human referential signals, for example pointing. The aim of the present study was to investigate whether dogs that seek more human contact in an unsolvable problem-solving paradigm also better understand human communicative cues in a pointing test. We also assessed between- and within-breed variation in both tests. 167 dogs were tested and were of the breeds German shepherd dog and Labrador retriever. The Labradors were separated into the two selection lines: common type (bred for show and pet) and field type (bred for hunting). A principal component analysis of behaviours during the problem solving revealed four components: Passivity, Experimenter Contact, Owner Contact and Eye Contact. We analysed the effect of these components on success rate in the pointing test and we found no effect for three of them, while a negative correlation was found for Owner Contact ($F_{(1,147)} = 6.892$; $P = 0.010$). This was only present in common-typed Labradors. We conclude that the ability to follow a pointing cue does not predict the propensity for human-directed social behaviour in a problem-solving situation and suggest that the two tests measure different aspects of human-directed social behaviour in dogs.

1. Introduction

In recent years, social cognition in dogs has been intensely studied. It seems that dogs during domestication have acquired unique abilities for interspecific social behaviour with humans (Miklósi and Topál, 2013). Dogs recognize and interpret human communicative signals and also communicate with humans in a way that is not found to the same extent in their wild ancestor, the grey wolf (*Canis lupus*) (Hare et al., 2002; Miklósi et al., 2003), nor in human's phylogenetically close relatives chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*) (Bräuer et al., 2006). In fact, dogs have been shown to behave more like human infants than wolves in response to human ostensive cues (Topál et al., 2009).

There are two commonly used ways to study interspecific social capabilities. Firstly, subjects' human-directed social behaviour is studied in a problem-solving paradigm, usually unsolvable, and secondly, subjects' skill to follow human communicative referential gestures is tested in a pointing test. In the first test type it has been shown that dogs readily communicate with humans through, for example, attention-seeking and attention-directing signals toward humans, sometimes

called showing or help-seeking behaviour (Hare et al., 1998; Miklósi et al., 2000). In the second class of tests, dogs have been shown to have an understanding of human pointing gestures and are able to follow them to find food in an object-choice paradigm (Hare et al., 1998; Miklósi et al., 1998). It seems that the understanding of this cue cannot be explained by simple local enhancement (Hare et al., 1998; McKinley and Sambrook, 2000), and some research even suggests that dogs in fact understand the communicative intent of the sender (Szetei et al., 2003; Tauzin et al., 2015).

Interestingly, comparative studies have shown that wolves do not seek human contact to the same extent when faced with a problem (Miklósi et al., 2003; Udell, 2015; Heberlein et al., 2016) and dogs perform better in the pointing task than both wolves (Hare et al., 2002; Virányi et al., 2008) and chimpanzees (Kirchhofer et al., 2012). Also, there are studies indicating that the ancient, feralised dog breed the Australian dingo performs between that of wolves and modern dogs both in pointing understanding and spontaneous eye contact (Smith and Litchfield, 2010; Johnston et al., 2017). This suggests that these are behaviours that have been affected by domestication.

Not all dogs perform equally in these two tests, however. In both

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types of social interactions there are individual differences as well as differences between groups of dogs (Gácsi et al., 2009a). While primitive breeds, for example the New Guinea singing dog, also show interspecific communicative skills, documented breed differences show that selection can affect these abilities (Wobber et al., 2009; Passalacqua et al., 2011; Udell et al., 2014). For example, Wobber et al. (2009) showed that both historical working and non-working breeds performed above chance level in a pointing test, although dogs of working breeds performed more successfully than dogs of non-working breeds. However, the background of the dogs, for example the amount of training, might differ between breeds and this might have influenced the result. It is not known how recent selection has affected the interspecific communication in dogs. This can, for example, be studied in recently diverged breeds where types are selected for different purposes.

The fact that there are differences in human-directed communicative skills between breeds suggests that there is a genetic basis for these behaviours, which is a prerequisite for selection. Consistent with this, genetic studies have found moderate heritability estimates and identified candidate genes for human-directed social behaviour during problem solving (Hori et al., 2013; Persson et al., 2015; Persson et al., 2016). These skills are also affected by experiences during ontogeny such as training for different tasks (Marshall-Pescini et al., 2009). Additionally, pet dogs seem more skilled than shelter dogs which, presumably, have less human communication experience (Udell et al., 2010). It is thus not clear how much of the communicative skills that can be explained by ontogeny and how much by phylogeny.

We investigated whether these two communicative skills, to follow human gestures and to seek human contact, reflect a common underlying general ability for interacting with humans, perhaps as genetically correlated traits evolving during domestication. Alternatively, the two traits could be genetically unrelated, and selected independently of each other. To distinguish the two possibilities, we examined the correlation between the behaviour of dogs in each of the two experimental tests, firstly assessing the ability to follow human referential gestures, and secondly, the ability to seek human contact in a problem-solving situation. To investigate how these traits have been selected in different breeds we used both German shepherd and Labrador retriever dogs. Also, to investigate how these behaviours have been affected by recent selection criteria we compared two recently separated types of Labrador retriever, one selected for show and pet qualities and the other for hunting behaviour.

2. Methods

The study was approved by Linköping local Ethical committee of The Swedish National Board for Laboratory Animals (approval no. Lpk 85-07).

2.1. Subjects

A total of 167 dogs of the breeds Labrador retriever (Labrador) and German shepherd dog (GSD) participated in this study after their owners were recruited on a voluntary basis through social media. These two breeds were chosen because both are common breeds and they are of equal size. Both Labradors and GSDs were also recruited for participation in other studies. Due to noncompliance in the pointing test (participating in less than half of the choices; see description below) or failing the motivation test for the problem solving (see description below), 12 dogs were excluded from the analysis. Additionally, two Labradors were removed due to unknown ancestry. Out of the remaining dogs, 32 were GSDs (16 females and 16 males) and 121 were Labradors (63 females and 58 males). Labradors were further classified as either common type or field type based on titles (e.g. field-trial champion) of ancestors in their pedigrees. If ancestors for at least three generations back were bred for field work, the dogs were classified as

field-type Labradors. If none of the ancestors had field titles, they were instead classified as common-type Labradors and most had ancestors with show titles. Most Labradors were clearly of one type or the other and no dogs with dubious or mixed ancestry were included in the study. Type classification was additionally confirmed by kennel information and physical phenotype. For pedigrees, Swedish Kennel Club's online registry was used (Hunddata, <http://hundar.skk.se/hunddata/>), and k9data.com (<http://www.k9data.com/>) with pedigrees of Labradors from other countries. Based on this analysis, 60 Labradors were classified as common type (35 females and 25 males) and 61 as field type (28 females and 33 males).

To obtain some background information about the dogs, dog owners also answered a questionnaire. They were asked the following: 'Is this your first dog?', 'Does your dog live together with other dogs?', 'How many hours do your dog on average spend alone each day?' and 'How many hours do you on average activate (walks, training etc.) your dog each day?'. Also, on a Likert scale from 0 to 4, strongly disagree to strongly agree, they were asked the following: 'I got this dog because I wanted a nice companion dog', 'I got this dog because I wanted a dog good for training', 'I train often with my dog', 'I play often with my dog', 'I often correct my dog' and 'I often reward my dog with treat or play'. Labrador owners had the additional question 'I often train fetch with my dog'.

The mean age (years) of the GSDs was 3.34 ± 0.427 (\pm SEM) and of the Labradors 2.43 ± 0.195 . Within the Labrador breed, the mean age of the common type was 2.10 ± 0.228 and of the field type 2.75 ± 0.311 .

2.2. Experimental design

Data was collected between August and November 2014. Tests were carried out at seven different locations in Sweden. All dogs included in the analyses participated first in a problem-solving test followed by a pointing test. Both tests were video recorded with a full-HD camcorder (Canon Legria HF G25) for later analysis. The experiments were performed in a marquee measuring 3×3 m in order to achieve a uniform environment at the different locations. Three of its sides had canvas walls and the fourth was closed off with a fence (Fig. 1).

The treats used were pieces of Frolic® Complete, unless the dog had allergies and the owner brought approved treats. Prior to the testing a motivation test was performed to assure that the dog was motivated to eat the treat. The plate used was similar to the compartments used in the problem-solving test, but did not have a lid (see description below).

There were two persons testing approximately half the dogs each as well as analysing the videos. Tests and observational analysis were therefore coordinated by the two experimenters, and also by three supervising test leaders, to ensure a high accordance between them. Both experimenters and test leaders were females.

2.2.1. Problem-solving test

The problem-solving paradigm we used has previously been described in detail by Persson et al. (2015) and is shown in Fig. 1A. The test apparatus was a plate with three identical compartments covered by Plexiglas lids, each with six 0.5 cm odour holes. All compartments contained treats. Two lids could easily be slid to the side and thereby opened while the lid in the middle was screwed on and could not be opened.

The dog owner held the dog in the front right corner of the marquee while the experimenter placed the test apparatus on the ground in the middle of the back side of the marquee, approximately 40 cm from the wall and 2 m from the dog. The experimenter placed herself in the front left corner and signalled to the owner to release the dog, after which the owner and experimenter remained passive and facing the apparatus throughout the test. If the dog escaped the marquee under the canvas, it was quickly called back inside and the owner went back to being passive. If the dog had not opened any of the compartments after 1 min, the

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