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Review article

Neural processes of vocal social perception: Dog-human comparative fMRI studies

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ABSTRACT

In this review we focus on the exciting new opportunities in comparative neuroscience to study neural processes of vocal social perception by comparing dog and human neural activity using fMRI methods. The dog is a relatively new addition to this research area; however, it has a large potential to become a standard species in such investigations. Although there has been great interest in the emergence of human language abilities, in case of fMRI methods, most research to date focused on homologue comparisons within Primates. By belonging to a very different clade of mammalian evolution, dogs could give such research agendas a more general mammalian foundation. In addition, broadening the scope of investigations into vocal communication in general can also deepen our understanding of human vocal skills. Being selected for and living in an anthropogenic environment, research with dogs may also be informative about the way in which human non-linguistic and linguistic signals are represented in a mammalian brain without skills for language production.

1. Introduction

In recent years the ethological study of human-dog relations emerged as an exciting and so far neglected topic in comparative behavioural investigations. In contrast to many other approaches in this field (c.f. 'comparative cognition', see Shettleworth, 2010 for an exhaustive review), often relatively arbitrarily chosen animal species are compared to each other or to humans. Here, we compare the behaviour and relevant underlying mechanisms of two species that have been living alongside each other for at least 16,000–32,000 years (Miklósi, 2014). Although there is some debate about details of dog domestication, there are strong arguments that this process enabled dogs to survive in small human groups in many of which they have been considered as true social partners (Serpell, 1995). Thus, human and dog comparisons both at the level of performance (behaviour) and underlying mechanisms (mental and neural processes) can help elucidate (1) how humans and dogs achieve similar cognitive performance, (2) where the differences and limits of these achievements are in one or the other species, (3) what the contribution of the social environment is, and (4) whether we can provide some evidence for a genetic factor in case of dogs.

The inclusion of dogs in studying vocal behaviour in mammals is also interesting because so far only relatively few species have been studied in detail, many of them in captivity, or while living in remote places. Dogs represent a new clade (Canidea) to be added to the set of mammals that can be included in comparative investigations. In addition, domestication has certainly changed the vocalisation patterns in dogs (see below) that makes this species very attractive to study acoustic communication.

In humans, the research focus on auditory communication has been on perception and production of language, with a specific interest in the evolution of this phenomenon. Systematic comparative work on mammals may help gain further insights, and dogs, selected for living in an anthropogenic environment – and especially family dogs, i.e., dogs living in human families and consequently being surrounded by human linguistic input – have the potential to contribute to our understanding of the evolution of language.

Our aim in the review is threefold. First, we overview the wide range of behavioural interactions between dogs and humans that happen in the auditory space and play an important role in the communication of the two species. Second, we review the neural processes that support and control such behavioural interactions and are responsible for the emergence of mental representations. Third, we summarize a few recent studies aimed to shed light on these neural processes in dogs (and humans) using a non-invasive method, functional magnetic resonance imagining (fMRI). We argue that both the

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dog specifically and canines broadly may provide be a useful mammalian clade to study the evolution of both the perception and production of vocal signals in mammals.

2. Dog-human communication: vocal parallels

Humans are very communicative, thus any species they cohabitate with has been probably selected for enhanced communicative abilities. Dogs provide a good example because they are able to develop and utilise a very flexible signalling system when communicating with humans (Miklósi, 2014). Both species rely on using both visual and acoustic signals, however, the latter may be more advantageous for evolutionary reasons. Many canine visual signals involve tail or ear movements which do not have their counterparts in human visual signals. Similarly, human visual signals often include hand motions for which no canine parallel exists. In contrast to the partly incompatible structure of human and dog visual signals, non-linguistic vocal signalling systems of both species show a much greater overlap due to the conservative structure of their sound production systems.

2.1. The conservative vocal system of Canidea

There has been relatively little interest in Canidea vocalisation, despite the fact that domestic dogs use a wide range of vocal signals and most of the ethologically-inspired research was carried out with captive wolves (*Canis lupus*). Early reviews (Cohen and Fox, 1976; Tembrock, 1976) based on *ad hoc* samples of a few canine species revealed up to 15 vocal categories. Most of these discrete vocalisations are relatively easily discerned by the human ear and are characterised by a wide range with regard to fundamental frequency, formant frequency, format dispersion, and tonality. The most common types of these vocalisations (bark, growl, scream, and whine) are shared among main canine genera (*Canis* and *Vulpes*).

The functional value of these vocalisations has not been investigated in much detail. *Ad libitum* observations indicate that vocal communication among canines plays an important role in organising group life by determining inter-individual distance, form of interaction, and synchronicity. Vocalisations may also stand for identity and position in the hierarchy, they play a role in directing attention, and may indicate changes (events) in the environment. Functionally speaking, canines vocalise in many social interactions including territorial and dominance aggression, mating, and playing (Cohen and Fox, 1976). However, there is little quantitative data concerning the true function of these vocalisations, that is, how these signals benefit the sender and influence the behaviour of the social partner.

Fox (1970) has also observed that there is a positive association between increased sociality and vocal repertoire. More sociable *Canis* genera and within *Canis* the more sociable wolves display more forms of vocalisations than fox-species living solitarily. This difference in signalling is even larger by the more frequent use of mixed sounds and sequential combination of two vocalisations in gregarious species such as wolves. It is assumed that these variations allow for more specific expressions of inner states.

2.2. Domestication and dog-human cohabitation

The emergence of dogs (estimated between 16,000–32,000 years before present, Wang et al., 2013) is closely associated with human activities (Miklósi, 2014). Today, the most widely accepted conceptualization is that during a relatively gradual evolutionary process (domestication) humans allowed today's dogs' ancestors to join their groups and this process selected for dogs that had the genetic potential to develop human-compatible social behaviours. Overall genetic difference between wolves (sharing the common ancestor with recent dogs) and dogs is relatively small (less than 0.01%) albeit systematic gene-level comparisons indicate several major differences that have significant effects on phenotype (for review see Ostrander and Ruvinsky, 2012). This is mirrored by great diversity in dog breeds, including with regard to physical appearance and behaviour.

Apart from anecdotic stories (Fentress, 1967), independent recent experimental evidence (Virányi et al., 2008) revealed that, despite intensive socialisation, wolves and dogs significantly differ in their social behaviour (Range et al., 2015), especially toward humans (Topál et al., 2009a,b). A similar tendency manifests among dog breeds (more wolf-like versus less wolf-like breeds), although only few quantitative studies exist (Passalacqua et al., 2011).

There is some evidence that selective environment has some specific effects on vocal behaviour in foxes. The approximately 40-year long selection for tame behaviour in foxes originally bred for fur resulted in important differences in vocal production between selected and non-selected individuals (Gogoleva et al., 2012). Tame foxes emitted more whines and pants and cackle sounds in the proximity of humans in comparison to non-selected animals which typically mooed and snorted in the same situation. The significance of these differences is not clear but it suggests that even small genetic changes can modify the vocal repertoire significantly.

Similar observations can be made about the acoustic structure (frequency range, tonality and length of barking trains) of dog barks, in that it exhibits considerably greater variability than wolves' (Feddersen-Petersen, 1991, 2000). Other vocalisations are more comparable in these species but available data also suggest that dogs use most sounds in a wider range of social interactions. This could be explained by either direct genetic effect on the vocal production system or by assuming that environmental and social input may allow for a more flexible deployment of vocal signals in dogs.

The large effect of developmental experience on dog has important consequences on the vocal behaviour of this species in many respects:

(1) *Developmental signal ritualization*: Dogs but not wolves use bark as a play signal (Feddersen-Petersen, 2000). Dogs may utilise this signal both toward dogs and humans, and they also respond if humans initiate play by a specific vocalisation (Rooney et al., 2001). It was suggested that, even at a young age, most puppies get excited during play and vocalise, mostly bark, during interaction. During repeated interactions, the specific form of barking gradually assumes the meaning of "let's play". So puppies or adult dogs may deploy this vocalisation in the presence of the other dog to initiate play. A similar process also ensures that dogs may attribute similar function to human vocal signals if they precede a playful interaction. These could be human non-linguistic sounds or even real words. Schassburger (1993) reports that wolf pups yelp exclusively if exposed to harmful stimuli or events. In contrast, Cohen and Fox (1976) indicate that in adult dogs yelping may be emitted in a handful of different situations, including greeting, solicitation of play or showing submission. They hypothesise that yelping in dogs may be a species-specific vocalisation. Similarly to barking, use of this vocalisation may be affected by developmental ritualization.

(2) *Flexibility of learning about vocal signals*: Dogs seem to show enhanced interest for human speech. A recent study has shown that even young puppies pay attention to a human talking to them (Ben-Aderet et al., 2017). Although even well-trained dogs show limited capacity of understanding human language (Pilley and Reid, 2011), a typical family dog may still learn about some aspects of the human vocal output spontaneously (Andics et al., 2016, see below), which can amount to owner-reported knowledge of 20–70 human vocal expressions (Pongrácz et al., 2001).

(3) *Intentional control of vocal production*: There has been a long-standing debate about whether non-human animals are able to control their vocalisations (e.g., Gruber and Grandjean, 2017), with the alternative being that specific vocalisations are strongly associated with specific motivation states, thereby allowing little