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The full citation:

Pongrácz, P. 2017. Modeling evolutionary changes in information transfer. Effects of domestication on the vocal communication of dogs (*Canis familiaris*). *European Psychologist*, 22: 219-232. doi: 10.1027/1016-9040/a000300

Title

Modeling evolutionary changes in information transfer. Effects of domestication on the vocal communication of dogs (*Canis familiaris*).

Short title: Information transfer evolution modeled by dog vocalizations

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Abstract

Inter-specific communication provides good opportunity for studying signal evolution. In this theoretical paper, we hypothesized that vocal signaling in dogs may show specific changes that made it more suitable for interspecific communication in the anthropogenic niche. We assumed that (1) some dog vocalizations will diverge from the corresponding exemplars of wolves; (2) they provide comprehensible affective, indexical and contextual information for humans; (3) some aspects of dog vocalizations are more typical for the interspecific than to the intraspecific domain. We found that the most unique type of vocalization in the dog is barking. We proved that human listeners can contextually categorize dog barks, as well as attribute distinct inner states of dogs based on the barks. We found that dogs are sensitive to both contextual and individual-specific features of other dogs' barks. However, dogs showed almost no response to the bark emitted in isolation, which is one of the easiest to recognize by humans, indicating the possibility of a specific, new communicative role for barks, not present in its original function. Our conclusion is that the qualitative and quantitative proliferation of barks can be explained by mechanisms of evolution such as ritualization and adaptive radiation. Barks became suitable for conveying a more various set of information than the original barks of wolves did. Barks also became typical in such contexts where originally they were not used – such as the contact seeking calls of isolated specimens, apparently targeted at the human, and not to a canine audience.

Keywords: dog, vocalizations, evolution, adaptive radiation

The dog is considered an 'artificial species' by some authors (e.g. Miklósi & Topál, 2013) in a sense that it is a domesticated animal without any extant wild-living ancestor – and almost the entire dog population lives in a more or less tight association with humans (i.e. in an 'artificial environment'). Of course, this does not mean that the evolutionary aspects of the behavior of dogs would not be a worthy subject for ethologists – if someone needs to be convinced about this, it is enough to think about the hundreds of empirical and theoretical papers on dog behavior from the last 25 years. Dogs are also having an ever growing importance for the greater public (McConnell, Brown, Shoda, Stayton, & Martin, 2011), and not only by their sheer numbers (by some authors' estimations the global canine population may exceeded the staggering amount of 1 billion dogs – Coppinger & Coppinger, 2016), but especially in the industrialized (or 'Western') societies the social relationship between humans and companion dogs may reach the importance and complexity of human-human interactions (Kwan, Gosling, & John, 2008). The initial attraction to dogs may share common roots with our interest for 'anything that lives' – according to the framework of biophilia (Wilson, 1993), a theory that gained also empirical proof later (e.g. LoBue, Bloom Pickard, Sherman, Axford, & DeLoache, 2013). However, dogs were found providing much more complex psychological and physiological benefit to their owners than being an animated collectible around in the house (see for a review Amiot & Bastian, 2015). Not only that humans attribute sophisticated personality traits to their four-legged companions (e.g. Gosling, Kwan, & John, 2003; Turcsán, Range, Virányi, Miklósi, & Kubinyi, 2012), but the apparent capacity of dogs to provide unconditional affection, companionship, and support (e.g. Bonas, McNicholas, & Collis, 2000) can be a leading factor why this species occupies a central position in the life of many people, regardless to their age, gender, or social status. On the physiological level, various studies showed that pleasant interactions with, or even the mere presence of a dog has more positive effect on the hormonal response (oxytocin, dopamine, endorphins) and brain activity of the participants, than other, non dog-related stimuli (Odendaal & Meitjens, 2003; Sugawara et al., 2012). From the psychological aspect, dogs were found affecting positively the well-being of humans who encountered traumatic events (Barker, Barker, Dawson, & Knisely, 1997), or who had to perform in stressful situations (Allen, Blascovich, & Mendes, 2002). While the roots of social behavior and cognitive capacity in dogs originates from its genetic ancestors, the long process of domestication (including the challenges of recent and present times) exerted new and strong selective forces on the socio-cognitive traits of dogs as well. This new evolutionary process resulted in such characteristics which served as adaptations predominantly to the new, anthropogenic environment. Ethologists who are interested in the evolutionary processes as well as in – for example – communicative behavior, find the co-existence between humans and dogs an especially rewarding research field, because of the easy access to large numbers of experimental subjects of both species, that are willing to participate in tests, and which also offer new phenomena to be studied.

Signal evolution and interspecific communication

How did communication evolve - what kind of selection led to the development of various signals, is one of the central research areas in behavioral and cognitive sciences (e.g. Blumstein, 1999; Wiley, 1983). The communication between different, many times only distantly related species, theoretically provides an excellent opportunity for testing signal evolution, because the effect of genotype can be ruled out both from the aspects of mechanism (i.e. signal structure) and function (i.e. kin-selection). It was found for example that the broader was the audience of the Old World leaf warblers (*Phylloscopidae*), the more variable were their alarm calls (i.e. their evolution was faster) (Wheatcroft & Price, 2015). At the same time, exemplars for interspecific communication in *not-antipredator* context are still relatively rare, showing that either forces of selection did not commonly favor the effective

information transfer between species; or physical constraints prevented the development of such signals in larger quantities. Thus, the best known cases of interspecific communication mostly come from the domain of alarm signals (Kostan, 2002), and only a few exemplars show other functions, such as the famous ‘feeding site showing’ behavior of honeyguide birds (*Indicator indicator*) (Isack & Reyer, 1989).

One can hypothesize that the complexity of interspecific communication will depend on the multi facetedness of social interactions of the two species in question. As it was mentioned earlier, the basic idea behind our scientific approach to dog behavior was the paradigm stating that the most important species-specific feature of dogs is the capacity to get interactively integrated to the anthropogenic environment. This means that the human group represents the natural environment for the dog (e.g. Topál et al., 2009b), which required sophisticated adaptations from the dog, enabling it to survive and thrive. It has been already found that the socio-cognitive capacity of dogs may even exceed the performance of the great apes (the closest genetic relatives of humans) especially in tasks that involve cooperative sharing of information (e.g. Hare, Brown, Williamson, & Tomasello, 2002). Although the role of epigenetic processes (i.e. learning due exposure, or spontaneously from repeated interactions with humans) should not be underestimated (e.g. Udell & Wynne, 2008), careful comparison between performances of equally socialized wolves and dogs in various socio-cognitive experiments (Miklósi et al., 2003; Virányi et al., 2008; Gácsi et al., 2009) involving humans as partners provided insight to the effect of domestication (i.e. effect of selective forces) on dogs’ willingness and success in communicative and cooperative tasks. As an attempt to unify both theoretical approaches, we support the theory outlined by Miklósi and Topál (2013), who suggested that meanwhile dogs truly develop their capacities to follow human communicative signals and initiate interactions with humans through learning, contrary to the wolves, the roots of dogs’ social competence relies on an inherited capacity for early and spectacularly fast socialization to humans. Following the concept of ‘human behavioral complex’ (Csányi, 2000), communication is one of the important ingredients that are essential for successful group living. In the case of dog-human co-existence, our main research target was understandably the interspecific communication; however, specific forms of intraspecific signaling also provides interesting contrasts for a better understanding of the complexity of canine vocal behavior.

For detecting those changes in the signaling behavior of dogs that may have evolved because of the evolutionary need for more effective communication with humans, one should look for the following features:

(1) Are there qualitative and/ or quantitative differences between particular signals, and communicative behaviors of dogs and their closest wild relatives (here researchers usually mean the gray wolf (*Canis lupus*))? Comparative studies of dogs and intensively socialized wolves have already discovered that the socio-cognitive capacity of dogs may show marked differences when compared to the otherwise tame wolves, providing good evidence for the effect of domestication, for example on attachment behavior (Topál et al., 2005); learning and following of human visual cues (Virányi et al., 2008); and sensitivity to human ostensive cues (Topál, Gergely, Erdőhegyi, Csibra, & Miklósi, 2009a). At the same time, other results warrant against the easily drawn conclusion that dogs in general would ‘inherit’ (due their domestication) the highly skilled social competences in dog-human interactions. Today it is widely accepted among scientists that socialized wolves can perform similarly to family dogs in particular socio-cognitive tasks (like the two-way choice test), however, it takes a longer period of time (it requires more opportunity to learn) for a wolf than for a dog to learn these skills (Gácsi et al., 2009; Miklósi & Topál, 2013). Similarly important are the results that show how important is socialization and ontogenetic experience for dogs in the development of ‘normal’ levels of social competence with humans. For example, in absence of socialisation

(i.e. being reared in a kennel-environment), dogs do not understand the pointing cues (D’Aniello et al., 2017) and they refer to people by gazing less than family dogs (D’Aniello & Scandurra, 2016).

(2) Do humans recognize correctly the signals of dogs? An additional question here may also arise whether humans need excessive experience with particular signals for an effective understanding? There are results showing that dogs for example, provide gaze alternations as effective referential signals for humans in the case of hoping for a treat that is otherwise unapproachable for them – gaze alternations serve as a highly effective signal for eliciting and directing human attention (Polgárdi, Topál, & Csányi, 2000). While research on cats’ vocalizations showed that human listeners have difficulties in deciphering the contextual meaning of different meows of cats (Nicastro & Owren, 2003), with a slight advantage in the case of those subjects who had extensive experience with these calls. Besides the experience, structure can also affect the between-species understandability of signals, because genetic predispositions may determine both the detectability (Wiley, 2006) and meaning of particular messages (Meints, Racca, & Hickey, 2010).

(3) Are there particular signals in the dog’s repertoire that are more relevant to the interspecific domain than between-dog’s communication? As we mentioned earlier, dogs show specific sensitivity to human ostensive communication (e.g. Pongrácz, Miklósi, Timár-Geng, & Csányi, 2004) which is not the case when socialized wolves interact with humans (Topál et al., 2009a). However, are there situations when dogs use such human-directed signals that have different, or no meaning when perceived by other dogs? One could argue that establishing eye contact with humans – a frequently experienced behavior, especially in unsolvable, stressful situations (Miklósi et al., 2003), but also an easy-to-train response among experimental conditions (Bentosela, Barrera, Jakovcevic, Elgier, & Mustaca, 2008) would be a perfect candidate for this category. Staring at the opponent is considered as an agonistic signal among wolves as well as dogs (Gácsi, Vas, Topál, & Miklósi, 2013) therefore the capacity for using eye contact (and gaze alternations) with humans in non-agonistic contexts (Miklósi, Pongrácz, Lakatos, Topál, & Csányi, 2005), may show an evolutionary adaptation to the requirements of interspecific communication. Importantly, ontogenetic-environmental effects can modify dogs’ capacity for gazing towards the humans – as it was shown that without proper socialization, dogs look back to a human less likely in an unsolvable task situation, than family dogs with normal levels of socialization do (D’Aniello & Scandurra, 2016).

The potential importance of acoustic signals in dog-human communication

Similar to other Canid species living in the wild, dogs also communicate predominantly through the sensory channels of olfaction, vision and hearing. The possible relevance of dog-human acoustic communication emerges from among the other means of information transfer due to the limitations of our species in comprehending canine chemical and visual signals. Canine chemical signals play an important intraspecific role in sexual and individual recognition (Bradshaw & Nott, 1995); however, they may not be relevant for humans, for example because of the difference between the sensitivity of olfactory systems of the two species (Marshall & Moulton, 1981). Dogs’ visual signals, although they can be conspicuous, are strongly taxon-specific. While there is a significant overlap between the visual signals of wolves and dogs (Bradshaw & Nott, 1995), the opposite is true for dogs and humans. It was shown for example that young infants misjudge the emotional state of dogs based on the assessment of dog portraits (Meints et al., 2010). Four-year-olds typically thought that dogs depicted with aggressively exposed teeth were ‘happy’ – presumably because of the resemblance between human smile and the facial signs of canine aggression. We can assume

that most of the visual signals of dogs are hard to interpret correctly for humans without ample a priori experience with them.

Acoustic signals however, may convey in a more universal way, the signaler's inner state and particular indexical features. According to the so-called 'motivational-structural (MS) rules' coined by Morton (1977), the inner state of the individual is reflected by the acoustic features of the call that are dependent on the vocal production organs of an individual: harsh (broadband), lower-frequency vocalizations are used in agonistic contexts; tonal, higher-frequency calls in appeasing or non-agonistic contexts. More importantly, these 'rules' seem to apply to a wide range of species (at least among mammals and birds), which makes acoustic signaling a likely channel of interspecific communication. According to Morton's theory, in terms of the evolution of competitive signal production, the emission of harsh, low frequency sound is linked to a relatively larger body size. If the receiver responds as expected, such signals may also determine the outcome of an agonistic encounter. Due to their size-dependency, such vocalizations may help to solve confrontations without actual physical interaction in evolutionary terms ('expressive size symbolism', Morton, 1994).

The information encoded in acoustic signals

Acoustic signals are arguably one of the most complex methods of information transfer. Although there are many robust, simple vocalizations used by various species, we should also remember that human language, the most sophisticated natural communication system, is also primarily an acoustic one (although it is inevitably and effectively aided by simultaneous gestural signals as well, (see Hostetter, 2011).

Information encoded in the acoustic signals can be sorted into three basic categories (Taylor, Ratcliffe, McComb, & Reby, 2014). Indexical information refers to such attributes of the caller, such as body size, sex, age, etc. The inner state of the signaler, as in hunger, fear, aggression, happiness, is transferred as so-called non-referential information (affective communication, graded signals). Finally, when the vocalization denotes an entity of the environment, independent of the signaler's inner state, we may consider it as functionally referential information (Marler, Evans, & Hauser, 1992).

We have already mentioned the structural-motivational theory by Morton (1977) that explains the universality of affective signals with the interconnectedness between certain anatomical features and the likelihood of particular inner states. Another important factor in the evolution of communicative signals is thought to be ritualization (Hinde, 1981). According to this, originally there was a tight connection between certain inner states and the phenotypic phenomenon occurring parallel with them (such as vocalizations, postures etc.). During ritualization, this tight connection could be loosened, and the audible (visible, etc.) byproduct of the inner state could be intensified, becoming a more obvious signal, already representing the inner state behind. The more independent (and 'cheap') the signals became to produce, the possibility for dishonest signaling arose.

Indexical information that encodes the caller's body size is one of the often studied aspects of acoustic communication. Perhaps the best-known theory behind this is the independent source-filter theory (Fitch & Hauser, 2003). Briefly, according to this, the quality of sound is predominantly affected by two factors: the 'source', which means the vocal folds in mammals; and the 'filter', that is a more or less intricate 'tube' above the vocal folds, called the vocal tract. As the length of the vocal tract is usually in strong correlation to the body size, the acoustic parameters of a call affected mostly by the 'filter' may also correlate with the size of the body. Formant dispersion is known to be one major parameter of the sound having such indexical relevance (Riede & Fitch, 1999).

The investigation of the possible evolutionary changes in the vocal communication of dogs

1. Quantitative and qualitative differences between the vocal repertoires of the dog and its closest relatives

There are extensive comparative descriptions of the vocal repertoires of dogs, wolves and a few other closely related wild Canid species (Cohen & Fox, 1976; Tembrock, 1976). The authors enumerated the call types and the contexts where particular vocalizations seemed to be relevant. One of the rather remarkable outcomes of these early efforts was that a certain sort of vocalization, barking, turned out to be almost a ‘trademark’ for dogs. While grey wolves, which are the closest relatives of dogs, only bark in a few (agonistic, resource-holding) contexts and by emitting single or short bursts of barks only, dogs in general bark in a strongly repetitive manner and in almost every possible context (although considerable qualitative and quantitative breed differences can also be expected in the level of barkiness – see e.g. Hart & Miller, 1985; Feddersen-Petersen, 2000). From the ethologist’s point of view, at first this discovery represented more of a difficulty than an advantage. For decades, it seemed to be almost impossible to find a convincing theory that would explain the evolutionary background of such a hypertrophied means of vocalization in the dog – from the aspect of communication.

If dog barking is considered as a form of communication, the researcher should prove that barks can be characterized with context-specific acoustic features, and most importantly they elicit specific reaction from the receiver. Additionally, we may also expect that according to the biological definition of communication (Scott-Phillips, 2008) the response of the receiver should be advantageous for the signaler (i.e. the barking dog). Only if these requirements are fulfilled would it be plausible to consider dog barks as communicative signals. Until the late 20th century mostly non-communicative hypotheses existed as explanations of the evolution of abundant barking in dogs. These theories agreed that the barking behavior of dogs is an outcome of changes along (or due to) domestication, but at the same time they could not assign specific communicative function to the barking. For example, according to the ‘theory of neoteny’, barking is one of the ‘neotenic’ features of adult dogs, being characteristic at the same time to juvenile wolves (Schassburger, 1993). Another theory considers dogs’ barking as a general indicator of a state of excitement (Coppinger & Feinstein, 1991), emerging in the lack of strict counter-selective forces since domestication. Other authors consider barks as ‘minimally informative vocalizations’, referring to the acoustic and functional resemblance between ‘contagious barking’ among dogs and the well-known phenomenon of mobbing choirs in many other species (Lord, Feinstein, & Coppinger, 2009).

Research into the communicative function of dog barks gained new momentum when it was found that there are stable acoustic differences among barks originating from different contexts (Yin, 2002; Yin & McCowan, 2004). Although, indirectly these results indicated that dog barks may reliably show the inner state of the signaler, as the contexts that were used to elicit the barks could be connected to different motivational states of the dog (such as in the mentioned studies by Yin, separation, play and territorial aggression). Similarly, an important addition was the concept by Feddersen-Petersen (2000) to the theoretical framework of the evolution of dog barks. She hypothesized that while the vocal signals of wolves served predominantly as long-distance communication (howls), the domesticated dog’s new social environment also included humans and new selective forces favored short and mid-distance vocalizations – such as barks.

2. Do humans understand dog vocalizations?

We previously showed that there is well established evidence regarding the differences between the vocal repertoires of dogs and wolves, but until recently it was unknown whether dog barks (or, in fact, any other dog vocalizations) would convey other information for humans than the dogs is ‘excited’ (Coppinger & Feinstein, 1991). Our approach to the investigation of dog barks was inspired by the results and theories of Feddersen-Petersen (2000) and Yin (2002), already mentioned in the previous paragraph; furthermore, our main hypothesis was based on the notion that during domestication, the most relevant selective pressure on dogs shaped their behavior and cognitive capacity towards being compatible with the anthropogenic environment (e.g. Miklósi & Topál, 2013). As an indirect measure of this presumed adaptation, it is worth to mention that dogs are in general perceived more positively than other animals by humans (Sevillano & Fiske, 2016). To be able to answer the next question about signal evolution in the case of interspecific communication between dogs and humans, we need to see whether barks are informative to the ‘new audience’ of the dogs – humans.

Although Yin (2002) discovered that dog barks recorded in three contexts (‘play’, ‘isolation’, ‘disturbance by doorbell’) showed consistent acoustic differences, these early analyses did not go beyond the identification of different types of barks, based on a few main acoustic parameters, such as duration and mean dominant frequency. A few years later, new analyses were performed where a larger set of bark samples of the same dog breed (Mudi) were included from six contexts: ‘Stranger at the gate’; ‘Schutzhund training’; ‘Left alone’; ‘Preparing for a walk with owner’; ‘Asking for a ball’; ‘Play with owner’ (Pongrácz, Miklósi, Molnár, & Csányi, 2005). More importantly, we also included a new parameter to the analysis, interbark intervals, which characterizes how fast was the pulse of a given bark sequence. It was found that barks from the agonistic situations (‘Stranger’, ‘Schutzhund’) can be characterized with lowest fundamental and peak frequencies, meanwhile the interbark intervals were the shortest in these bark sequences. On the other hand, ‘Left alone’ barks had the highest fundamental and peak frequencies, coupled with longer interbark intervals. These findings strengthened the earlier notion of Yin (2002) and Yin and McCowan (2004), providing ample acoustic evidence that dog barks show characteristic and reliable differences among different contexts – a prerequisite for any receiver to be able to distinguish these.

Obviously, biological sounds can be described with a much higher number of acoustic parameters than tonality, fundamental frequency and interbark intervals. However, the analysis and interpretation of several dozens of parameters requires more sophisticated procedures. By employing a machine learning algorithm it was possible to include a vast array of parameters for the analysis of more than 6 thousand individual bark samples (Molnár et al., 2008). In this study evidence was found that barks, even when they were isolated from the original sequences (therefore lacking the potential information encoded in the interbark intervals), contained reliable cues both about the context and the individual dog that emitted the particular bark. With a slightly different mathematical approach (k -nearest neighbors supervised learning), recently it was found that single barks contain not only context and individual specific information, but they also convey the sex and age of the signaler (Larrañaga et al., 2015).

Having the knowledge that dog barks significantly differ from each other among contexts, there is a solid bioacoustical fundament for the experiments that tested whether human listeners are able to recognize contextual and inner state-related information in these vocalizations. In a series of playback experiments a methodology was employed where pre-recorded sequences from six contexts and several dozen dogs were presented to human participants. Subjects had to guess the context and rate each bark sequence along five emotion scales (Aggressive, Fearful, Desperate, Happy, and Playful). Bark sequences were recorded

from a single dog breed (Mudi), thus it was avoided that the additional acoustic variability likely to be encountered in the case of anatomically different breeds of dogs. Besides the main questions (do humans recognize different contexts / do humans attribute consistently inner states to particular contexts based on the acoustics of barks), it was also tested whether the amount/type of experience with dogs would affect the subjects' responses. Three empirical directions were followed to achieve this goal: (1) the possible effect of dog-related experience in sighted adults; (2) the possible effect of dog-related experience in sighted and sightless adults; and (3) the possible effect of age and experience with dogs in children.

The results showed that dog barks carry plentiful, various and easy-to-decode information for the human audience as well. More importantly, these vocalizations are 'understandable' for humans without the constraints of extensive learning, as it was found that adults with both ample (i.e. owners of Mudi dogs) and minimal dog-related experience (i.e. never owned a dog) were able to recognize the contexts significantly above chance level (Pongrácz et al., 2005). From the six contexts, listeners had the highest success rate of recognition in the case of the 'Stranger', 'Schutzhund' and 'Left alone' barks, meanwhile 'Before walk' and 'Asking for ball' barks were recognized only at chance level. Regarding the moderate-to-none effect of experience on adults' success in recognizing the context of barks, further support was gained from the experiment with sightless subjects. Adults with either congenital or later developed blindness performed equally with sighted controls in every aspect of contextual recognition of dog barks (Molnár, Pongrácz, & Miklósi, 2010). This result showed that visual experience about dog behavior is not of primary importance when deciphering the potential context of the vocalization. Finally, the effect of age turned out to have only a moderate effect in the success rate of listeners. When the performance of children 6, 8 and 10 years of age was compared to the adults', it was found that participants of all age groups recognized 'Stranger' barks above the chance level, the next easiest context was 'Left alone', meanwhile only the ten years old and adults recognized 'Play' barks (Pongrácz, Molnár, Dóka, & Miklósi, 2011). Regarding the inner state of barking dogs, based on the playbacks, human participants attributed feasible emotions to contexts in each of the above mentioned studies, regardless of their level of experience, age and sightedness (Pongrácz et al., 2005, 2011; Molnár et al., 2010). In details, agonistic barks such as the ones recorded in the 'Stranger' and 'Schutzhund' categories, were found highly aggressive and low in their scores of fearfulness, happiness and playfulness. 'Left alone' barks were significantly more desperate and fearful than any of the other contexts by the opinion of the subjects. 'Play' barks were found mostly playful and happy. Interestingly, 'Before walk' and 'Asking for ball' barks did not show an unambiguous pattern of attributed emotions, similar to the above mentioned difficulty with their contextual recognition.

Although the contexts where the bark samples were collected from show typical acoustic attributes, the natural variability of bark sequences, plus the individual peculiarities of a given dog and recording situation, makes it difficult to analyze the effect of acoustic parameters on the inner state scores. Therefore in another study artificial bark sequences were assembled from a pool of original single bark segments, where the selection of single barks was based on their fundamental frequency (low, medium, high); and tonality (low, medium, high). By adding interbark intervals (short, medium, long) to the segments, 27 types of bark sequences were created for the playback test, where the acoustic makeup of the sequences was more uniform than in the case of the natural recordings. It was found that adult human listeners decipher the possible inner states of dogs according to the predictions of the structural-motivational rules by Morton (1977). Low pitched barks were considered as 'aggressive', with only low scores of other emotions. High-pitched barks on the other hand were given low scores of aggression, and if they also had long interbark intervals, they were given high scores

of ‘happiness’. High-pitched barks that had high tonality values additionally were given the highest ‘despair’ scores (Pongrácz, Molnár, & Miklósi, 2006).

The results of the previously mentioned studies provide convincing evidence that humans can successfully recognize most of the commonly occurring contexts that were included in the sample collection. It is worthy to note that although the rating of emotions and the context categorization happened in separate turns during the testing, participants were mostly able to recognize those contexts where they also provided the most unambiguous rating of emotions. According to our hypothesis, the contextual ‘understanding’ of dog barks in humans is based also on the involuntary assignment of particular inner states to dog barks in the ‘first step’ of mental processing of auditory inputs. Where the assessment of the signaler’s inner state is not easy, human listeners may also face difficulty to figure out the context. The interconnectedness of contextual and affective information processing of vocalizations was further supported recently by Faragó et al. (2014), who provided evidence that the emotional content and valence of canine and human vocalizations show similar patterns in humans.

3. Are there specifically human-directed elements of the canine vocal repertoire?

The fact that dog barks provide affective and contextual information for the human listeners about the signaler is necessary but not enough evidence to prove that domestication caused such changes in the vocal repertoire of dogs that were driven by the specific evolutionary need for a more effective interspecific communication. To see whether some signals are better suited/ more relevant for the human audience than to the intraspecific domain of communication, it was necessary to test whether dogs show specific responses to the vocalizations that proved to be informative for humans.

One problem with the testing of dogs’ responses to barks in the laboratory is that there is no well-established ethogram for the behaviors elicited by barking. Apart from observations showing dogs are likely to join when they hear other dogs’ barking (e.g. Lord et al., 2009), until recently there were no empirical studies about intraspecific canine communication by barks. Later, as an initial approach, laboratory experiments were performed based on the habituation-dishabituation paradigm to see, whether dogs show signs of discrimination between the barks of different individuals (Molnár, Pongrácz, Faragó, Dóka, & Miklósi, 2009); and between barks from different contexts (Maros et al., 2008; Molnár et al., 2009). Dogs were placed in the middle of a room with their owners, and the sound playbacks came from a speaker that was positioned to one side (left or right) of the dog. Latency and duration of gazing towards the speaker was measured at the time of and after the playback. Additionally, in the study of Maros et al. (2008) variance of the subjects’ heart rate was measured with a portable device, mounted on the dog. At first subjects heard three times the same dog’s bark (from one particular context), then, depending on the actual test, the fourth playback was either the same dog’s bark from another context, or a bark from a different dog but same context as in the first three occasions. For controlling simple acoustic dishabituation, different mechanical noises (refrigerator, drilling machine) were played back in the 3+1 design. As contexts of barking, recordings from the ‘Stranger’ and ‘Left alone’ situations were used. The results of both the heart rate (Maros et al., 2008) and gazing behavior measurements (Molnár et al., 2009) showed that dogs were able to detect individual and contextual differences between the barks – meanwhile different mechanical noises did not elicit dishabituation in the subjects. Of course, these results provided only a theoretical possibility for the communicative role of barks, because the change in heart rate variance and the gazing towards the speaker can hardly be considered a specific response according to the context of the barks. However, in the following study (Pongrácz, Szabó, Kis, Péter, & Miklósi 2014) dogs were tested in their original living environment (suburban gardens), where bark samples of familiar and unfamiliar dogs, recorded in either ‘Stranger’ or ‘Left alone’ contexts

were played back from a hidden speaker located on the street. Dogs behavior before, during and after the playbacks was video-recorded. The results showed that both familiarity and context had an effect on dogs' responses. 'Stranger' barks, especially if they were emitted by unfamiliar dogs, elicited vivid approach, and exploration and barking from the subjects. Upon the barks of familiar dogs, subjects looked more often towards the house (where the familiar dog was locked in during the experiment). More importantly, dogs did not show any specific reaction to 'Left alone' barks, independent of the familiarity of the source (Pongrácz et al., 2014).

Based on the above mentioned results of the playback experiments in the field, we can assume that particular barks may serve as communicative signals for dogs as well – 'Stranger' barks elicited appropriate reaction (exploration, vigilance, response barks) from the subjects. There is also proof of the relevance of individual-specific cues of barks in a naturalistic setting (Pongrácz et al., 2014), this is in strong contrast with an earlier result where humans were not able to distinguish between individual dogs based on their short bark sequences alone (Molnár, Pongrácz, Dóka, & Miklósi, 2006). However, barks of 'Left alone' dogs did not have noticeable effect on the dogs that were moving freely in their home environment – although the earlier experiments in the laboratory (e.g. Molnár et al., 2009) proved that these barks were distinguishable from the 'Stranger' barks for dogs. Contrary to these results, we showed earlier that 'Left alone' barks were highly informative for human listeners, who successfully recognized them and attributed unambiguous affective states to these dogs. In a recent study it has been also discovered that 'Left alone' barks may have a specific effect on humans – it turned out that high-pitched barks (one of the main attributes of the separated/isolated dogs' vocalizations) received the highest 'annoyance' scores from human participants (Pongrácz et al., 2016). According to our theory of the communicative relevance of auditory nuisance, noise of biological origins may have a stressful effect on the listener because it effectively motivates a response that cannot be performed, or turns out to be unsuccessful. A well-known exemplar of this phenomenon is the cry of a baby, a highly alerting and difficult to ignore sound (Swain et al., 2008). It was also found that cat purrs, which sound like 'urging' or 'demanding' to human listeners, contain acoustic frequencies similar to baby cry (McComb, Taylor, Wilson, & Charlton, 2009) – a further evidence of the effectiveness of evolutionary parallels in acoustic communication. Based on our results the barking of left alone dogs is highly informative and urging for humans – most probably because of the acoustic structure that evokes emotional alarm reaction from human listeners.

Dog growls – are 'conservative' acoustic signals suitable for interspecific communication?

As a counterpart for dog barks in the canine 'vocabulary', growls can be regarded as 'conservative' from an evolutionary aspect, as they have similar occurrence contextually (and acoustically) in wolves and dogs (Cohen & Fox, 1976). Growls are emitted in a relatively narrow range of contexts, most of these are agonistic, but dogs also growl during play bouts. Previously we showed that dog barks went through considerable changes during domestication that resulted in at least one characteristic bark type ('alone' or 'separation' bark) that is mostly relevant for humans, but not for dogs (Pongrácz et al., 2014; 2016). The question is intriguing therefore, whether the conservative growls would be understandable for dogs and humans alike.

There is a wealth of bioacoustics research available dealing with the indexical information (regarding the caller's body size) encoded in dog growls. In general, two main approaches were followed in these studies: (1) researchers either experimentally manipulated the acoustic features of growls that were relevant for size communication (fundamental frequency, formant dispersion) (e.g. Taylor, Reby, & McComb, 2008; Taylor, Reby, & McComb, 2010);

or (2) researchers used unaltered growl sequences from different size dogs in their tests (e.g. Bálint, Faragó, Dóka, Miklósi, & Pongrácz, 2013; Faragó et al., 2010a). Notably, in these studies both humans and dogs were tested as listeners, and the results in general concluded that dog growls convey useful and readily decipherable information about the signaler's body size. From the acoustic parameters, formant dispersion was found to be the most reliable predictor of body size (Taylor et al., 2008), in agreement with the earlier mentioned source-filter theory (e.g. Riede & Fitch, 1999). A further interesting result regarding the reliability of communication about the body size was when it was found that dog growls from different contexts conveyed more or less accurate ('honest') signaler size. Employing the modality matching paradigm, where subject dogs were provided pictures of differently sized dogs with parallel growl playbacks, it was found that in the case of food-guarding (agonistic) growls, dogs preferred to look at the 'matching size' picture that showed a similarly sized dog to the growling one (Faragó et al., 2010a). However, when the playback was a playful growl, dogs preferred to look at the larger from the two depicted dogs (Bálint et al., 2013). The possibility that dogs growl themselves 'larger' during play fits well with one of the important characteristics of play signals: namely that these can be strongly exaggerated, resulting in a clear meaning of playfulness, instead of 'real' aggression (Feddersen-Petersen, 1991).

Although it was known from earlier research that humans react to size-related acoustic information encoded in dog growls (Taylor et al., 2008; 2009), an important detail still remained unknown, whether dogs would use 'acoustic size manipulation' in the case of communication with humans. In an experiment where either men or women approached the subject dogs in a mildly threatening manner (a so-called 'threatening stranger' paradigm developed by Vas, Topál, Gácsi, Miklósi, & Csányi (2005)), it was tested whether the body size or the gender of the approaching human affects the size-related information of the elicited growls. Our results showed that the apparent size of the threatening strangers did not affect the defensive response of dogs, however, dogs that had experience with both male and female owners at home, emitted growls of larger encoded own body size when they were approached by male experimenters (Bálint, Faragó, Miklósi, & Pongrácz, 2016). Besides being the first study providing evidence that dogs can modify their size-related signals according to the stress level in an agonistic encounter, it left open an interesting question for further analysis: whether humans would be able to recognize the difference between the original and modified apparent body size?

Besides the indexical content, dog growls are likely to convey information about the inner state of the signaler as well. A further question is whether there is a detectable difference between agonistic growls that originate from different contexts – for example, could listeners tell apart the growls of dogs that are defending their food or themselves from a threatening opponent. So far, the only research where the contextual/ affective content of dog growls were tested in the intraspecific domain was done by Faragó, Pongrácz, Range, Virányi, & Miklósi (2010b). In that study they used an experimental setup where dogs had the opportunity to obtain a large, 'unattended' bone, meanwhile in each experimental group one of the three growl types were played back: 'bone guarding', 'threatening stranger' and 'play'. The results showed that dogs withdrew from the bone only if they heard the context-appropriate bone guarding growls. As there was a clear difference between the responses to the two agonistic types of growls, there is a chance that (1) growls contain context-specific (functionally referential) information; or (2) 'bone guarding' growls convey higher levels of aggression, than 'threatening stranger' growls.

Finally, there are a few studies that tested human listeners with growl samples of various contexts. Taylor et al. (2009) found that the subjects were not able to discriminate between growls recorded in playful and an agonistic context – however, when they created resynthesized growl sequences, they found that bouts of shorter growls were perceived as

more playful by the human subjects. In a recent study (Faragó, Takács, Miklósi, & Pongrácz, 2017) human listeners were tested with natural (not modified) sequences of growls from the three contexts already mentioned in the Faragó et al. (2010b) study. Participants had to identify the context and also evaluate the affective state of the dogs on five emotional scales, used earlier for the dog barks (e.g. Pongrácz et al., 2006). It was found that contrary to the results of Taylor et al. (2009), listeners could recognize each context above chance level. Play-growls were found the least aggressive but highly playful, meanwhile ‘bone guarding’ and ‘threatening stranger’ growls were found mostly aggressive. Interestingly, participants thought that ‘bone guarding’ growls were significantly the most aggressive. Although it was found that the contextual recognition was highly successful in the case of human participants, this latter result shows a likely parallel with one of the explanations of the results of Faragó et al. (2010b), where one could hypothesize that the strong deterrent effect of ‘bone guarding’ growls was due to the highest level of encoded aggression.

Conclusions – outlining a new theory about the evolution of dog barks

It seems likely that different types of dog vocalizations went through markedly different evolutionary changes during domestication. While growls remained mostly in their ‘original’ form, with the exception of a few dog breeds, barks literally proliferated. With the help of our results, based on both the playback experiments with human and canine listeners who were tested with dog bark sequences of particular contexts, we are now able to formulate a well-supported new theory about the evolution and function of dog barks.

In the wild species of Canidae, barks are almost solely used in contexts where they convey warning or different levels of aggression (gray wolves: Lehner, 1978; Schassburger, 1987; 1993; African wild dogs (*Lycaon pictus*): Robbins, 2000; crab-eating foxes (*Cerdocyon thous*), bush dogs (*Speothos venaticus*), maned wolves (*Chrysocyon brachyurus*): Brady, 1981; red wolves (*Canis rufus*): McCarley, 1978; coyotes (*Canis latrans*): Lehner, 1978; red foxes (*Vulpes vulpes*): Newton-Fisher, Harris, White, & Jones, 1993; and dholes (*Cuon alpinus*): Volodin, Volodina, & Isaeva, 2001). More importantly in a recent study it was found that even in the dingo (*Canis lupus dingo*), the wild dog of Australia, barks occur only in the original, agonistic context (Déaux & Clarke, 2013). Although it is important to note that the subjects of the latter study were dingoes kept in enclosures and not as companions, it is somewhat reasonable to assume that the contextual proliferation of barks happened mostly in such dog populations that lived and evolved in the possible closest functional connection to humans. From the evolutionary aspect, the most important new feature of the ‘modern barks’ is the inclusion of the opposite end against aggression on the affective continuum – fear/desperation and happiness (e.g. Pongrácz et al., 2005, 2006). Empirical evidence was found that meanwhile dogs do not show interest towards one of the ‘new’ types of barks (left alone dog, Pongrácz et al., 2014), these barks are highly annoying (i.e. urging to intervene) for humans (Pongrácz et al., 2016) who easily recognize the context and connect no aggression but rather fear and despair to these vocalizations. In terms of signal evolution, the process that leads to a behavior with somewhat changed phenotype and modified meaning compared to the original form is called ritualization (Hinde, 1981). We hypothesize that in the new, anthropogenic environment, dog barks went through ritualization, gaining new roles to fulfill that proved to be adaptive during the interspecific communication with humans.

An interesting parallel can be drawn between the above described way acoustically modified barks became common in new communicative contexts and the process of adaptive radiation, widely discussed in ecology and evolutionary sciences regarding speciation (e.g. Benton, 1996; Otte & Endler, 1989). This phenomenon involves the theoretical, once uniform population, that through selection becomes adapted to moderately or strongly different new

niches, eventually resulting in a related group of new species. In our new model (see Figure 1 as an illustration), we could consider acoustically distinct vocalizations as ‘species’ and communicative contexts (or distinct affective states of the signaler) as ‘niches’. The model involves the need for effective intra- and inter-specific communication as forces of selection, and fitness could be assumed either on the level of a particular vocalization (i.e. how common it is in a particular context along the generations); or on the level of actual survival of the genes of a given signaler. According to our model, under a new force of selection – effective signaling towards humans – some of the original vocalizations of the dog’s ancestor, went through ‘adaptive radiation’, hence creating new ‘niches’ (i.e. signaling other affective states than aggression, in other than agonistic contexts) by the incorporation of new acoustic features. With this model we can even formulate hypotheses about the course of signal evolution in case of dog vocalizations. One of the crucial questions regarding adaptive radiation/ speciation is whether the divergence of niches (1) appeared in the early stage of evolution (‘habitat-first’ theory, resulting in closely related, allopatric species (Diamond, 1986)); or (2) the main diversification of niches happened only later along the course of speciation (Ackerly, Schwilk, & Webb, 2006). In case of (1) we would find the distinct niches populated by mostly closely related species, while in case of (2) distinct niches would be created by more loosely related species. The fact that now we know about the information conveyed not only by barks, but another type of dog vocalization, the growls, allows us to elaborate better the theory of ‘adaptive radiation’ of vocalizations in the dog. We can consider the acoustically different barks as ‘closely related species’, meanwhile growls would represent another cluster of closely related ‘species’ that are at the same time related only loosely to barks. We showed that barks and growls can both convey the same affective states (i.e. practicing similar ‘niches’) – such as aggression, or playfulness (e.g. Pongrácz et al., 2006; Taylor et al., 2009; Faragó et al., 2017). At the same time barks diversified considerably from the ancient form of agonistic signal, creating new ‘niches’ such as conveying non-aggressive negative affective states, such as fear, frustration and despair. Based on these features, we assume that for the evolutionary ‘speciation’ barks would rather follow option (2) in adaptive radiation, where the distinct communicatory ‘niches’ developed only later in the course of diversification of the acoustic signals themselves.

According to our hypothesis about the evolutionary changes in dog barks during domestication (Pongrácz, Molnár, & Miklósi, 2010), the first step could be a spontaneous inflation of acoustic variability of barking vocalizations due to relaxed selection (Price, 1999) in the anthropogenic environment. At the same time, this new environment also raised new challenges (e.g. short or mid-distance signaling to a ‘new audience’; new sorts of social interactions), which were possible to tackle by means of vocalizations due to the universal rules of acoustic information encoding. Why barks become the most typical form of vocalization in dogs, can be explained by the fact that this type of signal had the opportunity acoustically for changing the most. Unlike the rather long, undivided howls, growls and whines, bark sequences consist of short units which opens up the possibility for quantitative proliferation. Additionally, by means of the variable lengths of interbark-intervals, it offers another effective way to encode information about the inner state of the signaler (Pongrácz et al., 2006). Besides the complexity of segmentation, bark sequences show a spectacular variability of other acoustic parameters as well, from which the easiest to analyze are the harmonic-to-noise ratio and frequency components. Compared to the generally low-pitched, harsh barks of wolves, dog barks radiated to the other extremes (tonal, high-pitched) of acoustic possibilities. This made it possible that while these vocalizations still remained in the category of ‘barks’, they can be used now as vocal phenotypes of other inner states, unlike the purely agonistic barks of wolves. On the theoretical level, it would be a fascinating

evolutionary enigma whether a similarly informative communication system could have evolved in dogs, based on howls, growls or whines instead of barks.

Research directions for the future

After almost two decades of research on the information content, function and evolution of dog vocalizations, luckily there are still plenty of unknown areas, thereby offering new challenges for the ethologist. The constant advance in technology allows us to include such strategies and methods that connect behavioral research with cutting edge neurobiology (e.g. Andics, Gácsi, Faragó, Kis, & Miklósi, 2014; Andics et al., 2016; Faragó et al., 2014). There is still a major lack of applied research regarding dog vocalizations, although both from the aspect of animal welfare (e.g. new methods in diagnosing separation-related disorder) and the peaceful coexistence of dog owners and the less dog enthusiastic part of society (e.g. nuisance barks – Pongrácz et al., 2016), it would be time for further employment of some of the empirical results on canine acoustic communication. Through a better understanding of dog communication and its effects on human behavior, this would help to enhance the quality of dog-human coexistence and could also improve the reputation of dogs and dog ownership, which is more and more important in a world where both populations are steadily growing. Finally, dog vocalizations offer an excellent opportunity for large-scale genetic and evolutionary research, exploiting the already present lines of purpose-selected breeds, where the proximate and ultimate role of vocalization in the process of adaptation could be readily investigated.

Acknowledgments

Much of the research mentioned in this paper has been funded by grants provided by the Hungarian Ministry of Education OTKA K82020 and by the Hungarian Academy of Sciences, MTA (01 031). The author wishes to express his gratitude to Anna Gábor for creating the illustration for the manuscript, Tamás Faragó and Antal Dóka for the sonograms and drawing for the illustration, and Celeste R. Pongrácz for the English proofreading of the manuscript.

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Figure legend

Figure 1. Schematic depiction of theory of adaptive radiation applied to the changing communicative role of dog barks along domestication. On the bottom half of the disk, communicative contexts and the corresponding types of vocalizations are shown that were characteristic to the hypothesized ancestor of the domestic dog. On the upper half, we show the phase after the domestication, where barks became typical in each of the communicative contexts. Around the disk, in the outermost ring, there are sonograms illustrating the acoustic structure of typical vocalizations to that category (in case of the upper half, only bark sonograms were used). Little black pictograms of a human or a dog show the assumed receiver species for the given vocalization. ‘?’ besides the dog pictogram marks the lack of empirical knowledge about the within-species role of barking in that context.

