

A Review of Human Perceptions of Emotions From Animal Vocalizations

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The study of the evolution of emotional communication dates back to Charles Darwin and has a rich history rooted in ethological research. The evolution of emotional communication is a growing field of research that explores how animals express and perceive different emotions. Studies continue to shed light on the complexity and universality of emotional communication in the animal kingdom. This review article examines the literature on human perceptions of emotions from animal vocalizations, addressing the acoustic variables that predict the way vocalizations are interpreted, whether people are generally more accurate with gauging arousal or valence from vocalizations, any patterns with respect to species, and subject variables that influence perceptions. By reviewing and synthesizing the existing literature, this article seeks to provide a comprehensive overview of the current understanding of human perceptions of emotions in other species and highlight avenues for future research in this field.

Keywords: communication, cats, animal vocalization

Emotional communication is a fundamental aspect of social interaction, allowing individuals to convey and perceive emotions, thereby facilitating coordination, bonding, and adaptive responses. The evolution of emotional communication in animals has captivated researchers for decades, with early contributions from influential figures such as Charles Darwin (1872). While the study of emotional communication has predominantly focused on human-to-human interactions, there is a growing recognition of the importance of understanding emotional communication across species. One method of research in this topic is the testing of heterospecific emotion perception - perception of emotion from another species' signals. In the last decade, there has been increasing research investigating human perception of emotion from other species' vocalizations. Exploring how animals express and perceive emotions provides valuable insights into the evolutionary roots and universality of emotional experiences. Furthermore, studying emotional communication can help contribute to animal welfare, advance knowledge of evolutionary pressures that shape behaviors, and enhance human-animal interactions.

In order to understand the current direction of the study of emotional communication, it is important to understand

the dimensional view of emotion (Mendl et al., 2010), which suggests that any emotional state can be characterized by where they lie on the dimensions of valence (positive or negative classification) and arousal (activation of the sympathetic nervous system). For example, the emotion of fear could be described as having high arousal and negative valence whereas the emotion of sadness could be characterized by low arousal and negative valence. The dimensional view of emotion has gained prominence due to its ability to capture the complexity and variability of human emotional experiences. It allows for a more nuanced understanding of emotions by considering them as continuous variables rather than discrete categories. This dimensional way of characterizing emotions is especially helpful when studying how humans perceive animal emotions as each dimension is hypothesized to have consistent acoustic correlations. The current article is a review of the literature on human perception of heterospecific vocalizations, focusing on four questions that have emerged as central within this area of research. First, it explores the acoustic variables that predict the way vocalizations are interpreted and how they contribute to emotional understanding. Second, it investigates whether individuals tend to be more accurate in gauging arousal or valence from

vocalizations. Third, it examines any patterns observed in emotional perception across different species, shedding light on potential species-specific characteristics. Finally, it explores the subject variables that influence perceptions of emotions from vocalizations, such as individual differences and contextual factors. This article aims to offer a comprehensive overview of the present comprehension regarding human perceptions of emotions in other species and identify potential directions for future research by extensively examining and synthesizing the existing literature.

ACOUSTIC VARIABLES

When it comes to predicting people's responses to animal vocalizations, there are different acoustic variables that can be important depending on the context and species being studied. Pitch, also known as fundamental frequency (F0), is a key factor that can influence human perception of animal vocalizations. The F0 is the frequency of the lowest frequency component of a sound and determines the perceived pitch of the sound. Many mammals and other species experience a tensing of vocal folds when the sympathetic nervous system is activated, resulting in a higher F0 when more aroused. Different animals can have vocalizations with varying F0, and this can convey different emotions or information. For example, in a study by Pongracz et al. (2005), they found that the F0 and duration of dog barks were important cues for humans in recognizing different types of barks, such as alarm barks and play barks. Similarly, Tallet et al. (2010) found that the F0 contour and duration of piglet vocalizations were important cues for human listeners in identifying the emotional content of the vocalizations.

Duration, or the length of a sound, is another important acoustic variable that can affect human perception of animal vocalizations. The length of a vocalization can convey different meanings, such as the level of urgency or intensity of an animal's communication. In some studies, duration has been found to be a more important predictor of human responses to animal vocalizations than pitch. For example, McComb et al. (2009) found that duration alone was the most important predictor of emotional valence in cat vocalizations. Meanwhile, in a study by Farago et al. (2014), both pitch and duration were important predictors of human recognition of emotional states in dog vocalizations.

In addition to pitch and duration, other temporal parameters, such as rhythm and tempo, can also be important predictors of human responses to animal vocalizations. In a study by Filippi et al. (2017), the rhythmic structure of macaque vocalizations was found to be a key factor in determining their emotional content. However, there is also mixed evidence and variability across studies regarding the importance of these acoustic variables in predicting human responses to animal vocalizations. For example, some studies have found that contextual factors, such as the familiarity of the listener with the species, can influence the relative importance of different acoustic variables. Some studies have even found a difference in F0 during positive valence in vocalizations of different species. For example, Jovanic and Gouzoules (2001) found that rhesus monkeys and gray mouse lemurs produce calls during positive contexts that are characterized by low frequencies, whereas vocalizations made by dogs in positive situations were characterized by high frequencies (Yin & McCowan, 2004). Overall, while pitch, duration, and temporal parameters can all be important predictors of human perception of animal vocalizations, the specific cues that are most influential may depend on a variety of factors, including the context, species, and listener.

AROUSAL VS. VALENCE

The accuracy of perception regarding arousal and valence varies from study to study. Overall, arousal perception accuracy tends to be higher than chance, but valence perception accuracy can vary across species and contexts. Valence is also less studied compared to arousal in the context of emotional vocalizations in part due to the difficulty of finding calls with a positive valence, especially those that have a similar arousal level to calls with a negative valence (Briefer, 2012).

In general, humans tend to rate vocalizations with a higher F0 as having greater arousal. As discussed previously, vocalizer arousal does generally correlate with vocalization F0 in many animal species, therefore this "pitch rule" often leads to accurate judgments of arousal (Filippi et al., 2017). However, using F0 as a sole indicator of arousal can also lead to inaccurate judgments of arousal in cases where the F0 of an animal vocalization is dependent on body size, age, or sex of the animal rather than the animal's arousal.

More research is needed to determine the accuracy of this “pitch rule” in a wider range of species.

Conclusive and repeated research has been done to support the idea that humans are fairly accurate with rating the arousal of animal vocalizations, although the variation in species is still fairly limited. Research by Filippi et al. (2017) found that humans accurately rated the arousal of vocalizations of nine species including hourglass treefrogs, American alligators, black-capped chickadees, common ravens, domestic pigs, giant pandas, African bush elephants, Barbary macaques, and humans. Another study found that humans accurately categorized pig calls into various categories of contexts based on valence and arousal (Tallet et al., 2010).

Less research has been conducted on the accuracy of the valence of animal vocalizations, however some studies have found significant results. A study by Greenall et al. (2022) found that humans accurately rated the valence of vocalizations by mammalian species including humans, horses, pigs, goats, cattle, and boars. It has also been found that even when participants could not accurately categorize the contexts of certain animal vocalizations, they could still accurately judge the arousal and valence (Kamiloglu et al., 2020). Another study found that participants, regardless of age or previous experience, were able to accurately categorize the valence of horse whinnies (Merkies et al., 2021).

Overall, more research is needed to determine a more precise conclusion on how humans rate the arousal and valence of animal vocalizations, how often these methods lead to accurate judgements, and how the accuracy differs based on species.

VARIATION ACROSS SPECIES

Previous research on human perceptions of animal vocalizations have focused largely on mammals, especially those closely related to humans and those that are commonly kept as pets. Regarding patterns with respect to species, it seems that humans are generally more accurate in perceiving emotional vocalizations in species they are most familiar with, such as dogs, cats, and domesticated animals. There is evidence to suggest that familiarity with a species can enhance perception accuracy. However, it is not consistently found that humans are more accurate with closely related species

compared to distantly related species. Much of the current literature is based around human perceptions of vocalizations of commonly domesticated species such as dogs and cats, and more research is needed to establish findings for other species that humans may not have experience with.

It has also been found that familiarity with some specific species can improve accuracy in emotional judgements. For example, McComb et al. (2009) found that individuals that had owned a cat performed significantly better than non-cat owners in judging urgency and pleasantness of cat vocalizations. Another study looked at how humans with different experience levels interpreted pig vocalizations. They found that ethologists studying pigs showed more accurate contextual recognition than students with no pig expertise (Tallet et al., 2010). On the other hand, one study found that experience level with horses did not affect the accuracy of categorizing valence of horse vocalizations. Another study found a facilitating effect of experience where humans with cat experience more accurately classified the context of single cat calls, but not bouts of cat calls (Nicastro & Owren, 2003). Furthermore, Pongracz et al. (2005) found that humans rated the emotional content of dog barks in a similar manner and with similar accuracy regardless of prior experience. It is possible that familiarity with a species may affect perceptions depending on the type of animal or vocalizations or the context of the experience.

Some species that have been featured in many studies of human perception include domesticated dogs, cats, pigs, and horses. A consistent finding across many studies is that humans appear to have the ability to accurately perceive dog vocalizations (Farago et al., 2017; Nicastro & Owren, 2003). It has also been found that humans can accurately judge the vocalizations of domesticated farm animals such as pigs and horses (Filippi et al., 2017; Greenall et al., 2022; Merkies et al., 2021; Tallet et al., 2010). Such research enhances our understanding of human-animal communication and the potential for cross-species understanding, but the evolutionary considerations that can be drawn are limited as these are species with which humans have had significant domestication or interactions with.

In regards to evolutionary relatedness to humans, there is evidence to suggest that humans use the same acoustic variables to judge vocalizations of animal calls regardless

of how distant the species are from humans, but there are varying results. Filippi et al. (2017) found that in a study of nine species spanning all classes of air-breathing tetrapods, human participants were able to identify higher levels of arousal using similar acoustic variables for all nine species. On the other hand, one study by Greenall et al. (2022) found that humans could not accurately judge the arousal of wild boar, Przewalski's horse, and cattle vocalizations but could accurately judge the arousal of pig, horse, goat, and human vocalizations. More research is needed to explore the ability of humans to accurately perceive arousal and valence from vocalizations of a wider array of species both closely and further related to humans.

PARTICIPANT CHARACTERISTICS

The previous research suggests that subject variables such as species, context, and individual differences can all play a role in the perception of animal vocalizations, but the extent to which they do so consistently across species is not entirely clear. Some studies suggest that there may be some universality in the perception of vocal emotions across species. For example, Belin et al. (2008) found that human listeners could recognize basic emotions in dog vocalizations, and Fritz et al. (2018) found that humans and dogs show similar neural responses to emotional sounds. Furthermore, Pongracz et al. (2005) found that the vocalizations of different animal species (dogs, cats, humans) were perceived differently by human listeners, suggesting that there may be some variation in how humans interpret vocal cues across species.

However, other studies suggest that individual differences and context can play a significant role in the perception of animal vocalizations. For example, Farago et al. (2014, 2017) found that individual differences in vocalization production and perception were related to social behavior in non-human primates, suggesting a role for a social experience in shaping vocal communication. Briefer (2012) and Kamiloglu et al. (2020) found that context, such as the presence of a conspecific or human, can influence the perception of dog vocalizations.

When considering gender as a subject variable in the perception of animal vocalizations, there is some evidence to suggest that gender can play a role in how individuals perceive and interpret vocal cues. For

example, Maruščáková et al. (2015) found that female participants rated piglet vocalizations as more positive than male participants, indicating that gender can influence how individuals perceive and interpret animal vocalizations. Similarly, Filippi (2017) found that female participants were better than male participants at identifying different emotional states in dog vocalizations.

However, other studies have not found consistent gender differences in the perception of animal vocalizations. Scheumann et al. (2017) found that there were no gender differences in the ability of human participants to recognize the emotional content of chimpanzee vocalizations, and Parsons et al. (2019) found no gender differences in the ability of participants to recognize the emotional content of dog vocalizations.

In summary, while there is some evidence for universality in the perception of vocal emotions across species, the overall evidence on subject variables and consistency in the perception of animal vocalizations is mixed, with some studies suggesting that individual differences and context can play a significant role in shaping vocal communication and others suggesting that there may be some variation in how humans interpret vocal cues across species.

CONCLUSION

Based on the reviewed literature, scientific understanding of animal emotional communication and human perception of it appears to be mixed. While there is evidence for some universality in the perception of vocal emotions across species, the overall picture suggests that subject variables, individual differences, and contextual factors play significant roles in shaping the human perception of animal vocalizations. Humans generally demonstrate high accuracy in perceiving emotional vocalizations in species with which they are familiar, such as dogs, cats, and domesticated animals. However, there is a lack of consistent findings regarding the influence of evolutionary relatedness on perception accuracy. Studies have shown that familiarity with specific species can enhance perception accuracy, but the specific impact varies depending on the animal or vocalization type. Alongside this, the amount of research conducted in regards to domesticated species compared to those undomesticated or familiar may play a crucial role in this finding.

Regarding the acoustic variables predicting human responses to animal vocalizations, factors such as pitch, duration, and temporal parameters have been identified as important cues. However, the relative importance of these variables can vary depending on the context, species, and listener. While pitch and duration have been found to be influential in some studies, the importance of other parameters like rhythm and tempo has also been observed. Moreover, contextual factors such as listener familiarity with the species can influence the relative importance of these acoustic variables. Thus, the specific cues that predict human perception may depend on a variety of factors. When it comes to accuracy in perceiving arousal and valence, studies indicate that humans tend to be more accurate in perceiving arousal compared to valence. The "pitch rule," associating higher F0 with greater arousal, generally leads to accurate judgments. However, the accuracy of this rule may be influenced by factors such as body size, age, and sex of the vocalizing animal. While more research is needed, current evidence suggests that humans have some degree of accuracy in rating arousal and valence, with varying results across species.

In conclusion, human perception of animal emotional communication is a complex and multifaceted phenomenon. While there are instances of universality in emotional perception across species, subject variables, individual differences, and contextual factors can significantly influence the accuracy of human judgments. Scientific understanding of emotional communication is particularly enhanced in species that humans are familiar with, such as dogs, cats, and domesticated animals. Acoustic variables like pitch, duration, and temporal parameters play important roles in predicting human responses, although their relative importance can vary. The accuracy of perceiving arousal tends to be higher than valence, but further research is needed to establish a clearer understanding of these perceptual processes and their evolutionary implications. Further research in the field of emotional communication evolution holds the promise of unraveling the intricate mechanisms underlying the evolution of emotional expressions, providing invaluable insights into the origins and adaptive functions of emotions across species, and deepening our understanding of the fundamental aspects of human and animal behavior.

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