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Physiological and Behavioural Responses of Animals to Human Emotions: They Suffer, Too

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Abstract: *Neurophysiological research highlights that emotion is a complex process with an adaptive function, that is crucial for survival. A fundamental element of this dynamic is emotional contagion, the automatic tendency to share and synchronise emotional states, which is not limited to the human species but is significantly evident in animals such as dogs, horses, and rodents, suggesting a profound interspecific connection. Human–Animal Interactions (HAI) generate measurable positive effects, classified as social, psychological, cognitive, and, most notably, physiological (Beetz et al., 2012; Barker & Wolen, 2008). The review by Beetz and colleagues (2012) confirms that contact with animals reduces stress (via decreased cortisol levels) and improves cardiovascular health. This well-being is largely mediated by the release of oxytocin, a key hormone for social bonding and relaxation, creating a positive feedback loop between species and confirming that emotional contagion is a shared neurobiological process.*

Keywords: *emotion; neurophysiology; emotional contagion; human–animal interaction; physiological responses; oxytocin; canis familiaris.*

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1. Introduction. The Neurophysiological Conception of Emotion

Emotions are increasingly understood as multicomponent processes that integrate physiological activation, expressive behaviour and subjective experience, serving crucial adaptive functions across species (Plutchik, 2001). Within this framework, emotional contagion – the automatic tendency to converge with the affective state of another – has been described in humans as a basic form of social attunement and as the most elementary level of empathy. Classic models emphasise facial mimicry, vocal synchronisation, and postural alignment as pathways through which one individual's emotion is transmitted to others, often without conscious awareness (Hatfield et al., 1993; Schoenewolf, 1990; Viola, 2019).

In parallel, research on Human–Animal Interactions (HAI) – understood here as structured or spontaneous encounters in which humans and non-human animals affect each other's behaviour, physiology and emotional states – has shown that contact with animals can influence human stress, cardiovascular activity, mood and social behaviour, and that these effects are at least partly mediated by neuroendocrine mechanisms such as oxytocinergic pathways (Beetz et al., 2012; Viola, 2019). More recent work extends this perspective by suggesting that the influence is not unidirectional: animals also appear to detect and mirror human emotional states, with measurable behavioural and physiological changes in dogs, horses, rodents and other species. This line of evidence supports the notion of interspecific emotional contagion, where emotional states propagate across species boundaries through shared biological systems.

Despite the rapid growth of this literature, current reviews tend to focus on either specific outcomes (e.g., psychosocial benefits of HAI, therapeutic applications) or on single species and contexts (e.g., dogs as a model of attachment, horses in equitation and sport). Others address emotion in animals mainly at a conceptual level, emphasising the risks of anthropomorphism without systematically linking theory to physiological data. As a result, there is still a lack of integrative work that jointly examines behavioural and physiological indices of interspecific emotional contagion across multiple species and that places detailed experimental studies in dogs within a broader comparative framework.

This review is intended to address this gap. First, it outlines a neurophysiological conception of emotion and clarifies the distinction between emotional contagion and more complex forms of empathy. Second, it synthesises key findings on HAI with an emphasis on objective indicators such as cortisol, heart rate and heart rate variability (Beetz et al., 2012), and oxytocin. Third, it presents and critically examines two recent experimental studies in dogs – Grigg et al., (2022) on simultaneous behavioural and cardiac measures in handling contexts, and Huber et al., (2017) on dogs' responses to emotional sounds – using them as case studies to illustrate methodological strengths, limitations, and divergent results. Finally, it broadens the focus to other species (rodents, horses, pigs, cows, and others), integrating evidence that animals can react to human emotional signals conveyed through acoustic, visual, and chemical channels.

At the same time, this work has a deliberately circumscribed scope and does not aim to be an exhaustive systematic review of all available studies on emotion or HAI. It concentrates on vertebrate species for which both behavioural and physiological indices of emotional contagion have been reported, and it focuses primarily on a limited set of measures (cortisol, cardiac activity, oxytocin) rather than covering neuroimaging, genetics, or detailed individual-differences approaches. The literature on invertebrates, wild free-ranging populations, and large-scale epidemiological data on pet ownership is not systematically addressed. Moreover, the review does not attempt a formal meta-analysis or quantitative synthesis of effect sizes, but instead provides a qualitative integration of findings.

Within these boundaries, the aim of the article is to show that interspecific emotional contagion can be understood as an emergent property of shared neurophysiological mechanisms, to highlight where current empirical evidence is well-substantiated or inconsistent, and to indicate conceptual and methodological directions for future research on the emotional coupling between

humans and other animals. In this article, we therefore focus specifically on the physiological and behavioural indices of interspecific emotional contagion that emerge in the context of Human–Animal Interactions. Rather than offering a general overview of the benefits of Animal-Assisted Interventions, we ask under which conditions human emotional states are mirrored in animals through convergent changes in autonomic activity, endocrine responses and behaviour, and when such mirroring does not occur. This thematic focus guides the selection of the literature and the interpretation of the empirical findings presented in the following sections.

2. Scope and Method

For this research, studies were included if they (a) examined emotional processes in Human–Animal Interactions, (b) reported at least one behavioural and one physiological index of the animal's state (e.g., heart rate, heart rate variability, cortisol, oxytocin), and (c) involved vertebrate species. The focus is on vertebrate species and on experimental or quasi-experimental paradigms in which human emotional states or emotionally salient stimuli are explicitly manipulated or assessed. Also, we have excluded the studies that focused solely on human outcomes without animal measures, relied exclusively on self-report, or dealt with invertebrate models, wild free-ranging populations or large-scale epidemiological data on pet ownership. Broader literature on invertebrates, wild free-ranging populations, neuroimaging and large-scale epidemiological studies of pet ownership falls outside the scope of this review and is not treated in detail. Vertebrate species were prioritised because they share broadly comparable neuroendocrine and autonomic architectures with humans, which facilitates the interpretation of behavioural and physiological indices of emotional contagion across species.

3. The Concept of "Emotional Contagion"

The phenomenon of emotional contagion, theorised by Elaine Hatfield and colleagues, manifests as "the unconscious imitation and synchronisation of another person's expressions and body language (faces, voices, postures, movements) that drive people towards shared emotional states" (Hatfield et al., 1993). In general, emotional contagion denotes the process by which observing an individual's behaviour induces others to reflexively reproduce the same behaviour.

A more extensive definition is proposed by Schoenewolf, who suggests that 'emotional contagion is the transfer of feelings and actions between people, leading to shared emotional states and behaviours' (Schoenewolf, 1990). A typical example is the rapid spread of fear among group members, which enables the majority of individuals to react quickly and escape potential danger. We can, therefore, define emotional contagion as the automatic capacity to assimilate the emotions of others and experience them intensely: the observer enters the emotional state of the other, is stimulated by their emotions, and may be overwhelmed by them.

In contrast to empathy (Hoffmann, 2008), emotional contagion does not involve awareness that the perceived emotion originates from another person; it does not involve complex cognitive processes, and attention remains centred on the self rather than the other. Conversely, an empathic response implies the capacity to feel what others feel and to attribute these experiences to others without confusing them with one's own (Blikhar et al., 2023).

In humans, emotional contagion manifests in readily observable ways, such as the tendency to laugh or cry in response to the emotions of others. However, recent studies have demonstrated that animals are also sensitive to these dynamics, perceiving and reacting to human emotional states in ways that involve both behavioural and physiological components. This confirms the idea that emotions are not isolated phenomena but processes that integrate cognitive, physiological, and social aspects (Beetz et al., 2012). Dogs, in particular, show a pronounced ability to perceive the emotions of their owners or familiar people. Several experiments have found that dogs respond to human emotional signals, such as crying or anger, with measurable behavioural and physiological changes, for example, variations in heart rate and modulation of behavioural activity. This

phenomenon, known as interspecific emotional contagion, suggests that dogs not only recognise human emotions but can also be directly influenced by them (Yong & Ruffman, 2014).

Horses also exhibit similar sensitivity: recent studies have observed that they react to human emotional signals, such as fear and joy, through variations in heart rate, exploratory behaviour, and body postures. These responses indicate that horses perceive human emotions and translate them into their own physiological and behavioural states, confirming the existence of an interspecific emotional contagion that can influence human–animal interaction and the well-being of the horse (Jardat et al., 2025).

Although fewer in number, several studies conducted on mice have demonstrated that emotional contagion is also present in rodents: mice can detect the emotional state of other individuals, such as fear, and modulate their own behaviour and physiological responses accordingly. These results suggest that emotional contagion is not limited to domestic or large species but is a widespread phenomenon even in small social mammals, with significant implications for the study of emotion as an evolutionary phenomenon (Langford et al., 2006).

Overall, emotional contagion between humans and animals shows that emotions are multicomponent, interactive phenomena influenced by physiological, behavioural, and social-contextual factors. This recognition has important ethical and practical implications: it underscores the need to consider human emotional states when interacting with animals, both in domestic settings and in professional or therapeutic contexts, to ensure their well-being and to more fully comprehend the complexity of shared emotions across different species.

4. Scientific Experimentation on Human-Animal Interactions

The analysis of animals' physiological responses to human emotions provides a valuable perspective for understanding the neurophysiological processes that underlie emotional states in both species and for exploring the complex interplay between behavioural and physiological responses of domestic and non-domestic animals. The present section does not aim to review all psychosocial or clinical outcomes of Human–Animal Interactions. Instead, the studies are selected because they are informative for **interspecific emotional contagion**, that is, for the extent to which the emotional state of the human is reflected in the animal at the physiological and behavioural level. Particular attention is given to work that reports changes in heart rate, heart rate variability, cortisol or oxytocin in both partners, or that describes systematic alterations in animal behaviour in response to human affect. Other, more general effects of Animal-Assisted Therapy and Education are mentioned only insofar as they help to contextualise these contagion processes.

Several studies conducted on dogs have shown a strong correlation between the physiological stress levels experienced by pet owners and the stress levels of their companion animals, suggesting the existence of emotional contagion across species. Similarly, research on horses has demonstrated that they are capable of physiologically responding to the emotional states of riders, particularly to negative emotions such as fear. Even experimental investigations on rodents have provided important models for analysing the fundamental mechanisms of emotional contagion, revealing that mice modify their behaviour and physiological parameters when interacting with stressed counterparts.

Overall, these results delineate a coherent and scientifically founded framework, highlighting that emotional contagion is not an exclusively human characteristic but derives from neurophysiological processes shared with many other animal species.

In recent decades, scientific research has dedicated increasing attention to the study of Human–Animal Interactions (HAI), with the intent of clarifying how these relationships can influence not only behaviour but also the physiological processes and emotional states of the species involved (Barker & Wolen, 2008; Beetz et al., 2012; Rabbitt, Kazdin, & Hong, 2014). A fundamental contribution in this area is represented by the review conducted by Beetz et al., (2012), which provides a systematic analysis of approximately seventy experimental studies published

between the 1990s and 2010. The authors propose an integrated interpretation of the results, highlighting how many of the positive effects associated with human–animal interactions can be attributed to the activation of specific neurophysiological mechanisms, particularly those connected to the release of oxytocin, the most socially relevant hormone (Beetz et al., 2012).

In their review, the effects of human–animal interactions are classified into four main categories:

- Social Effects: At the social level, evidence shows that the presence of an animal can promote communication, empathy, and prosocial behaviours. For example, Hergovich et al., (2002) and Kotrschal and Ortbauer, (2003) found that the presence of a dog in a school context increases positive interactions among children and helps reduce aggressive behaviours.
- Psychological Effects: From a psychological perspective, the companionship of an animal or direct contact with it is associated with a decrease in anxiety, fear, and feelings of loneliness. Studies conducted in hospital environments and elderly residential facilities confirm these benefits, highlighting an improvement in general emotional well-being (Kaminski and Nitzschner, 2013).
- Physiological Effects: From a physiological standpoint, several studies have shown that the presence of an animal can cause measurable variations in bodily parameters, such as heart rate, blood pressure, and cortisol levels (Stapleton et al., 2019), the primary stress-response hormone. Allen et al. (1991, 2001, 2002) demonstrated that pet owners tend to have more stable blood pressure and a quicker recovery after stressful situations compared with those without pets. Furthermore, research on patients with cardiac diseases found that a dog visit can significantly reduce levels of epinephrine and norepinephrine, confirming the relaxing and physiologically beneficial effects of animal interaction.
- Cognitive Effects: Beetz et al. (2012) report a series of cognitive studies, mainly conducted with children, indicating that the presence of a dog can enhance concentration, motivation, and learning abilities. In particular, studies by Hall et al. (2016) show that children tend to make fewer errors and complete tasks more quickly when a dog is present in the classroom, suggesting a facilitating effect of the animal on cognitive and attentional processes.

One of the most significant findings concerns the synchronisation of cortisol levels between humans and animals. During their interaction, Barker et al. (2005) observed that doctors and nurses experiencing occupational stress recorded a marked drop in cortisol after 20 minutes spent with a dog, whereas a break without animal contact did not produce the same effect. Similarly, Odendaal et al., (2003) found that stroking a dog, whether one's own or a stranger's, resulted in a decrease in cortisol and an increase in oxytocin, dopamine, and endorphins, indicating a direct neurochemical impact (Kaminski and Nitzschner, 2013).

In another study, Beetz et al., (2012) analysed children with insecure attachment styles and observed that, in stressful contexts, cortisol levels were significantly lower when the children were accompanied by a dog compared with when they were in the presence of an adult or a peer. Analogously, Viau et al., (2010) confirmed these effects in children with Autism Spectrum Disorders: the mere presence of an assistance dog was sufficient to reduce the cortisol peak upon waking, promoting better physiological stress regulation.

Cardiovascular measurements constitute another relevant research area. Studies by Allen et al. (1991, 2001, 2002) demonstrated that owners of dogs or cats exhibit lower blood pressure and faster stress recovery times, especially when the interaction is with their own animal compared with a human family member. Cole et al., (2007), focusing on cardiac patients, found a reduction in catecholamines and heart rate during AAT sessions. Finally, Motooka et al. (2006) highlighted that walking with a dog increases Heart Rate Variability (HRV), an indicator of relaxation and autonomic nervous system balance.

Numerous studies reported by Beetz et al., (2012) emphasise the positive influence of animal interactions on mood and anxiety. Kaminski et al., (2002) observed that hospitalised children

showed lower anxiety levels and an increase in positive affectivity following dog-assisted therapy sessions compared to traditional therapy. Shiloh et al. (2003) conducted an experiment in which participants stroked a live animal (a rabbit or turtle) or a stuffed animal: only contact with the live animal caused a significant reduction in anxiety. Subsequent clinical studies, such as Lang et al. (2010) on patients with schizophrenia , confirm that the presence of a dog during therapeutic interviews decreases tension and facilitates emotional communication.

In the educational context, studies by Gee et al. (2007, 2009, 2010) and Kotrschal and Ortbauer (2003) demonstrated that the presence of an animal, particularly a dog, increases children's motivation and ability to concentrate (Gee et al., 2007, 2009, 2010; Hall, Gee, & Mills, 2016; Kotrschal & Ortbauer, 2003; Mombeck et al., 2023). According to the authors, the animal acts as a relational mediator, reducing social pressure and creating an emotionally secure environment that facilitates learning. These results have contributed to the development of Animal-Assisted Education (AAE) projects, which are now widely disseminated in European schools. (Kaminski and Nitzschner, 2013). A relevant contribution of Beetz et al., (2012) is the identification of oxytocin as the neurophysiological mediator of the benefits of human-animal interactions. Experimental studies (Odendaal, 2000; Handlin et al., 2011; Petersson, Handlin, & Uvnäs-Moberg, 2017) have shown that stroking or maintaining eye contact with one's dog causes an increase in oxytocin levels in both humans and the animal. Nagasawa et al. (2009) further documented a direct correlation between the duration of reciprocal gaze and urinary oxytocin levels in owners, suggesting a positive feedback loop between the two. Since oxytocin is associated with relaxation, trust, and the strengthening of social bonds, it likely represents the main biological mechanism underpinning interspecific emotional contagion (Odendaal, 2000; Handlin et al., 2011; Petersson, Handlin, & Uvnäs-Moberg, 2017). In summary, the study by Beetz et al., (2012) represents a benchmark in the scientific study of human–animal relationships. The collected evidence indicates that contact with animals, particularly those with whom a stable affective bond is established, produces positive effects detectable at both the psychological and physiological levels. These include stress reduction, improved cardiovascular health, decreased anxiety, and increased motivation and empathy. The hypothesis that oxytocin acts as a biological mediator offers a coherent explanation, paving the way for further research on interspecific emotional contagion. Beetz et al., (2012) emphasise that human–animal interaction goes beyond simple perceived well-being: it is a shared neurobiological process in which emotions and physiological states can mutually influence each other, confirming the deep evolutionary connection between humans and animals. (Kaminski & Nitzschner, 2013)

5. Evaluation of "the relationship between the emotional states of dogs and their human handlers, using simultaneous behavioural and cardiac measures" *(Grigg et al., 2022)*

This study was selected as a case example because it directly tests the hypothesis of "emotional contagion between dogs and unfamiliar human handlers" (Grigg et al., 2022), combining behavioural observation with simultaneous measures of heart rate and heart rate variability in both partners.

The study conducted by Grigg et al., (2022) focused on analysing the connection between the "emotional states of dogs and their unfamiliar human handlers" in a controlled manipulation context. The research, carried out between April and December 2019, involved 40 adult dogs paired with unfamiliar human handlers. The objective was to assess whether, and to what extent, the dogs' physiological and behavioural states were influenced by human emotions and to examine the effects of a brief mindfulness session on the stress levels of both (Kabat-Zinn, 1994).

The literature indicates that factors such as the owner's personality, the quality of the human–animal interaction, and training strategies, especially when prolonged over time, can influence the behaviour and well-being of dogs. The purpose of "the present study was to verify whether the emotional state of a human handler correlated with that of the dog during routine

manipulation exercises, under conditions of a brief interaction with an unfamiliar handler" (Grigg et al., 2022). The exercises were performed both before and after the introduction of a mild verbal distress factor, aimed at inducing a psychological emotional state in the human participant.

Stress levels in both "dogs and humans can be assessed through various tools including behavioural measures, such as body language and behaviours indicative of tension, and physiological indicators, including stress hormone concentration or variations in cardiac activity. Specifically, the analysis of cardiac activity and Heart Rate Variability (HRV) is widely used as a reliable indicator of stress and emotional state in both humans and animals" (Grigg et al., 2022). Research highlights that HRV can represent a significant indicator of bodily functions related to "stress, adaptability, and general health. In particular, lower HRV values at rest are generally associated with states of stress, anxiety, worry, or panic attacks" (Grigg et al., 2022).

Maros, Dóka and Miklósi (2008) employed a metric system applied to a harness to record RR intervals in dogs, observing an increase in Heart Rate (HR) during physical activities. No significant variations in HRV were found in relation to body position or movement. However, HRV was higher when the dogs oriented towards a preferred toy, leading the authors to suggest that this parameter may serve as a useful indicator of the state of attention in dogs (Grigg et al., 2022).

All "research protocols for this study were reviewed and approved by the Institutional Animal Care and Use Committee (IACUC) of the University of California, Davis. Forty healthy adult dogs (>1 year) of any breed and weighing approximately 20 lbs (about 9 kg) were used in this study. Dogs underwent screening before inclusion to ensure the safety of all participants; dogs exhibiting excessive fear or aggression towards humans and those with high levels of socialisation and obedience training (such as working, assistance, or therapy dogs) were excluded" (Grigg et al., 2022; Dochow et al., 2015).

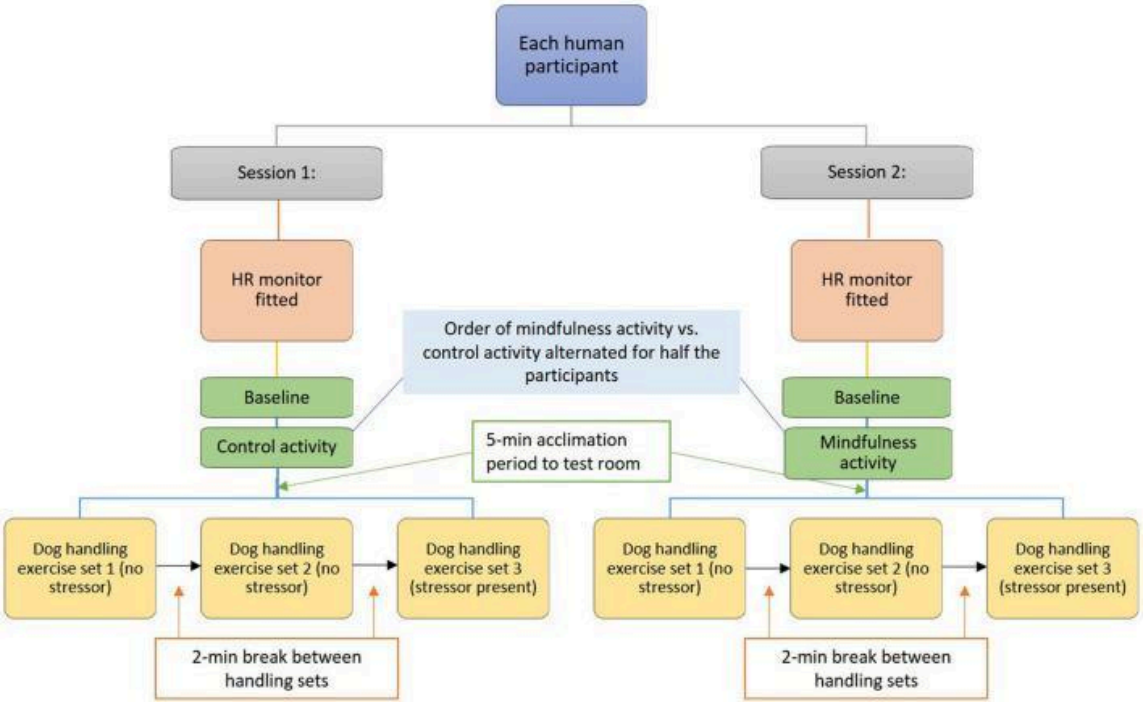


Figure 1. Sequence of data collection sessions and handling sets. Reproduced from Grigg et al. (2022), Animals, 12(13), 1680, https://doi.org/10.3390/ani12131680, under the terms of the Creative Commons Attribution (CC BY) license. No changes were made.

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Each human participant took part in two experimental sessions, separated by approximately one week. In both sessions, "physiological parameters—heart rate and heart rate variability—were

recorded using a Polar H10 heart rate monitor for both the handler and the dog"(Grigg et al., 2022). The two sessions involved: a brief mindfulness practice and a subsequent control activity such as reading or neutral conversation.

After a five-minute acclimatisation phase in the test room, each human–dog pair performed three consecutive sets of dog manipulation exercises, separated by two-minute intervals. The first two sets took place under neutral conditions, while a verbal stress factor was introduced in the third set to slightly increase the handler's level of emotional arousal.

The analysed physiological variables included mean heart rate, heart rate variability, and high-frequency power, the latter used as an indicator of parasympathetic nervous system activity, see Figure 1 (Grigg et al., 2022).

Concurrently, the dogs' stress behaviours were video recorded and subsequently analysed with the BORIS software, from which a Stress Index (SI) was elaborated. The SI was obtained by combining the sum and frequency of behaviours indicative of tension or discomfort .

The data analysis showed a significant reduction in stress levels in the dogs over the course of the experimental session. Specifically, the mean heart rate was higher in the first set of exercises and showed a progressive drop in the subsequent sets, while the Heart Rate Variability increased, indicating greater parasympathetic system activity and, consequently, a more marked state of relaxation. Similarly, the behavioural stress index recorded a significant decrease from the first to the third set, confirming an observable reduction in behaviours associated with tension or discomfort.

These results indicate that progressive familiarisation with the experimental context, the handler, and the manipulation procedures exerted a calming effect on the dogs, regardless of the type of pre-experimental activity performed by the human handler. Regarding the physiological indicators of the human handlers, the experimental conditions did not yield statistically significant differences. The mindfulness practice did not lead to statistically relevant effects on either heart rate or heart rate variability. Furthermore, no consistent correlations emerged between the physiological parameters of the dogs and those of the handlers, suggesting the absence of evident emotional contagion in situations of brief interaction with unfamiliar operators.

The most significant finding of the study concerns the observation that the repetition of sessions and increasing familiarity with the environment produce a progressive reduction in stress levels in dogs. This evidence has important practical implications in contexts such as veterinary clinics and shelters, where staff continuity and procedural predictability can substantially contribute to improving animal welfare.

In summary, the study confirms that rapid familiarisation and a predictable context are effective in reducing stress in dogs when manipulated by unfamiliar people. However, no signs of emotional contagion between human and dog emerged under the experimental conditions considered, likely due to the brevity of the interaction, the lack of familiarity between the participants, and the relatively modest intensity of the stressor employed. These results highlight the importance of adopting management strategies that promote calm, consistency, and predictability in human-animal interaction, with positive implications for the welfare of dogs and safety in professional activities in which they are involved. (Grigg et al., 2022)

6. Study of "Emotional contagion in dogs (canis familiaris) to emotional sounds of humans and conspecifics" (Huber et al., 2017)

This second case study complements Grigg et al. (2022) by examining rapid "emotional contagion in dogs exposed to emotional sounds", using a strictly acoustic paradigm in which the valence and source of the vocalisations are experimentally controlled.

Emotional contagion represents an essential component of empathy, understood as the correspondence of emotional states between individuals. The present research investigates this phenomenon, directly comparing emotional sounds originating from two species, humans and dogs,

and by considering opposing emotional valences (positive versus negative) in order to gain new insights into the mechanisms of empathy.

Huber et al., (2017), citing de Waal (2008) mention that “empathy is an eminently social phenomenon, and can be defined as the ability to be influenced by and share the emotional state of another”. They also noted that “Preston and de Waal (2002) proposed a multilevel conception of empathy, in which the most basic level is precisely represented by emotional contagion—an automatic, unconscious correspondence of emotional states between individuals” (Huber et al., 2017).

The objective of the study conducted by Huber et al., (2017) was to investigate the phenomenon of “emotional contagion in dogs in response to acoustic stimuli of different” origins. To this end, the authors conducted a sound playback experiment, analysing three dimensions simultaneously for the first time:

- **Emotionality**: comparing neutral environmental sounds with emotional sounds produced by humans and dogs;
- **Species**: comparing dogs' reactions to emotional human sounds versus those of conspecifics;
- **Emotional Valence:** analysing the differences in canine responses to sounds of positive and negative valence from both species.

The “dogs' behavioural responses were assessed both towards their owners and towards a loudspeaker transmitting the stimulus” Huber et al., (2017).

7. Methodology

The study included 53 adult companion dogs, of at least 1 year of age, taken “from the Clever Dog Lab database of various breeds and mixed breeds with private owners. Testing was conducted in two identical experimental rooms at the Clever Dog Lab at the University of Veterinary Medicine Vienna, each measuring metres. The two rooms were connected by an internal door.

In each room, three wooden separation panels were arranged in a semicircle. Behind each panel, a wooden box was placed to conceal an external loudspeaker from which the acoustic stimuli were played. The loudspeaker was moved by the experimenter between the three boxes in each room in random order for each trial, in order to vary the situational context and reduce the risk of habituation in the canine subject, see Figure 2.

On the opposite wall, centrally positioned relative to the median panel, a blanket intended for the dog was placed on the floor, while a chair for the owner was located next to it. The experiment was structured into two sessions, each consisting of four trials. In each session, four different acoustic stimuli were played, organised according to specific criteria deemed more appropriate than a completely balanced design” (Huber et al., 2017).

In the first session, the first and last stimuli of each session “were always emotional, while the second and third were non-emotional” (Huber et al., 2017). This methodological choice was adopted to maximise the temporal interval between emotional stimuli, thereby reducing the risk of residual effects from the first influencing the response to the subsequent one.

In the second session, this arrangement was inverted, such that stimuli from both species alternated valence between the two experimental sessions.

To prevent habituation phenomena in the subjects, several control measures were adopted: the experiment was divided into two separate sessions (mean interval: 18 days), with the playback of four sound stimuli per session; the test rooms were changed after each test; and the loudspeaker position varied randomly in every trial. In this way, the situational context was always different, reducing the possibility of habituation and a subsequent decrease in the dog's response.

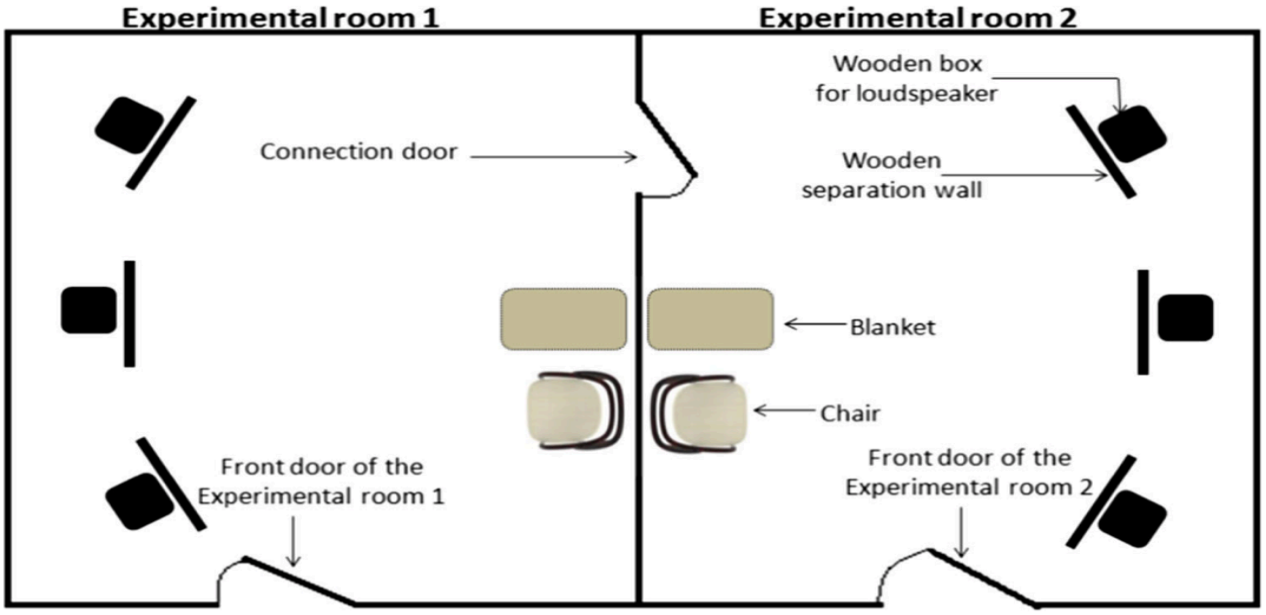


Figure 2. Schematic sketch of the experimental rooms (1 and 2) with the required objects (three wooden separation walls and boxes per room to hide the loudspeaker, one blanket, and one chair per room). Reprinted from Dogs show evidence of rapid emotional contagion, by L. Huber, J. Popovová, T. Riener, J. Salobir, & J. Cimarelli, 2017, Scientific Reports, 7, Article 13424 https://doi.org/10.1038/s41598-017-06412-3. © The Author(s) 2017

For each trial, the dogs' behavioural responses were analysed using continuous sampling during the 20 seconds of stimulus playback and the subsequent 30 seconds.

The observed variables were organised into three main behavioural categories:

- Owner-oriented behaviours;
- Loudspeaker-oriented behaviours;
- Indicators "of arousal and negative emotional states"(Huber et al., 2017).

8. Study Results

- **"Emotionality" Dimension:** Comparison between emotional and non-emotional sounds. The results show that dogs react more intensely to emotional sounds compared with neutral ones" (Huber et al., 2017). During the listening of emotional sounds, they reduced attention towards the owner but increased interest towards the loudspeaker, indicating greater engagement with the sound source. Furthermore, the dogs exhibited higher levels of arousal and stress (RRS - restlessness and stress score) and greater immobility, signs of increased emotional activation. Neutered and older dogs showed more moderate emotional responses, while the second session registered a general reduction in reactivity, suggesting a possible habituation effect.
- **"Species" Dimension:** Comparison between emotional canine and emotional human sounds. No relevant behavioural differences emerged between dogs' reactions to emotional human sounds and canine sounds, with the exception of greater immobility observed in response to canine sounds, indicative of more intense emotional activation. It was also found that "dogs were more likely to approach their owners after listening to positive human sounds" (Huber et al., 2017), highlighting a selective sensitivity to positive emotions expressed through human vocalisations.
- **"Emotional Valence" Dimension**: Comparison of positive valence sounds with negative valence sounds: Dogs showed greater arousal and immobility in response to negative

sounds, regardless of whether the sound originated from humans or conspecifics. Furthermore, in the second session, dogs looked at the owner for a shorter duration, suggesting a possible effect of familiarisation or a decrease in social attention over time.

The results suggest that dogs' responses "to negative emotional sounds can be interpreted as being based on emotional contagion" (Huber et al., 2017). In the presence of emotional sounds, dogs showed greater attention towards the loudspeaker and an increase in behavioural indicators associated with negative emotional states.

9. Discussion

The evidence reviewed in this work indicates that emotional contagion is a widespread phenomenon that extends beyond the human species and is rooted in shared neurophysiological mechanisms. Throughout the article, our guiding question has been when and how human emotional states are mirrored in animals through convergent physiological and behavioural changes. Studies on dogs, horses, rodents, pigs, cows and even phylogenetically distant species such as crocodiles and wild ungulates converge on the idea that animals can perceive and react to human emotional states through coordinated behavioural and physiological changes. In this framework, the dog appears as a particularly sensitive model, but not as an isolated case: rather, it represents a salient example of a broader interspecific predisposition to decode emotionally relevant signals.

A first level of integration concerns the physiological data emerging from Human–Animal Interactions (HAI). Research on companion animals and assistance dogs shows that contact with humans can modulate "heart rate, heart rate variability (HRV), blood pressure, and cortisol levels" (Grigg et al., 2022), often in the direction of stress reduction and improved autonomic balance. These effects have been documented both in everyday contexts and in clinical or educational settings, and are frequently accompanied by increases in oxytocin, a hormone linked to social bonding and relaxation. Taken together, these findings support the view that emotional contagion between humans and animals is mediated by a neuroendocrine system capable of synchronising the states of both partners, especially when a stable affective relationship is present.

The two case studies examined in detail highlight complementary aspects of this phenomenon. Grigg et al., (2022) "did not find clear evidence of emotional contagion between dogs and unfamiliar handlers" in a brief handling context, despite careful measurement of cardiac and behavioural indices. The main result was a progressive reduction in canine stress across repeated sessions, attributable to familiarisation with the environment and procedures rather than to the handler's emotional state. By contrast, Huber et al., (2017) observed robust behavioural indications of emotional contagion in dogs exposed to emotional acoustic stimuli from humans and conspecifics. In this study, dogs reacted more intensely to emotional than to neutral sounds, showed heightened arousal and immobility in response to negative vocalisations, and modulated their orientation towards the owner and the loudspeaker depending on the valence and source of the stimulus.

9.1. Integrative Analysis and Methodological Considerations

In light of this central question, the studies reviewed here can be interpreted as probing different boundary conditions for interspecific emotional contagion.

When the available findings on interspecific emotional contagion are considered together, a more complex and nuanced picture emerges. Grigg et al., (2022) report no clear "evidence of emotional contagion between dogs and unfamiliar handlers" during routine handling, despite detailed behavioural coding and simultaneous cardiac measures. By contrast, other studies document marked behavioural and, in some cases, physiological reactivity to human or conspecific emotions, suggesting at least partial contagion. Huber et al., (2017) show that dogs differentiate between emotional and neutral vocalisations from humans and conspecifics and exhibit heightened arousal and freezing in response to negative sounds. Yong and Ruffman (2014), and more recent

work such as Jardat et al., (2025) likewise describe robust orienting, vigilance, and stress-related behaviours when dogs are exposed to emotionally salient auditory stimuli.

These apparently divergent results can be partly explained by differences in relational context, the nature of the emotional trigger, and the measurement strategy employed. Grigg et al., (2022) used unfamiliar handlers in a relatively mild, repeated handling situation, where the human's emotional state may have been only weakly perturbed and poorly externalised. In contrast, studies employing owners or familiar humans often start from a stronger pre-existing bond, which may facilitate emotional coupling and increase the salience of subtle cues. Similarly, paradigms based on clearly negative or highly arousing stimuli (e.g., distress cries, fearful voices, intense frustration) are more likely to elicit detectable responses than routine manipulations framed as part of a standard procedure. The modality of stimulation also matters: acoustic and chemosensory signals can travel without direct physical contact and may trigger rapid orienting and autonomic changes, whereas purely tactile or postural cues may be less distinctive or more easily confounded with learned associations to handling itself.

Methodological characteristics further contribute to variability in outcomes. Cortisol is a widely used stress marker, but its slow temporal dynamics, circadian rhythm, and substantial inter-individual variability make it sensitive to the timing of sampling, prior events, and basal differences between animals. Single pre–post measurements may miss transient peaks or under- or overestimate changes if collection is not carefully aligned with the stressor. Heart rate variability (HRV) offers a window into autonomic regulation, but is vulnerable to artefacts from movement, posture, and signal quality, and short recording windows or differences between devices (e.g., sport heart-rate belts versus clinical ECG) can complicate comparison across studies. Behavioural scoring, although indispensable, is influenced by the choice of ethogram, observer training, and the treatment of ambiguous behaviours. In several studies, systematic reporting of inter-rater reliability and blinding procedures is limited or absent, which makes it difficult to assess the robustness of the observed patterns.

A similar caution applies to oxytocin. Differences in sampling matrices (e.g., saliva, urine, blood), assay techniques and timing of collection relative to the interaction can yield heterogeneous oxytocin values and complicate direct comparison across studies. These methodological factors need to be considered when interpreting oxytocin findings in the context of interspecific emotional contagion.

Taken together, these considerations suggest that absence of evidence for emotional contagion in certain paradigms does not necessarily constitute evidence of absence, but may instead reflect threshold and design issues: small changes in human emotional expression, weak or mixed-valence stimuli, or insensitive measurement protocols can all reduce the likelihood of detecting cross-species convergence. Conversely, studies that report strong contagion effects often combine highly salient emotional cues, close human–animal relationships and multimodal measurement (behavioural, cardiac, endocrine). Future research will benefit from explicitly designing studies to test the conditions under which emotional contagion is amplified or attenuated, rather than treating it as a simple present/absent phenomenon.

9.2. Cross-species Perspective and Theoretical Implications

The broader literature across species reinforces this interpretation. Rodent studies demonstrate that mice can modify their behaviour and physiological responses when exposed to stressed conspecifics, and that their reactions are associated with activation of limbic structures such as the amygdala (Becker & Huber, 2023). Horses exhibit changes in heart rate, exploratory behaviour, and posture in response to human fear or joy, suggesting a capacity to internalise the emotional state of the handler. Pigs and cows respond to human vocal and chemical signals associated with stress by adjusting their vigilance and social behaviour (De Luca, Rossi, & Zalaquett, 2021). These findings have been extended by citizen-science research showing that

family pigs and dogs differentiate human emotional vocalisations and adjust their behaviour accordingly **(**Nawroth & Marino, 2024**).**

Even crocodiles and wild moose have been shown to react selectively to human and primate distress calls or to human voices, indicating that sensitivity to emotional cues related to threat or suffering may be an evolutionarily ancient adaptation (Huchard & Mathevon, 2023; Olsson, Ericsson, & Frank, 2022; Bhardwaj et al., 2022).

From a theoretical standpoint, these converging findings support models that conceptualise emotional contagion as the most basic level of empathy. At this level, the process is largely automatic, does not require explicit perspective-taking, and is mediated by perception–action mechanisms that link the observation of another's state to one's own bodily responses.

Neurophysiological systems "involving the autonomic nervous system, the hypothalamic–pituitary–adrenal axis" (Dupont, Martin, & Rossi, 2019) together with neuromodulators such as oxytocin, dopamine and endogenous opioids, likely play a central role in this coupling. It is plausible that oxytocinergic pathways, in particular, have been shaped by domestication processes, contributing to heightened sensitivity to human socio-emotional cues in certain species. Domestication may have further refined these mechanisms in certain species, such as dogs, enhancing their sensitivity to human signals, but the basic architecture seems conserved across many taxa.

A simple conceptual model can help organise these heterogeneous findings (see Figure 3). Human emotional states are first instantiated at the physiological level, through changes in autonomic activity (e.g., heart rate, HRV), endocrine responses (e.g., cortisol, oxytocin), and expressive channels such as voice, posture, facial expression, and chemosignals. These internal changes generate a set of external cues – acoustic, visual, tactile, and olfactory – that are available to the animal. The animal, in turn, perceives and interprets these cues using species-specific sensory and cognitive systems, leading to adjustments in its own autonomic balance, endocrine activity and overt behaviour. Finally, the animal's responses (e.g., approach, avoidance, vigilance, appeasement) feed back into the human's emotional and physiological state, either dampening or amplifying the original reaction. In this sense, interspecific emotional contagion can be viewed as a dynamic, bidirectional loop linking human physiology and behaviour to animal perception and responses, rather than as a one-way process that affects only the animal.

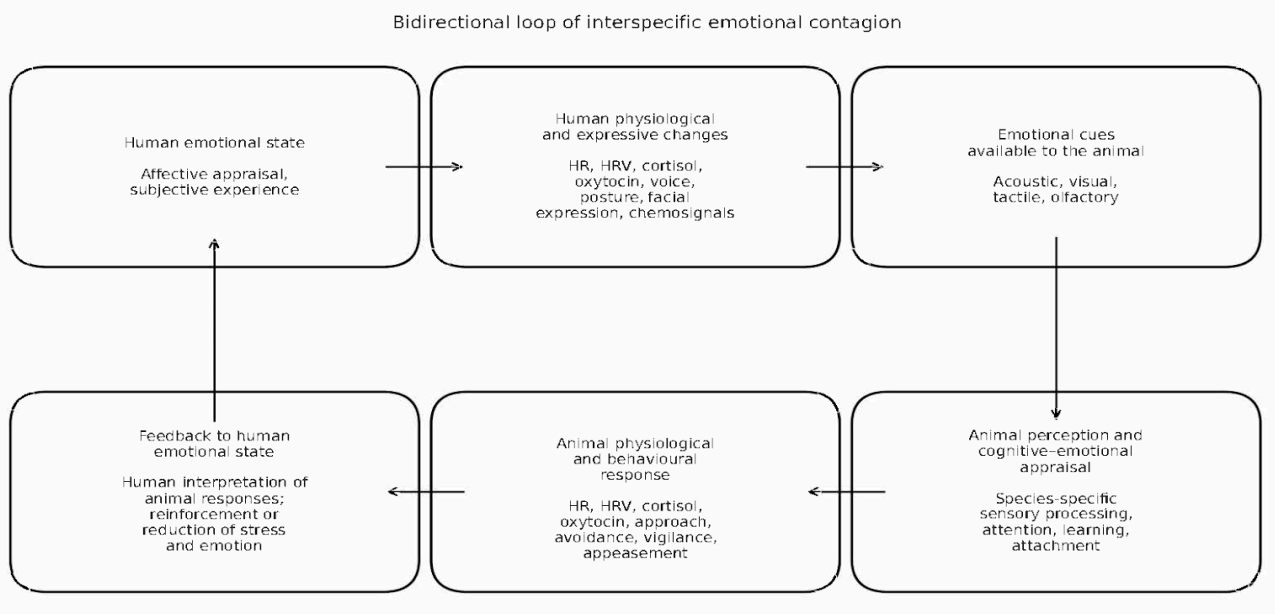


Figure 3. Bidirectional loop of interspecific emotional contagion. Concept of the authors

9.3. Limitations and Future Directions

The existing literature presents important limitations. Many studies are based on relatively small samples, often drawn from specific populations (e.g., pet dogs from urban environments), which limits generalisability. Experimental paradigms vary considerably in terms of stimuli, procedures, and outcome measures, making direct comparison difficult and sometimes leading to apparently conflicting results. Behavioural coding is not always accompanied by rigorous assessments of inter-rater reliability, and physiological measures can be affected by confounding factors such as movement, circadian rhythms, or prior experiences. In addition, the directionality of the effects is not always clear: in some cases, it is difficult to distinguish whether the animal is reacting to the human's emotion, to contextual cues, or to learned associations.

Future research should address these limitations through more standardised and multimodal designs. Studies that simultaneously combine behavioural, cardiac, and endocrine measures in both human and animal partners would allow for a more precise mapping of synchrony dynamics. Longitudinal designs could clarify how emotional contagion develops over time within a relationship and how it is influenced by factors such as training, attachment style, or previous trauma. Cross-species comparisons using homologous protocols would help determine which aspects of emotional contagion are species-specific and which reflect general mammalian mechanisms. Finally, greater attention should be paid to individual differences, both in humans (e.g., personality traits, emotion regulation skills) and animals (e.g., temperament, breed, prior learning), which may significantly modulate susceptibility to contagion (Khavula et al., 2024).

The ethical and applied implications of these findings are considerable. In domestic contexts, recognising that animals can absorb human emotional states underscores the responsibility of owners to manage their own stress and emotional reactivity, particularly in the presence of sensitive individuals such as dogs or horses. In professional settings—veterinary clinics, shelters, farms and therapeutic programmes—attention to the emotional climate, staff continuity, and the predictability of procedures can contribute substantially to animal welfare. In Animal-Assisted Therapy and Education, a better understanding of emotional contagion mechanisms may improve intervention design, maximising benefits for human participants while protecting the animals from chronic stress or emotional overload.

10. Conclusions

The available evidence supports the idea that emotional contagion between humans and animals is an emergent property of shared neurophysiological systems, shaped by evolution and further refined by domestication and individual experience. Dogs stand out as a particularly responsive species, but similar processes are observable in many other animals, from rodents to horses and pigs, and even in more distant taxa. Emotional contagion thus appears not as an isolated curiosity of companion animal behaviour, but as a general feature of social life in vertebrates.

By integrating behavioural and physiological indicators across species and paradigms, this review highlights both the robustness and the fragility of current findings. Robust, because multiple lines of evidence converge on the capacity of animals to detect and mirror human emotional states; fragile, because methodological differences and contextual factors can easily obscure or mimic contagion effects. A more systematic consideration of these factors—relational history, stimulus salience, measurement sensitivity—will be essential to refine theoretical models and to interpret empirical results correctly.

Ultimately, viewing interspecific emotional contagion as a dynamic, bidirectional process has implications that extend beyond academic debates. It invites a reconsideration of the moral and practical significance of human relationships with other animals, emphasising that our emotional lives are not strictly private, but are continuously shared, transmitted, and transformed in contact with other species. Understanding how this process unfolds, and under what conditions it promotes

or undermines welfare, remains a central task for future research at the intersection of affective science, comparative cognition, and animal welfare.

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