

ADVANCED REVIEW

Emotional contagion in nonhuman animals: A review

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Abstract

Emotional contagion, the emotional state-matching of an individual with another, seems to be crucial for many social species. In recent years evidence on emotional contagion in different animal species has accumulated. However, despite its adaptative advantages and its presumed simplicity, the study and direct demonstration of this phenomenon present more complexities than previously thought. For these reasons, a review of the literature on emotional contagion in nonhuman species is timely to integrate current findings. In this paper thus, we carry out a comprehensive review of the most relevant studies on emotional contagion in animals and discuss the main problems and challenges of the field. We conclude that more research is needed to broaden our understanding of the mechanisms and functions of emotional contagion and the extent to which this process is present in a wide variety of species. Furthermore, the comparative study of emotional contagion would benefit from the use of systematized paradigms including both behavioral and physiological measures and the simultaneous recording of the responses of the interacting individuals to reliably assess an emotional state-matching between them and reliable controls.

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1 | INTRODUCTION

Emotional contagion is broadly defined as the emotional state-matching of a subject with another (de Waal, 2008; Shamay-Tsoory, 2011). This automatic emotional response that matches the perceived emotion of another individual involves changes at the neurophysiological, cognitive, and behavioral dimensions. It has been considered as the most basic form of empathy (de Waal, 2007; Preston & de Waal, 2002), but it is not clear that all empathic behaviors involve a core process of emotional contagion (Isern-Mas & Gomila, 2019; Yamamoto, 2017). Emotional contagion has also been related to motor mimicry: motor mimicry has been considered as the underlying mechanism of emotional

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matching (Hatfield, Cacioppo, & Rapson, 1994; Preston & de Waal, 2002). When an observer mimics the display of another, induces in itself the perceived emotional state (Niedenthal, 2007; de Waal and Preston, 2017). The evidence of the relevance of motor mimicry in emotional contagion is extensive for facial displays (see e.g., Palagi et al., 2020; Campbell & de Waal, 2011; Davila-Ross et al., 2008; Norscia & Palagi, 2011; Palagi et al., 2009; Palagi et al., 2018; Palagi et al., 2019; de Waal and Preston, 2017). Motor mimicry, though, is interesting on its own, as it can occur without emotion contagion (for a review, see Chartrand & Lakin, 2013; Duffy & Chartrand, 2015). Overall, emotional contagion processes do not seem to be cognitively demanding and thus might be important evolutionary adaptations for a wide number of social species.

Emotional contagion may provide important adaptive advantages to species that need to interact with others and engage in parental care. For these species, adopting the same emotional state of their group, mate or offspring could be vital in certain contexts. For example, the rapid spread of fear among group members could allow that most individuals in a group escape from potential danger. Emotional contagion is a way to acquire valuable information about environmental threats without directly experiencing them (Decety et al., 2012; Preston & de Waal, 2002). Furthermore, being able to emotionally resonate with others may be crucial for effective communication and social cohesion (de Vignemont & Singer, 2006; Decety et al., 2012). Besides, emotional contagion may help promote social bonds, restore relationships after agonistic interactions, reduce stress levels, enhance social acceptance, and mark others as similar to self (Decety et al., 2012; Uchino et al., 1996). As a consequence, emotional contagion may provide the primary motivation for prosocial responses (de Vignemont & Singer, 2006; Decety et al., 2012; Yamamoto, 2017). And, in species endowed with further cognitive abilities, emotional contagion may underlie more complex empathic behaviors such as helping (Pérez-Manrique & Gomila, 2018). Finally, in many cases, parental care relies on the ability to be affected by the emotional expressions of the offspring, allowing parents to respond with care to the needs of their young (Darwin, 1897; Preston & de Waal, 2002). This capacity could thus provide an important fitness advantage for the offspring (Decety et al., 2012).

Despite the supposed importance of emotional contagion in numerous aspects of animals' social life and its presumed simplicity, the study and direct demonstration of this phenomenon present more complexities than would be expected, and neither its features are as well defined as assumed by most of the scientific community (Adriaense et al., 2020). Nevertheless, momentum in the study of emotional contagion in nonhuman animals has been gathering in the past decade. For these reasons, a review of the available evidence and pending challenges seems timely. We have decided to organize the studies on emotional contagion in groups of species, and order them according to the number of studies available. In so doing, we hope to provide a clear panoramic vision of the experimental paradigms, variables measured, and modulating factors, as a way to propose how to improve research in this field and get clearer results. After the revision of literature, we will discuss the methods, concepts and main problems of the field, and will propose solutions for future studies on emotional contagion in nonhuman animals.

2 | STUDIES ON EMOTIONAL CONTAGION IN NONHUMAN ANIMALS

2.1 | Mammals

2.1.1 | Rodents

Rodents have become consolidated as an ideal model for assessing emotional processes in animals and the neural substrates involved. In recent years, many studies have focused on emotional contagion of pain, distress and fear. These studies reveal that rodents are highly attuned to the affective state of their group partners (see reviews Hernandez-Lallement et al., 2020; Keum & Shin, 2016; Kim et al., 2019; Meyza & Knapska, 2018; Meyza et al., 2017; Mogil, 2012; Panksepp & Lahvis, 2011).

Studies on emotional contagion of negative emotions (fear, distress, and pain)

Studies on emotional contagion of fear, distress and pain in rodents can be broadly divided into five categories, depending on the type of stimulus to which the observer animal is exposed (Meyza et al., 2017): A conspecific receiving aversive physical stimulation, a fear-conditioned conspecific reacting to the conditioned stimulus, a distressed conspecific due to a previously experienced event, a conspecific in various degrees of pain, and a conspecific subjected to a social stressor.

1. The first category includes experiments in which rodents observe a conspecific (demonstrator) experiencing aversive stimulation (e.g., foot-shocks), in occasions paired with a conditioned stimulus (e.g., a tone). This paradigm serves to assess the observer's responses to demonstrators' fear and pain reactions. As rodents usually express fear by freezing (defensive immobility) (Sivaselvachandran et al., 2016), this is the most used behavioral variable in experiments assessing emotional contagion of fear.

In two seminal studies, a rat (*Rattus norvegicus*) had to press a lever to either obtain food while observing another rat receiving electrical shocks (Church, 1959) or to stop the shocks delivered to a conspecific (Rice, 1964). Both studies showed that the exposure to a conspecific's distress decreased the observers' rate of lever pressing, behavior that was interpreted as a signal of fear (Estes & Skinner, 1941). Interestingly, rats that during the training phase received a synchronous shock with a partner expressed a strong drop in lever pressing compared to the other groups (rats that received shocks in isolation, and the no-shock group). This behavior was observed even when rats were deprived of food (Church, 1959). However, in the experiment of Rice (1964), it was not clear whether this effect and the observers' fear-related responses were due to the features of the apparatus or triggered by the sight of the distressed conspecific.

Some recent and more controlled studies have provided mixed results on the response of rodents to the exposure of conspecifics being subjected to physical stressors. Four studies showed that neither the visual (Sanders et al., 2013) nor auditory (Atsak et al., 2011; Chen et al., 2009; Ueno et al., 2020) exposure to familiar or unrelated conspecifics receiving foot-shocks or to videos of foot-shocked cagemates elicited freezing responses in observer rodents. However, another series of studies provided positive evidence of this phenomenon. Mice (*Mus musculus*), degus (*Octodon degus*) and rats displayed freezing behavior in response to the sight of a familiar or unrelated demonstrator receiving electrical shocks (e.g., Allsop et al., 2018; Atsak et al., 2011; Carrillo et al., 2015; Gonzalez-Liencrez et al., 2014; Han et al., 2020; Jeon et al., 2010; Jeon & Shin, 2011; Keum et al., 2016; Keum et al., 2018; Lidhar et al., 2017; Pisansky, Hanson, et al., 2017; Pisansky, Young, et al., 2017; Sanders et al., 2013; Twining et al., 2017; Ueno et al., 2020; Yusufshaq & Rosenkranz, 2013). Besides, in rats, the demonstrators' behavior was modulated by the behavior of the observers: they froze more if witnesses froze more (Atsak et al., 2011; Han et al., 2020). Interestingly, genetic background modulated some of the mice's responses. For example, only mice from a gregarious genetic strain displayed a heart rate deceleration in response to the playback of vocalizations of conspecifics receiving shocks (Chen et al., 2009). That response has been related to empathic concern in humans (Zahn-Waxler et al., 1995). Also, this social breed and four more inbred mouse strains showed a significant increase in freezing behavior while observing a demonstrator being repeatedly shocked compared to five other strains (Keum et al., 2016).

Overall, the results of some of these studies showed that exposure to a conspecific experiencing an aversive event influenced the behavior of observer rodents. More precisely, observers displayed similar behavioral responses to those of the demonstrators, being freezing the most prominent response. However, a recent study has questioned whether this freezing behavior is an indicator of emotional contagion or it is rather a tendency to imitate the movements of others (Ueno et al., 2020). Ueno and collaborators reported that observer mice ate the same amount of chocolate chips in the presence of a foot-shocked cagemate than in the presence of an undisturbed mouse, whereas demonstrators ate no chocolate while receiving the shocks. According to the authors, this outcome indicates that observers were more strongly motivated by food than by the emotional responses of their mate, suggesting that freezing behavior does not reflect empathy-like behavior. Furthermore, in support of this hypothesis, this study also showed that observers' freezing behavior did not correlate with the degree of pain experimented by demonstrators.

2. In the second group of studies on emotional contagion of fear, demonstrators are first fear-conditioned and then subjected to a fear-memory retrieval task in which only the conditioned stimulus is presented (e.g., a tone). During the fear-memory retrieval, the observers' reactions to a frightened demonstrator are registered. In these studies, the display of freezing behavior by the observer is also interpreted as evidence of the social transfer of fear among rodents. Overall, prairie voles (*Microtus ochrogaster*) and rats with previous experience with the aversive event but not with the conditioned stimulus, displayed significant freezing in response to the reactions of the frightened individual (e.g., Burkett et al., 2016; Kim et al., 2010; Pereira et al., 2012). Furthermore, some of the observer's responses occurred concurrently with those of the demonstrator (Burkett et al., 2016).

A more controversial issue is which of the demonstrator's responses triggered the observed freezing behavior. It has been proposed that fear-induced 22-kHz ultrasonic vocalizations (USVs) may play a role in this "fear transmission" in rats (Kim et al., 2010). This hypothesis is supported by the fact that observers' freezing was blocked by specific lesions in the thalamus, which prevented auditory information flow to the forebrain (Kim et al., 2010). However, some studies (Jones & Monfils, 2016; Pereira et al., 2012) showed that most of the demonstrators did not emit

distress calls at all during the fear-memory retrieval task, and yet observers displayed freezing behavior. This result casts doubt on the role of USVs in this process. An alternative explanation is that other auditory cues could be involved in this process. In fact, Pereira et al. (2012) reported that freezing of the demonstrator could be detected through the lack of movement-evoked sound. They showed that the sudden cessation of locomotion sounds triggered freezing only in experienced observers, even when the test was performed in the dark.

Vicarious fear learning: Social interaction with a frightened, distressed or emotionally aroused conspecific has been found to result in long-lasting changes in behavior modulating learning and memory (Meyza et al., 2016). Vicarious fear learning and social acquisition of defensive, avoidance or conditioned fear responses have been interpreted as a proof of emotional contagion. In these studies, observer rodents are usually first exposed to a demonstrator reacting to a conditioned stimulus either during the conditioning procedure (e.g., paired with an unconditioned stimulus like shocks) or during a fear memory retrieval (without unconditioned stimulus). Then, observers are tested to examine their responses towards the conditioned stimulus. In this way, it is possible to assess whether observers learned from the demonstrator's emotional responses to fear certain cues. This social transfer of information and subsequent learning from emotional cues have been observed in rats, mice deer mice (*Peromyscus maniculatus*) and degus (e.g., Allsop et al., 2018; Bredy & Barad, 2009; Bruchey et al., 2010; Chen et al., 2009; Ito et al., 2015; Jeon et al., 2010; Jones et al., 2014; Jones & Monfils, 2016; Kavaliers et al., 2003; Kavaliers et al., 2005; Knapska et al., 2010; Lidhar et al., 2017; Nowak et al., 2013; Panksepp & Lahvis, 2016; Twining et al., 2017; Yusufshaq & Rosenkranz, 2013). However, the use of this type of measurements to assess emotional contagion is controversial. It has been claimed that these paradigms do not measure emotional contagion, instead, they use it as a tool to study the cognitive impacts of observing distress in others (Hernandez-Lallement et al., 2020). That is, as changes in memory and learning do not involve an emotional observable response, they are considered as secondary processes related to emotional contagion (Hernandez-Lallement et al., 2020). Furthermore, observational learning can occur in these tasks without implying the sharing of emotions (Keum et al., 2018).

3. In the third group of experiments, observer rodents were exposed to a distressed conspecific which had undergone an aversive event (e.g., fear conditioning episode). In this case, the demonstrator was still stressed due to the previous aversive and/or painful event. Thus, this protocol serves to evaluate the observer's responses to demonstrator's distress cues. These studies used different indicators to assess the occurrence of emotional contagion: behavioral reactions (e.g., percentage of freezing time), and physiological and neural responses. Again, the existing evidence is mixed:

On the one hand, rats, mice and voles showed several signs of distress and fear when exposed to a distressed conspecific. Rats displayed an increased arousal/vigilance state (Knapska et al., 2006; Knapska et al., 2010), and fear responses (increased freezing and self-grooming) (Rogers-Carter et al., 2018). Besides, after the exposure, only female rats presented an amygdalar activation similar to that of demonstrators, being the amygdala a part of the limbic system involved in fear processing and emotional reactions (Knapska et al., 2006; Mikosz et al., 2015). Similarly, mice also spent significantly more time immobile when exposed to a fear-conditioned cage mate than when exposed to an unaltered partner (Ueno et al., 2020). And, only a gregarious strain of mice displayed increased activation in the prefrontal cortex and the amygdala (Meyza et al., 2015). In turn, prairie voles mimicked the anxiety and fear like behaviors (self-grooming and freezing) of a stressed familiar vole (Burkett et al., 2016). Furthermore, when voles could not interact physically with their distressed partner, they presented significantly elevated plasma corticosterone which correlated with that of the demonstrator. Therefore, the behavioral and physiological responses displayed by observers and demonstrators were alike, suggesting an emotional state-matching between them. On the other hand, rats' responses did not differ when interacting with distressed or control rats (Mikosz et al., 2015). And, when visual but not auditory or odor cues emitted by the distressed partner were blocked, no significant differences in observer mice' freezing were observed (Ueno et al., 2020).

4. The fourth category encompasses studies assessing social modulation of pain by registering changes in pain sensitivity or pain thresholds in individuals exposed to a conspecific in pain (see reviews Hernandez-Lallement et al., 2020; Martin et al., 2014; Mogil, 2015). To do so, a noxious stimulus is administered to observers and demonstrators and then, they are tested in dyads or isolation. In mice, modulation of pain sensitivity (hyperalgesia) was observed in familiar (cagemates) but not in stranger dyads or individuals tested alone (e.g., Langford et al., 2006; Laviola et al., 2017; Martin et al., 2015). Furthermore, observers presented altered pain sensitivity in a different modality and displayed pain behaviors (writhing) that were influenced and co-occurred with those of the cagemate. These pain behaviors were dependent on visual information (Langford et al., 2006). However, this protocol in which both, observer and demonstrator are in pain, does not allow to distinguish between the effects of vicariously felt pain and

physical pain (Yu et al., 2019). A series of studies have tried to overcome this impediment by first exposing mice and rats to an individual in pain (cagemate or stranger), and then isolating them and examining their pain responses (Du et al., 2020; Li et al., 2014; Li, Yu, et al., 2018; Lü et al., 2017; Yu et al., 2019). Again, only observers which interacted with familiar individuals showed enhanced pain-related behaviors, increased mechanical but not thermal pain sensitivity, and enhanced nociceptive neuronal activity. Furthermore, these responses seemed to be mediated by the medial prefrontal cortex and the locus coeruleus (Li et al., 2014; Lü et al., 2017), brain structures related to empathy for pain in humans (Singer et al., 2004; Yu et al., 2019).

5. Finally, a series of studies used social defeat as a social stressor to assess the effects on the physiological, cognitive and behavioral responses of observer rats and mice (see Carnevali et al., 2020 for a review). After several days of viewing aggressive encounters between conspecifics, observers displayed different responses including increased anxiety and depression-like behaviors strikingly similar to that of defeated conspecifics. Both, witnesses and demonstrators, also displayed increased levels of serum corticosterone (a glucocorticoid involved in stress responses), deficits in body weight and increases in mean arterial pressure and heart rate (Carnevali et al., 2017; Finnell et al., 2017, 2018; Iñiguez et al., 2018; Miao et al., 2018; Patki et al., 2014; Patki et al., 2015; Sial et al., 2016; Warren et al., 2013, 2014)(Warren et al., 2013).

Studies on emotional contagion of positive emotions

There is an important lack of studies investigating emotional contagion of positive emotions in rodents (Hernandez-Lallement et al., 2020). One of the few available studies is that of Saito et al. (2016). They tested whether rats display positive or negative emotional contagion after hearing conspecific USVs (50 kHz USVs emitted in positive contexts and 22 kHz USVs emitted in negative contexts) via a cognitive bias task. This task serves to measure affective states via operant conditioning. Rats were first conditioned to respond differently to two sounds, each of which signaling either a positive or a negative outcome. Then, they were exposed to an ambiguous cue (frequency falling between the two conditioned stimuli). After being exposed to positive vocalizations rats responded to ambiguous cues as positive (optimistic bias), and negative after being exposed to negative vocalizations (pessimistic bias). Suggesting that rats were indeed influenced by the emotional cues of conspecifics. Another experiment showed that observation of reward delivery to another rat modulated the emission of USVs in observers and the release of dopamine (neurotransmitter involved, among other things, in reward processes and reinforcement learning) (Kashtelyan et al., 2014). Interestingly, rats seemed to experience a mixture of affective states while observing their conspecific receiving the treat but not when the reward was delivered to an empty box. On the first trial of conspecific observation, a strong release of dopamine and the highest rate and amplitude of positive calls (50 kHz) were registered. When the rat obtained the reward for itself, a release of dopamine was also observed, suggesting a positive emotional state matching between rats. However, during the following trials, dopamine release was reduced and the rate of negative calls (22 kHz) increased. Moreover, during these trials, observers rapidly oriented away from the rewarded rat. The authors suggested that these data could be indicative of a negative affective state (e.g., frustration) in the observer when watching another individual eating.

Factors influencing emotional contagion responses

Certain variables seemed to influence rodent responses in these studies: previous experience, familiarity, genetic background, rearing conditions, gender, stress levels and repeated exposure to the stimulus. For example, observer mice and rats displayed fear behaviors only if they previously had a shock experience similar to that of demonstrators (Atsak et al., 2011; Carrillo et al., 2015; Sanders et al., 2013). Specific genetic variations and the rearing conditions also influenced emotional contagion of fear and distress in rats and mice. Distinct mouse strains responded differently to the sight (S. Keum et al., 2016) and sound (Chen et al., 2009) of conspecifics receiving shocks. Besides, isolation-reared rats showed significantly less freezing behavior observing a demonstrator receiving foot-shocks compared to pair-housed rats (Yusufshaq & Rosenkranz, 2013). However, when it comes to familiarity the results are not so clear cut. On the one hand, a familiarity bias was reported in mice and degus fear responses: observers showed more freezing behavior when they were socially related to demonstrators (e.g., Gonzalez-Liencre et al., 2014; Jeon et al., 2010; Jeon & Shin, 2011; Lidhar et al., 2017; Pisansky, Young, et al., 2017). On the other hand, Sanders et al. (2013) did not find any familiarity bias in the freezing levels of observer mice, and the administration of oxytocin render male mice sensitive to the distress of strangers (Pisansky, Young, et al., 2017). Elevated stress levels could be responsible for the absence of emotional contagion in stranger dyads (Martin et al., 2015). In fact, blockade of glucocorticoid synthesis or receptors for adrenal stress hormones elicited the same pain behaviors among stranger and familiar pairs of mice and humans.

Moreover, the induction of stress impaired the previously observed behavioral responses in familiar dyads (Martin et al., 2015).

A recent meta-analysis (Hernandez-Lallement et al., 2020) found that, indeed, some of those factors had a significant modulatory effect on rodents' emotional contagion responses: breed (mice), prior experience with the stimulus (rats), social testing conditions, age or the sensory modality of the demonstrator cues. Conversely, they found no effect of sex and familiarity on emotional contagion of pain or fear. However, the authors remained cautious about these last results. In the case of sex, they relied on few data points and in the case of familiarity, the negative results could be due to important between-study differences in familiarity length (e.g., number of days rodents were together before the test). Furthermore, further analysis revealed a familiarity effect on pain contagion in mice, but only when demonstrators were subjected to abdominal pain.

2.1.2 | Nonhuman primates

Several anecdotal reports have described possible cases of emotional contagion in nonhuman primates, especially in chimpanzees: mothers briefly whimpering when they heard their offspring whimper (de Waal, 2008); chimpanzees becoming excited upon seeing another individual become aroused (O'Connell, 1995); or the scaling up of group arousal through the emission of excited vocalizations (Fritz & Koelsch, 2013).

The empirical study of emotional contagion in nonhuman primates started mainly in the '60s, with several experiments with rhesus macaques (*Macaca mulatta*). These monkeys received electric shocks while a conspecific observed their reactions (Masserman et al., 1964). The sight of a distressed individual affected the behavior of the observer up to the point that most of the macaques would suffer hunger rather than obtain food at the expense of shocking a partner. In their turn, Miller and colleagues carried out a set of experiments in which two macaques engaged in a cooperative-conditioning paradigm. In these studies, the demonstrator had access to the conditioned stimulus that was paired with noxious stimuli and the responder had access to a lever that, if operated, avoided aversive stimulation for both macaques. Importantly, the responder could see the face of the demonstrator during the testing sessions. The experiments showed that (1) macaques do react to the emotional expressions of other individuals (Miller et al., 1963; Mirsky et al., 1958); (2) observers did not respond when a monkey puppet or a rat received the shock (Miller et al., 1959); and that (3) macaques exhibited the same heart rate (HR) response when experiencing distress and when perceiving distress in others (Miller, 1967).

Several studies have more recently assessed the behavioral and physiological responses of chimpanzees to the sight and sound of emotional expressions of conspecifics. Berntson et al. (1989) exposed infant chimpanzees to conspecifics' emotional vocalizations and recorded changes in HR and behavior. Conspecific laughter had an acceleratory influence in HR and evoked vocalizations similar to adult threat-barks. Conversely, screams evoked decelerating HR responses. These findings indicate that cardiac responses of infant chimpanzees differentiate between scream and laughter stimuli. However, infants' reactions to laughter were more reminiscent of a defensive reaction than of a positive emotional state.

In another study (Parr & Hopkins, 2000), chimpanzees' tympanic membrane temperature (Tty) was measured while they watched three types of emotional videos: positive, neutral or negative. Tty is an index of brain temperature changes that, in turn, indicates variations in physiological arousal (Hopkins & Fowler, 1998). Right Tty increased significantly in response to the negative emotional videos and left Tty increased in response to the positive videos, but not significantly. This outcome might suggest lateralization of emotional processing in chimpanzees. Moreover, during negative videos chimpanzees responded with strong visual orientation, piloerection, pant-hooting vocalizations and bluff-displays, indicators of a high arousal state. In a similar experiment (Parr, 2001), chimpanzees watched three categories of negative emotional videos. A decrease in peripheral skin temperature (an indicator of negative arousal) was recorded when chimpanzees viewed videos of individuals injected with needles or videos showing needles but not when watching videos of a conspecific chasing the veterinarian. There were no significant differences in the responses to the sight of conspecific injected and the sight of needles themselves. Thus, it was not clear that the physiological changes were triggered by the perception of another's distress rather than by the sight of an aversive stimulus like needles.

Furthermore, two studies have used infrared thermography to examine changes in skin temperature in wild and captive chimpanzees exposed to different types of emotional stimuli (Dezecache et al., 2017; Kano et al., 2016). Kano et al. (2016) registered nasal temperature, cortisol level, HR and behavioral responses of chimpanzees exposed to play-back sounds or videos of conspecifics fighting. Chimpanzees showed changes in excitement behavior and HR-variability

in response to these stimuli but not in salivary cortisol. Furthermore, chimpanzees' nasal temperature decreased in response to the playbacks and videos of conspecific agonistic interactions. In turn, Dezechache et al. (2017) assessed changes in surface body temperature of wild chimpanzees upon hearing different conspecific vocalizations. Overall, they found that aversive vocalizations induced larger decreases in temperature in the nasal area compared to neutral vocalizations, data that match that obtained with captive individuals (Kano et al., 2016). In turn, neutral calls produced larger increases in temperature in the ear region than aversive ones. Moreover, the vocalizations that were associated with more dramatic temperature changes were the aggressive barks, vocalizations that have been proposed to be highly emotional (Dezechache et al., 2017). Overall, it has been reported a link between a decrease in nasal temperature and negative emotional states (Adriaense et al., 2020). Therefore, these findings suggest the occurrence of contagion of negative emotions in chimpanzees. However, there are still discrepancies and inconsistencies in the data on facial temperature and its relationship with emotional states, thus, more research is needed to extract solid conclusions based on thermal results. Furthermore, the use of aggressive vocalizations as stimuli might not be the best to assess emotional contagion since they can trigger fear responses in the listener without involving the sharing of emotions.

In turn, tufted capuchin monkeys (*Sapajus apella*) appropriately associated the emotional valence of conspecifics' expressions with a container, preferring to reach the one that elicited positive expressions in the demonstrator (Morimoto & Fujita, 2011, 2012). However, no clear responses indicative of emotional contagion between observers and demonstrators were registered, despite demonstrators displaying overt emotions during the experiment (Morimoto & Fujita, 2012).

Finally, a study assessed the occurrence of visual contagion of grooming, affiliative behavior associated with positive and relaxed states, in a group of semi-free-ranging female Barbary macaques (*Macaca sylvanus*) (Berthier & Semple, 2018). In this group, observing conspecifics groom produced a reduction of behavioral indicators of anxiety and an increase in the number of different affiliative behaviors. These results suggest that both being groomed and observing others grooming, induce, in fact, a positive state in macaques and that this state can be transferred to bystanders. However, this study does not allow to differentiate whether these outcomes were the result of emotional or behavioral contagion.

2.1.3 | Swine and bovids

Interest in whether emotional contagion is found in swine and bovids has been related to animal welfare in farms. Some evidence of emotional state matching has been found, but experimental control in this area needs improvement.

Some interesting research has been done on the reactions of farm animals to distressed conspecifics. Anil et al. (1997;1996), for example, investigated the stress responses of pigs (*Sus scrofa domestica*) and sheep (*Ovis aries*) witnessing the process of slaughtering of conspecifics. They did not find any specific stress-related changes in pigs or sheep when witnessing stunning or slaughter, although the levels of stress-related hormones and HR tended to be high during the process due to human contact and handling. Both studies lacked rigorous controls, so they were not able to distinguish between effects due to the experience of the observers and those triggered by the slaughter.

Reimert et al. (2013) assessed the responses of naive pigs (observers) to the emotional responses of a trained pen mate (demonstrator). The demonstrator had had experience with the auditory and visual cues that signaled rewarding and aversive events, and the naive pig observed its reactions during the anticipation and experience of the events. The behavior of both pigs matched, displaying behaviors indicative of positive emotions (e.g., play) during the rewarding events and behavioral indicators of negative emotions (e.g., tail low, increased level of defecation and urination, low-pitched vocalizations, etc.) during the aversive events. Salivary cortisol measurements supported these behavioral observations, indicating that both pigs were aroused by the events. The authors ruled out the possibility that naive pigs were just copying the behaviors from the demonstrators since, during the events, observers could not see the demonstrators only hear them.

In two follow-up studies, Reimert et al. (2015, 2017) used the same paradigm to examine the influence of intranasal doses of oxytocin (neurohormone that has been related to empathic processes) on observer pigs' behavior, and whether the emotional responses of the demonstrator had long-term effects on observers' emotional state. Oxytocin did not significantly affect observers' behavior, except by increasing the number of negative vocalizations (Reimert et al., 2015). Surprisingly, it affected the behavior of the demonstrators which had not received oxytocin. Thus, the authors concluded that oxytocin may play a role in pig auditory or olfactory communication. In turn, the emotional state of a pig subjected to either a positive or negative treatment affected (positively and negatively, respectively) the state of

observers in the period after the treatment (Reimert et al., 2017). However, the positive emotional state elicited in the observer pigs could also be due to the exposure to traces of peat and chocolate raisins present on the demonstrator body after the treatment, rather than triggered by emotional contagion.

Another study (Goumon & Špinková, 2016) showed that piglets responded to the sight of a frightened pen mate with greater attention and more indicators of fear than to the sight of an unaltered mate. Furthermore, experienced observers reacted more strongly than naïve ones. The authors stated that these responses could be indicative of emotional contagion of fear between piglets.

Baciadonna et al. (2019), using a habituation–dishabituation–rehabilitation playback paradigm, showed that goats (*Capra hircus*) seem to distinguish the valence of conspecific calls. Goats were exposed to conspecific calls of the same type (contact call) but differing in their valence (positive and negative). First, they were habituated to listen to a positive or negative call. Then, in the dishabituation phase, the valence of the call was reversed and was followed by a final call from the habituation phase as control. When the valence of the call was reversed, goats look more towards the speaker. Furthermore, whereas the valence of the call did not affect goats' HR, in the habituation/rehabilitation phases HR variability tended to be higher when goats were exposed to positive vocalizations than when exposed to negative ones.

2.1.4 | Canids

Dogs are a very interesting animal model to study inter-species emotional contagion due to their close bond with humans. It has been reported that during positive interactions there is a physiological and hormonal synchronization (Odendaal & Meintjes, 2003) and a positive correlation of HR variability changes (Katayama et al., 2019) between dogs and their owners. Moreover, dogs seem to discriminate human emotions (Deputte & Doll, 2011) and emotional expressions of human faces (Müller et al., 2015). Even human odors excreted during emotional situations of different valence could distinctly affect dogs' behavioral and cardiac responses (D'Aniello et al., 2018).

Using different paradigms, several studies have evaluated the occurrence of emotional contagion between dogs and humans. In one of them, dogs were exposed to 4 conditions: two in which their owner or a stranger pretended to cry and two in which they hummed a song (Custance & Mayer, 2012). Dogs oriented significantly more often towards their owner or the stranger during the crying condition. Furthermore, most of the dogs approached the person in a submissive way and two dogs produced mild distress vocalizations. When the stranger was pretending to cry, dogs sniffed, nuzzled and licked him instead of seeking out their owner for comfort. Thus, the authors suggested that dogs' reactions were driven rather by emotional contagion than by personal distress (a self-focused, aversive emotional response triggered by the perception of another's distress [Batson, 1991]).

Sümeği et al. (2014) examined whether the owner's stress level could be contagious to the dog using as an indicator the registered changes in dogs' performance in a spatial working memory task (remember the location of a ball). This paradigm is supported by data showing a significant effect of perceived stress on subjects' cognitive performance in memory tasks (McEwen & Sapolsky, 1995). Task completion was indeed affected by dog owners' anxiety state: dogs showed better performance in the task after interacting with their stressed owner. A stressful period in which dogs were separated from their owners also improved dogs' performance in the test.

Yong and Ruffman (2014) assessed whether humans and dogs showed signs of emotional contagion responses to three auditory stimuli: a human infant crying, a human infant babbling and 'white noise'. They found that, only after the crying condition, cortisol levels increased significantly from the baseline in both species. Moreover, dogs behave in a submissive and alert manner in response to crying. Similarly, Huber et al. (2017) exposed dogs to positive and negative sounds of humans or conspecifics and nonemotional sounds and measured their behavioral responses. Dogs displayed significantly more indicators of arousal and negative emotional states (e.g., more time freezing) when hearing negative sounds compared to positive ones, irrespectively of the species producing the sound. These results suggest an inter and intra-specific contagion of emotional valence.

To date, three studies have assessed prosocial rescue behavior in dogs and whether this behavior relies on emotional contagion (Carballo et al., 2020; Sanford, 2017; Van Bourg et al., 2020). In these experiments, dogs had the opportunity to free their seemingly trapped owner from a compartment. Dogs were tested in one condition in which the owner displayed signs of distress and in different control conditions (e.g., the owner hummed or read inside the box). In general, dogs released their owner more often in the distress condition compared to the control conditions. However, only one of the studies provided clear evidence that dogs were affected by the distress cues emitted by their owners (Van Bourg

et al., 2020): dogs displayed significantly more behavioral stress responses in the stress condition than in the control ones.

Finally, a study tested whether dogs experience emotional contagion and direct empathy-like behaviors towards familiar individuals (dogs that lived together) after hearing conspecifics' distress whines (Quervel-Chaumette et al., 2016). Each dog participated in three conditions in which they were first exposed to the playback of three stimuli: either familiar whines (from their partner), stranger whines or control sounds. Then, they were reunited with their partners. Whereas dogs displayed higher alertness and more stress-related behaviors in the whine conditions compared with the control condition, none of these responses was influenced by familiarity. That is, dogs did not respond differently to whines according to the identity of the caller. Unlike the study of Yong and Ruffman (2014), no increase in salivary cortisol levels was found. Dogs spent more time near their partner and engaged in more affiliative behaviors after the whine conditions than after the control condition.

2.1.5 | Elephants

Elephants have complex social behavior and share close bonds with family members, features which make them a very interesting study species for emotional contagion research (Plotnik & de Waal, 2014). However, there are not many empirical studies with well-defined controls assessing emotional contagion, and most of the available data come from anecdotal reports. The available evidence suggests that when a member of a group experiences distress, the others react emotionally.

Although anecdotal reports have been called into question for several reasons (see Bates & Byrne, 2007), they can provide valuable data. For example, Douglas-Hamilton et al. (2006) carried out a rigorous observational report using long-term associations records, GPS tracking data and direct observations of a group of African elephants (*Loxodonta africana*). They reported the behavioral responses of different elephants towards a dying and deceased matriarch. For example, when the injured matriarch fell to the ground showing signs of distress such as temporal gland secretion (related to stress, excitement or fear in elephants [Gorman, 1986]), an unrelated matriarch rapidly approached her displaying signs of excitement too, as tail raised, emission of vocalizations and temporal gland secretion. This female also tried to lift her. Sikes, in 1971 (Schulte, 2000) described a similar case in which an elephant was mortally wounded and could not rise. The other group members tried to lift it, but they failed, so they started circling the injured individual (an indicator of stress in elephants [Ranaweerage et al., 2015]). Similar observations were made in Asian elephants (*Elephas maximus*). Sharma et al. (2020) registered the responses of an adult female to an injured and dying calf. This female tried to lift the calf and emitted a series of vocalizations (trumpets) that could be indicative of her distress. Jointly, these studies indicate that elephants are affected by the sight of a suffering individual. During those situations, they displayed both behavioral and physiological signals of distress that, sometimes, appeared to match those of the distressed individual suggesting the occurrence of an emotional state-matching.

Regarding empirical evidence of emotional contagion in elephants, we can only mention the study of Plotnik and de Waal (2014). They investigated affiliative tendencies between Asian elephants living in an elephant camp after distressing events (e.g., conspecific intimidation or aggression, group separation, environmental threat). The behavioral and emotional state of observer elephants matched those of individuals that had undergone a distressful event. More specifically, bystanders adopted the agitated behavior of the distressed individual (e.g., ears presented forward, erected tail, vocalizations, urination and defecation). Following a distress display, observers engaged in significantly more reassuring responses towards the distressed individual and directed more contacts to other elephants than during control periods with no distress displays. However, this study lacked well-defined controls to distinguish between the observer's behaviors triggered by the perception of distress in others from the behaviors elicited by the distressing event itself.

2.1.6 | Horses

In recent years, research on emotional processes of domestic horses (*Equus caballus*) has experienced great advances. These animals recognize and remember human emotional facial expressions (Nakamura et al., 2018; Trösch et al., 2019), and use those memories to adapt their behavior in subsequent interactions with humans (Proops et al., 2018). Furthermore, human anxiety might be contagious to horses. A study reported that when a person

accompanying a horse became aroused about a possible future event both, horses and humans, displayed an increased HR (Keeling et al., 2009). In another study, horses' behavioral and physiological responses were registered while they watched videos of positive and negative interactions of a conspecific with a human (grooming and veterinary procedures respectively) (Trösch et al., 2020). Horses displayed indicators of positive emotional states (positive facial expressions, contact-seeking behavior and decreased HR) during the positive videos and indicators of negative emotional states during the negative ones (negative facial expressions and increased HR). The authors proposed two explanations for these outcomes: observer's responses could have been driven by either an emotional contagion with the actor horse or by a reaction to the valence of the human's behaviors in the videos. In turn, Briefer et al. (2017) measured the behavioral and physiological reactions of horses to a specific type of vocalizations, whinnies, emitted by familiar or unfamiliar conspecifics during negative (social separation) or positive (reunion) situations. Although horses responded differently depending on the emotional valence of the whinnies, there was no clear evidence for an emotional state-matching between horses.

2.2 | Birds

The response to others' distress has also been studied in several bird species. The evidence available also suggests that emotional contagion can be found in social species of birds. Calls are an important way to express emotional arousal and thus influence others' state in these animals.

Using a similar paradigm to that of Church (1959) with rats, Watanabe and Ono (1986) tested pigeons (*Columba livia*) obtaining equivalent results. First, pigeons were trained to peck a lever that supplied food, and then, during these training sessions, they were repeatedly exposed to an individual being shocked. Pigeons showed a suppression of the response, not pecking the lever after witnessing the demonstrator's distress responses. Apparently, the conspecifics' distress became an aversive stimulus for them.

Wascher et al. (2008) assessed the responses of semi-tame free-roaming greylag geese (*Anser anser*) while they observed social and nonsocial events. Geese HR responses were significantly greater in social contexts. Significantly higher maximum HR and a greater HR increase were recorded in response to agonistic interactions in which a familiar individual (partner or kin) was involved. HR was also significantly higher when the bystander observed unrelated higher-ranking individuals interacting. The authors remained cautious of interpreting the HR results as an indication of emotional involvement, but they highlighted that the specificity of the arousal caused by witnessing social interactions points in that direction.

In turn, Perez et al. (2015) examined the responses of female zebra finches (*Taeniopygia guttata*) to males' stress-induced calls. Calls of males treated with corticosterone elicited an increase of this glucocorticoid levels and behavioral changes in females compared to control calls. Females' responses matched those of stressed males only when the calls were emitted by their mate, not by an unfamiliar male. Also using playback, Liévin-Bazin et al. (2018) tested the occurrence of emotional contagion in cockatiels (*Nymphicus hollandicus*). These birds displayed higher attention levels and were more active (e.g., emitted more calls) during the playback of distress calls than during the exposure to white noise. Moreover, the degree of affiliation influenced their responses: they displayed more stress-related behaviors (e.g., erected crest, increased locomotion and avoidance of the loudspeaker) in response to their partner's calls than in response to control sounds.

Edgar et al. carried out a set of studies assessing emotional responses of hens (*Gallus gallus domesticus*) after the perception of distress in their chicks or familiar individuals. First, they evaluated whether hens responded to an aversive stimulus (air puff) directed at them or their chicks (Edgar et al., 2011). Hens displayed increased alertness, decreased preening behavior and a reduction in eye temperature only when they were either exposed to the air puff or the sight of their chicks receiving the air puff. Exclusively during this last condition, hens showed increased HR and emitted more vocalizations. Although neither the valence nor the emotional component of hen's responses were clear, adult hens usually avoid environments associated with the reported physiological and behavioral changes (Nicol et al., 2009). Similar physiological and behavioral results were found in 9-week old domestic chicks using the same paradigm, in this case, chicks observed familiar broods receiving the air puffs (Edgar & Nicol, 2018).

A subsequent study (Edgar et al., 2013) investigated whether hens' behavioral and physiological responses to chick distress were mediated by their knowledge about the situation and by chicks' distress cues. Hens displayed indicators of a negative emotional state (e.g., increased vocalizations and walking rate [Edgar et al., 2011; Nicol et al., 2009]) when they perceived their chicks to be threatened, regardless of their chicks' responses to the situation. These responses may

serve to stimulate chicks to move away from the perceived danger and to enhance chicks' learning of the potentially threatening situation (Edgar et al., 2013). Furthermore, hens only displayed stress-induced hyperthermia when their perception of threat matched that of their chicks, suggesting that their responses were influenced and enhanced by chicks' distress cues. Thus, hens' responses may be driven by the integration of distress signals and hens own learned associations of the situation (Edgar et al., 2013). Conversely, hens did not display behavioral or physiological reactions in response to the mild distress of an unrelated but familiar conspecific (Edgar et al., 2012).

A recent study used the cognitive bias task to test emotional contagion in ravens (*Corvus corax*) (Adriaense et al., 2019). Before the cognitive bias task, observer ravens were exposed to conspecifics that were manipulated to display a positive or negative affective state. After being exposed to conspecifics in a negative state, observers displayed a pessimism bias towards the ambiguous stimulus. However, they did not show an optimism bias after observing a conspecific in a positive state. Moreover, the demonstrators did not show statistically significant differences in their behavior when subjected to the cognitive bias test, neither in the positive nor negative condition. The authors pointed out that demonstrator results could have been unsuitable for interpretation due to procedural constraints.

Finally, two experiments examined positive emotional contagion within the context of play behavior in two social species of birds: kea parrots (*Nestor notabilis*) and ravens. Schwing et al. (2017) assessed whether play vocalizations of keas may elicit emotional contagion. The acoustic playback of play calls increased significantly the amount of play among both juveniles and adult wild keas compared with the control sound stimuli. Furthermore, these vocalizations seemed to induce playfulness rather than 'invite' to play since the keas, instead of joining in play that was already underway, started playing with other nonplaying keas or engaged in solitary play. These results support the authors' hypothesis that play calls may act as a contagion process of positive emotional states. Osvath and Sima (2014) also investigated whether the spread of play might be a case of positive emotional contagion in ravens. In the experimental condition, a toy known to elicit object play in the individual holding was introduced in the aviary and then play behaviors were measured. Ravens engaged in different categories of play during this experimental condition but not during the control conditions (no intervention and introduction of food in the aviary). Given that a category of play in one individual induced different categories of play in others, this result points to play mood contagion rather than a spread of specific motor patterns (Osvath & Sima, 2014). However, to better distinguish between the occurrence of emotional contagion and behavioral contagion (which could not imply the sharing of emotions), this kind of paradigms should also report an increase in other behavioral indicators of positive emotions, apart from play behavior itself (Briefer, 2018).

2.3 | Fish

To date, not many studies have focus on fish species, but the scarce evidence available suggests that fear displays can spread in groups of fish.

Two studies have examined emotional contagion of fear in zebrafish (*Danio rerio*) (Fernandes da Silva et al., 2019; Oliveira et al., 2017). Both works registered the behavioral changes triggered in zebrafish when visually exposed to anti-predator behaviors of other conspecifics. These displays induced antipredator reactions in observers similar to those of demonstrators (e.g., freezing, increased swimming speed, diving to the bottom). Observers also showed increases in cortisol levels (Oliveira et al., 2017). Furthermore, the responses of zebrafish were influenced by familiarity. They responded more strongly when observing a distressed familiar fish than when observing an unfamiliar demonstrator (Fernandes da Silva et al., 2019). The results suggest that fear contagion mediated the observers' responses in these experiments.

3 | MAIN FINDINGS AND PROBLEMS IN THE STUDY OF EMOTIONAL CONTAGION IN NONHUMAN ANIMALS

In a broad sense, the reviewed evidence supports the claim that certain animals are sensitive to the emotional displays of conspecifics. This suggests that the sharing of emotions could be widespread among vertebrates. But there is still a lack of empirical studies on emotional contagion in many animal species, as well as standardized experimental and conceptual approaches. The detailed consideration of the reviewed studies makes us point the following as the most important problems and challenges for this field:

3.1 | Standardized paradigms and concepts

first, many studies do not have a clear concept of emotional contagion and infer it from the evidence of other processes such as behavior contagion (see Adriaense et al., 2020 for a deeper review on this issue). As we have previously highlighted, to establish the occurrence of emotional contagion it is necessary to assess an emotional state in the demonstrator and the occurrence of an emotional state matching in the observer. In this endeavor physiological measures and context information are also required in addition to evidences of behavior contagion. Second, even if the studies use the same concept they differ in their methods. We noted that the procedures and stimuli used to assess emotional contagion varied greatly between studies (see Table 1). Whereas some paradigms directly registered physiological or behavioral changes in one or both individuals, others used indirect measures like fear-memory retrieval tasks to examine the influence of another's emotional displays in the observer's responses. The lack of a systematic paradigm makes it difficult to properly compare the available data. In fact, many of the contradictory and not conclusive results on the field may be due to this unstandardized use of different methods and protocols (Hauser, 2000). For example, in the case of rodents the reviewed studies measured different parameters, used different devices, intensities of the aversive stimuli and housing conditions. To properly compare results it is necessary that the studies from which they come use the same parameters and factors.

Depending on the species, emotional contagion processes could be displayed only under precise circumstances, and when interacting with certain individuals. Due to this variability of emotional responses, it is unfeasible and useless to design a single paradigm to assess emotional contagion in nonhuman animals. However, it would be useful at the time of comparing data from the same species to reach a consensus on which paradigm to follow. At the time of designing those paradigms, it is crucial to consider the ecological circumstances and socio-behavioral traits of the species. In this endeavor, data coming from anecdotal reports of wild animals could be a very useful tool. This information, apart from being a source of valuable information by itself (Boesch, 2020), could help establish which emotions to assess in each species, what are the best contexts in which to study emotional responses or what factors and variables must be taken into account. In some cases, thus, the same standardized procedure could serve to compare studies carried with different species, if they are influenced by the same variables and tested in similar contexts. Finally, to assess the factors influencing observers' emotional responses it is necessary to test the animals using the same protocol but varying one variable of the procedure (e.g., sensory modality of the stimuli) to register the occurrence of emotional changes.

3.2 | Assessment of emotional responses

for a certain process to qualify as emotional contagion it must include an emotional response. However, many studies fail to measure the different components required to establish the occurrence of an emotional state (neurophysiological, behavioral, and cognitive). Indeed, most of the studies only measure one component of the emotional response (see Table 1), and this could be problematic. Two individuals may match their physiological states but not their behavior, as different negative emotions trigger the same stress responses in the observers. Moreover, certain cues can transmit information that triggers automatic behaviors in witnesses without involving the sharing of emotions. Through observational learning, individuals could have learned to react in a certain way in presence of specific signals. These responses could resemble those arising from emotional contagion. Therefore, assessing the occurrence of an emotional state-matching between individuals using only behavioral variables is risky. So, we agree with Adriaense et al. (2020) in that a better approach to reliably assess the occurrence of emotional contagion is to measure several components of an emotional state through the recording of different behavioral and physiological measures (Paul et al., 2005). This approach also allows differentiating between behavioral and emotional contagion. In cases where this is not possible, an alternative could be to test the animals using the same stimuli but modifying the circumstances in which the observer is tested (e.g., introducing a preferred food item in the experimental enclosure; Ueno et al., 2020). In the case of contagion of fear or distress, observers are expected to display emotional responses when the demonstrator displays signs of fear or discomfort under almost any situation.

The question of which emotions get matched is also crucial. The diversity of emotional contagion responses and the fact that it is observed in many different contexts suggest that these processes could be multipurpose, serving independent functions in different situations and varying depending on the behavioral ecology of the species. Therefore, the type of emotions transferred between individuals might differ across species (Yamamoto, 2017), a fact that might explain some of the variability observed in animals' emotional contagion processes. For instance, due to its survival

TABLE 1 Summary of measures and stimuli used in the reviewed studies on emotional contagion

Stimulus*	Measures				
	Behavioral changes	HR	Physiological and hormonal changes	Cognitive performance	Others
Stressed conspecific	Behavioral changes Rhesus macaques (Miller et al., 1963) Prairie and meadow voles (Burkett et al., 2016) Rats (Knapska et al., 2010; Mikosz et al., 2015; Rogers-Carter et al., 2018) Mice (Ueno et al., 2020) Asian elephants (Plotnik & de Waal, 2014; Sharma et al., 2020) African elephants (Douglas-Hamilton et al., 2006; Schulte, 2000) Pigs (Goumon & Špinka, 2016) Zebrafish (Fernandes da Silva et al., 2019; Oliveira et al., 2017)	HR Pigs (Goumon & Špinka, 2016)	Physiological and hormonal changes Temperature changes Chimpanzees (Parr & Hopkins, 2000) <i>video</i> Hormonal changes (cortisol, corticosterone) Prairie voles (Burkett et al., 2016)	Cognitive performance Changes in memory/ Learning Cognitive bias	Others Changes in pain sensitivity

(Continues)

TABLE 1 (Continued)

Stimulus*	Measures				Others		
	Physiological and hormonal changes		Cognitive performance				
	Behavioral changes	HR	Temperature changes	Hormonal changes (cortisol, corticosterone)	Changes in memory/Learning	Cognitive bias	Changes in pain sensitivity
Stressed conspecific (only auditory cues)	Mice (Chen et al., 2009)	Chimpanzees (Bernison et al., 1989)	Horses (Briefefer et al., 2017)	Dogs (Quervel-Chaumette et al., 2016)	Rats (Saito et al., 2016)		
	Dogs (Huber et al., 2017; Quervel-Chaumette et al., 2016)						
	Goats (Baciadonna et al. 2019)	Mice (Chen et al., 2009)					
	Horses (Briefefer et al., 2017)						
	Cockatiels (Liévin-Bazin et al., 2018)	Goats (Baciadonna et al. 2019)		Zebra finches (Perez et al., 2015)			
	Zebra finches (Perez et al., 2015)	Horses (Briefefer et al., 2017)					
Stressed human	Dogs (Carballo et al., 2020; Custance & Mayer, 2012; D'Amiello et al., 2018; Huber et al., 2017; Sanford, 2017; Van Bourg et al., 2020; Yong & Ruffman, 2014)	Dogs (Carballo et al., 2020; D'Amiello et al., 2018; Katayama et al., 2019; Sanford, 2017) Horses (Keeling et al., 2009)		Dogs (Carballo et al., 2020; Yong & Ruffman, 2014)	Dogs (Sümegei et al., 2014)		

TABLE 1 (Continued)

Stimulus*	Measures					Others
	Behavioral changes	Physiological and hormonal changes	Temperature changes	Hormonal changes (cortisol, corticosterone)	Cognitive performance	
Conspecific experiencing negative stimulation	Rhesus Macaques (Miller et al., 1959; Mirsky et al., 1958; Wechkin et al., 1964)	Rhesus Macaques (Miller, 1967; Miller et al., 1966)	Chickens (Edgar et al., 2011; Edgar et al., 2012; Edgar et al., 2013; Edgar & Nicol, 2018)	Rats (Twining et al., 2017; Yusufishaq & Rosenkranz, 2013)	Changes in memory/ Learning	Changes in pain sensitivity
	Rats (Church, 1959; Han et al., 2020;; Rice, 1964; Twining et al., 2017; Yusufishaq & Rosenkranz, 2013)					
Mice	(Allsop et al., 2018; Atsak et al., 2011; Carrillo et al., 2015; Chen et al., 2009; Gonzalez-Liencres et al., 2014; Jeon et al., 2010; Jeon & Shin, 2011; Keum et al., 2016; Keum et al., 2018; Pisansky, Young, et al., 2017; Pisansky, Hanson, et al., 2017; Sanders et al., 2013; Ueno et al., 2020; Ueno et al., 2020 (video))	Chickens (Edgar et al., 2011; Edgar et al., 2012; Edgar et al., 2013)		Deer mice (Kavaliers et al., 2003)	Mice (Allsop et al., 2018; Chen et al., 2009; Ito et al., 2015; Jeon et al., 2010; Pisansky, Young, et al., 2017)	
	(Sehoon Keum et al., 2018)					
Pigeons (Watanabe & Ono, 1986)				Pigs and Sheep (Anil et al., 1996; Anil et al., 1997)	Deer mice (Kavaliers et al., 2003, 2005)	

(Continues)

TABLE 1 (Continued)

Stimulus*	Measures				Others		
	Physiological and hormonal changes		Cognitive performance				
	Behavioral changes	HR	Temperature changes	Hormonal changes (cortisol, corticosterone)	Changes in memory/ Learning	Cognitive bias	Changes in pain sensitivity
	Chickens (Edgar et al., 2011; Edgar et al., 2012; Edgar et al., 2013; Edgar & Nicol, 2018)	Pigs and Sheep (Anil et al., 1996; Anil et al., 1997)			Degus (Lidhar et al., 2017)		
Conspecific in pain	Pigs and Sheep (Anil et al., 1996; Anil et al., 1997)	Rats (Li et al., 2014)			Rats (Li et al., 2014)		
	Rats (Du et al., 2020; Li et al., 2018; Li et al., 2014; Lü et al., 2017)						
Mice (Langford et al., 2006; Martin et al., 2015)	Mice (Du et al., 2020; Langford et al., 2006; Martin et al., 2015)						
Fearful demonstrator	Rhesus macaques (Miller et al., 1959) (<i>pictures</i>)				Mice (Bredy & Barad, 2009; Nowak et al., 2013; Panksepp & Lahvis, 2016)		
	Rats (Jones et al., 2014; Jones & Monfils, 2016; Kim et al., 2010; Knapska et al., 2010; Pereira et al., 2012)				Rats (Bruchey et al., 2010; Jones et al., 2014; Jones & Monfils, 2016; Knapska et al., 2010)		
	Prairie voles (Burkett et al., 2016)						

TABLE 1 (Continued)

Stimulus*	Measures				Others
	Behavioral changes	Physiological and hormonal changes	Cognitive performance	Others	
	HR	Temperature changes	Hormonal changes (cortisol, corticosterone)	Changes in memory/Learning	Changes in pain sensitivity
Agonistic interactions of conspecifics	Chimpanzees (Kano et al., 2016) (<i>video, playback</i>)	Chimpanzees (Kano et al., 2016) (<i>video, playback</i>)	Chimpanzees (Kano et al., 2016) (<i>video, playback</i>)	Chimpanzees (Kano et al., 2016) (<i>video, playback</i>)	Rats (Patki et al., 2014)
	Rats (Carnevali et al., 2017; Finnell et al., 2017; Finnell 2018, Patki et al., 2014, 2015)	Rats (Carnevali et al., 2017; Finnell et al., 2017, 2018)	Rats (Kano et al., 2016) (<i>video, playback</i>)	Rats (Carnevali et al., 2017; Finnell et al., 2017, 2018, Patki et al., 2014, 2015)	
Aggressive vocalizations of conspecifics	Mice (Íñiguez et al., 2018; Li, Xu, & Wang, 2018; Miao et al., 2018; Warren et al., 2013, 2014)	Greylag geese (Wascher et al., 2010)	Mice (Íñiguez et al., 2018; Warren et al., 2013, 2014)	Mice (Íñiguez et al., 2018; Warren et al., 2013, 2014)	
	Tufted capuchin monkeys (Morimoto & Fujita, 2012)	Horses (Trösch et al., 2020)	Chimpanzees (Dezecache et al., 2017)	Pigs (Reimert et al., 2013, 2015)	Ravens (Adriaense et al., 2019)
Conspecific experiencing a negative event	Pigs (Reimert et al., 2013, 2015)	Horses (Trösch et al., 2020)			

(Continues)

TABLE 1 (Continued)

Stimulus*	Measures				Others		
	Physiological and hormonal changes		Cognitive performance				
	Behavioral changes	HR	Temperature changes	Hormonal changes (cortisol, corticosterone)	Changes in memory/Learning	Cognitive bias	Changes in pain sensitivity
Conspecific experiencing a positive event	Tufted capuchin monkeys (Morimoto & Fujita, 2012) Pigs (Reimert et al., 2013, 2015) Rats (Kashatelyan et al., 2014) Horses (Trösch et al., 2020)	Horses (Trösch et al., 2020)		Pigs (Reimert et al., 2013, 2015)		Ravens (Adriaense et al., 2019)	
Positive interactions of conspecifics	Barbary macaques (Berthier & Semple, 2018) Ravens (Osvath & Sima, 2014)		Chimpanzees (Parr & Hopkins, 2000) (video)				
Positive vocalizations of conspecifics	Horses (Briefer et al., 2017) Keas (Schwing et al., 2017)	Chimpanzees (Bertson et al., 1989) Horses (Briefer et al., 2017)	Chimpanzees (Dezecache et al., 2017) Horses (Briefer et al., 2017)			Rats (Saito et al., 2016)	

*Stimulus: *Stressed conspecific/human*: exposure to a human or a conspecific which is under stress; *Stressed conspecific (only auditory cues)*: exposure to the sounds emitted by a conspecific under stress; *conspecific experiencing negative stimulation*: exposure to a conspecific which, in that moment, is receiving painful stimulation (the aversive stimulus is present); *conspecific in pain*: exposure to a conspecific that has been subjected to a treatment inducing pain (e.g., injection of venom) (the aversive stimulus is not present); *fearful demonstrator*: exposure to a conspecific which is frightened due to a previous treatment; *agonistic interactions of conspecifics*: exposure to two or more conspecifics interacting in an agonistic manner (e.g., fights); *aggressive vocalizations of conspecifics*: exposure to aggressive vocalizations of conspecifics; *conspecific experiencing a negative event*: exposure to a conspecific being subjected to an unpleasant event, without causing harm or fear in the individual (e.g., frustration); *conspecific experiencing a positive event*: exposure to a conspecific enjoying a pleasant situation; *positive interactions of conspecifics*: exposure to two or more conspecifics interacting in a positive way (e.g., play); *positive vocalizations of conspecifics*: exposure to vocalizations emitted by conspecifics during positive situations (e.g., play).

advantages, the contagion of negative emotions such as fear could be widespread among animals and be displayed in several contexts; while the contagion of positive emotions could be restricted to a reduced number of social species. This is a question for further research.

3.3 | Assessment of contagion processes

even though evidence has been found suggesting possible cases of emotional state-matching in chimpanzees, elephants, birds, rodents or pigs (Burkett et al., 2016; Douglas-Hamilton et al., 2006; Langford et al., 2006; Parr & Hopkins, 2000; Perez et al., 2015; Reimert et al., 2013, 2017; Warren et al., 2013) the number of studies specifically assessing an emotional match between individuals is still small. Moreover, many of the reviewed studies did not register the responses of both individuals (observers and demonstrators) to assess the occurrence of an emotional convergence. Although emotional contagion is broadly defined as the emotional state-matching of an individual with another, even in humans it is not well established whether the emotional response triggered by the perception of another's emotional state is isomorphic or not to the perceived affective state (de Vignemont & Singer, 2006). The transmission of certain emotions might not imply a perfect emotional match. There may be differences in arousal or a mismatch between the behaviors or the physiological states of observers and demonstrators even if an emotional transfer has taken place. For example, in the case of distress contagion, likely, the observer's emotional response triggered by the perception of a conspecific in distress differ in magnitude from that of the demonstrator. Therefore, more research is needed to clarify this issue.

Furthermore, the evidence is not always powerful enough to rule out an alternative interpretation of individuals' emotional convergence in terms of distress, instead of contagion. Studies need to exclude the possibility that the emotional-state matching is due to the observer responding to environmental aversive cues rather than the demonstrator emotional state. Thus, the demonstrator's emotional cues must be the main source of emotion induction in the observer. A good way to do so is to control that the observer cannot perceive the stimulus which triggers demonstrator's emotional response, as proposed by Adriaense et al. (2020). In experimental paradigms, therefore, it is crucial the election of the appropriate emotional stimulus to induce contagion in the observer: 1) this stimulus must be the emotional state of the demonstrator and 2) this state should trigger a similar emotional state in the observer. Not all emotions may be equally effective in triggering the same emotional state in both individuals. For example, inducing frustration or anger in the demonstrator may induce different emotional states of the same negative valence in the observer. That is, demonstrator's frustration or aggressive displays could trigger distress or fear responses in the observer due to the probability of becoming the target of redirected aggression. Based on the results of the reviewed studies, emotions such as fear or positive emotions are good candidates to assess emotional contagion because they seem to induce similar emotional states in both individuals.

4 | CONCLUSION

The reviewed studies show that certain animals seem to be affected by the emotional displays of others, suggesting that the sharing of emotions could be widespread among social species capable of emotions. Emotional contagion seems to be related to the ecological circumstances and socio-behavioral traits of the species and thus present a great variability across the animal kingdom. Therefore, depending on the species, it could be triggered by a great variety of stimuli, modulated by different factors and be based on distinct mechanisms. This phenomenon thus could be far more complex and flexible than previously thought, and we should be cautious when generalizing about its functions and mechanisms between species. From this point of view, while it seems clear that emotional contagion involves some perception-action mediating systems (as suggested by Preston & de Waal, 2002), its workings look much more flexible and context-dependent than expected if it were an automatic response –what suggests an interaction of several components (as suggested by Yamamoto, 2017).

Overall, more research is needed to expand our understanding of the mechanisms and functions of emotional contagion and the extent to which this process is present in a wide variety of animal species. Simultaneously registering the different responses of observers and demonstrators would allow us to reliably establish the occurrence of an emotional state-matching between individuals. Furthermore, future studies should provide more evidence on the link between these processes, prosociality and complex empathic behaviors. The use of systematized paradigms including both behavioral and physiological measures and reliable controls to test different species are much needed in this endeavor.

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CONFLICT OF INTEREST

The authors have declared no conflicts of interest for this article.

AUTHOR CONTRIBUTIONS

Ana Pérez-Manrique: Data curation; methodology; writing-original draft; writing-review & editing. **Antoni Gomila:** Conceptualization; funding acquisition; methodology; supervision; writing-review & editing.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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