scientific reports

OPEN

Emotional contagion of fear and joy from humans to horses using a combination of facial and vocal cues

Plotine Jardat[1,2]✉, Shinya Yamamoto[3,4,5], Monamie Ringhofer[6], Noa Tanguy-Guillo[2], Céline Parias[2], Fabrice Reigner[7], Ludovic Calandreau[2] & Léa Lansade[2]

Emotional contagion, the emotional state-matching of two individuals, has been documented in various species. Recent findings suggest emotional contagion could also take place between humans and domestic mammals. However, the range of targeted animal species and human emotions that have been studied is still limited, and the methodology to investigate emotional contagion in this context is not fully established. This study examined emotional contagion of fear and joy from humans to horses by measuring physiological (heart rate, infrared thermography) and behavioral responses (posture, laterality bias, facial expressions) to videos of human fear, joy, or neutral emotions. Horses (n = 45) exhibited higher heart rates and ear movements during the fear and joy videos compared to the neutral ones, suggesting heightened arousal. During fear videos, they showed a greater increase in eye temperature than during joy or neutral videos, and maintained an alert posture for longer than during neutral videos, expressing specific facial expressions including inner brow raising and blowing. During joy videos, they showed a higher right eye preference (indicating a higher left-hemisphere bias) than during neutral videos, suggesting a more positive emotional valence. These findings suggest that human facial and vocal cues of fear and joy trigger emotional contagion in horses, which may influence the human-horse relationship.

Keywords *Equus caballus*, Human-animal relationship, Animal cognition, Animal behavior

Emotions are internal states that enable individuals to adapt to situations through physiological and behavioral responses[1]. For social species, emotions can also have a social role, especially through emotional contagion, defined as the emotional state-matching of an individual with another[2]. Emotional contagion can help coordinate group behaviors or promote social bonds[2] and has been documented across various species. For example, in humans, exposure to odors collected from individuals in fearful or joyful contexts elicited corresponding facial expressions of fear or joy in the recipient[3,4]. Similarly, pigs demonstrated emotional state-matching behaviors, playing more frequently—a marker of positive emotion—in response to conspecifics anticipating a positive experience, and holding their tails low—a marker of negative emotion—when conspecifics anticipated a negative experience[5]. Horses also displayed emotion-specific reactions, showing contact-seeking behaviors in response to videos of conspecifics expressing positive emotions and adopting a high-neck posture with ears positioned forward when observing negative expressions[6]. Likewise, dogs exhibited more negative responses (e.g., panting or stretching) to conspecific vocalizations associated with distress (whines) compared to those associated with positive states (play barks)[7].

Emotional contagion could also occur between individuals of different species, although it has been less documented as an interspecific phenomenon. Interspecific emotional contagion may provide advantages, especially between domestic animals and humans, who live in close proximity. For example, it could help animals respond to dangers identified by humans or locate resources linked to positive human emotions. Domestic mammals have been found to perceive and react to human emotions, with results suggesting they could also be affected by human emotions through emotional contagion[8]. For example, cats expressed more

[1]Institut Français du Cheval et de l’Equitation, Pôle développement, innovation et recherche, Nouzilly, France. [2]INRAE, CNRS, Université de Tours, PRC, 37380 Nouzilly, France. [3]Institute for Advanced Study, Kyoto University, Kyoto, Japan. [4]Wildlife Research Center, Kyoto University, Kyoto, Japan. [5]Institute for the Future of Human Society, Kyoto University, Kyoto, Japan. [6]Department of Animal Science, Teikyo University of Science, Tokyo, Japan. [7]UEPAO, INRAE, 37380 Nouzilly, France. ✉email: plotine.jardat@ifce.fr

positive behaviors when their owners expressed joy rather than anger[9]. Horses' heart rate increased[10] and dogs licked their mouth more[11] when presented with angry human faces, indicating higher levels of stress. Goats and horses were more attracted to joyful expressions than angry or sad ones[12,13], which could be linked to the former prompting a more positive emotional state in them than the latter[13]. Emotional contagion could also explain horses' greater performance at discriminating human facial expressions of joy from other emotions, compared to discriminating sadness from other emotions[14]. Finally, horses' stronger attention toward humans speaking in pet-directed speech compared to adult-directed speech could also stem from a transmission of the positive emotional content of pet-directed speech[15].

However, the range of human emotions that have been studied in the context of human-animal interactions is still limited, with most studies focusing on joy and anger[8]. In dogs, a few studies explored reactivity to other human emotions, revealing asymmetrical brain processes in response to human anger, fear, happiness, sadness or surprise[16,17]. A few studies on horses indicate they could detect other human emotions: horses reacted differently to human facial expressions of disgust compared to joy[18], and differentiated human facial expressions of joy or sadness from anger, disgust, surprise or fear on pictures[14]. Horses also showed a preference for videos of joyful facial expressions compared to sad ones, with evidence of cross-modal recognition of these two expressions[13]. Recent studies on olfactory signals also showed horses can discriminate human odors produced in contexts of fear or joy[19,20].

In this study, we explored the phenomenon of interspecific emotional contagion between humans and domestic mammals. We focused on horses, a species with a long history of domestication, and for which sensitivity to human emotions has been demonstrated in previous research. This study specifically examined the emotions of fear and joy displayed by humans. Fear, triggered by the perception of (potential) danger, is a likely universal emotion that prompts a fight-or-flight response[21], and it seems adaptive to react to others' perception of threats[2], especially for prey species like horses. Intraspecific contagion of fear has been studied extensively and across various species from rodents[22] to fish[23]. Moreover, fear has been identified throughout literature as a good candidate to assess emotional contagion, as have positive emotions[2]. Here, we also studied a positive emotion, joy. Reacting to signals of human joy could also be adaptive for horses, as communication of positive emotions can provide social cohesion and promote social bonds, which are important for social species[2]. Previous studies have shown that human emotional odors can influence horses' physiology and behavior (Jardat et al. 2024—submitted), which could be attributed to shared olfactory pathways among mammals[24]. In contrast, emotional contagion from auditory and visual stimuli could involve more complex cognitive processes, and deserve dedicated investigation.

Using video projections to provide standardized stimuli, the aim of this study was to examine emotional contagion of fear and joy from humans to horses, recording their behavioral and physiological responses to videos of a human actor displaying fear, joy, or a neutral emotion. Previous studies have shown that horses react to images or videos of humans (e.g.,[15,25]) and perceive them as representing actual humans[6,26]. Thus, when watching videos of human emotions, if interspecies emotional contagion takes place between horses and humans, we could predict that horses' emotional valence and arousal would vary according to the emotional valence and arousal of the stimuli[27]. I.e., horses' emotional state would be characterized by higher arousal when the video was of fear or joy compared to the neutral emotion (measured by heart rate and facial expressions), and by a more positive valence when the video was of joy and a more negative valence when the video was of fear, compared to the neutral emotion (measured by variation in eye temperature, brain hemisphere bias and facial expressions).

Materials and methods

Ethics statement

All methods were carried out in accordance with the relevant guidelines and regulations, in accordance with the declaration of Helsinki, and informed consent was obtained for human participation from all subjects and/or their legal guardian(s). This study was subject to ethical auto-evaluation following the guidelines of the INRAe Ethics of Projects Committee, and all experimental protocols were approved by the Val de Loire Ethical Committee (CEEA VdL, Nouzilly, France, authorization number CE19-2022-1511-2).

This study was reported in accordance with ARRIVE guidelines. Animal care and experimental treatments complied with the French and European guidelines for the housing and care of animals used for scientific purposes (European Union Directive 2010/63/EU) and were performed under authorization and supervision of official veterinary services (agreement number F371752 delivered to the UEPAO animal facility by the veterinary service of the Département d'Indre et Loire, France). The horses lived in groups, were not food deprived during the experiment and did not undergo any invasive procedures.

Animals

The study involved 48 Welsh mares (Equus caballus) aged 8.2 ± 2.9 years (mean ± s.d.) reared and living at the Animal Physiology Experimental Unit PAO (UEPAO, 37,380 Nouzilly, France), INRAE. These mares lived in groups in indoor stalls bedded with straw, with environmental enrichments and access to an outdoor area 12 h a day. Fodder and water were available ad libitum. These horses are used only for research purposes and are handled daily by humans.

Stimuli

Four actors (two males and two females) from local theatre groups were filmed saying a text with three different expressions: joyful, neutral, or fearful. The text was a French sequence that meant "Oh, but how come, that is not possible, I have never seen that before. Oh wow, but no, it's impossible! Wait, are you really sure? No, I can't believe it, it's not possible". This text was chosen because it could plausibly express positive or negative emotions and conveyed a high intensity of emotion. The emotions expressed in the videos corresponded to the Facial Action Coding System[28] and were appraised by 17 people who did not take part in the experiment, confirming the expressed emotions were, respectively, joy, neutral and fear (see Supplementary Information—Figure S1). Sound level was measured with a sonometer and sound intensity was adjusted to ensure equivalent levels across all stimuli (60–70 dB from the location of the horse's head).

The stimuli shown to the horses consisted of 2 min-long videos composed of three 37 s-long sections showing a same actor, separated by 5 s of black screen (Fig. 1). A section consisted in three repetitions of the actor saying the text in one of the emotions. For each of the four actors, six different orders of presentation of the emotions were therefore possible. Horses were randomly assigned an actor and order of presentation. They had never seen or heard the faces and voices of these actors before the experiment.

Experimental set-up

The testing area consisted in a large stall (3.5 × 4.5 m). The horse was attached in the middle of the stall by two lose ropes, facing a projection screen on which the videos were projected such that the projected faces were approximately twice the size of a real person's face (Fig. 2)[13,25]. The sound was broadcast by a speaker placed just behind the screen at the top of it (the sound level was around 70 dB from where the head of the horse was located). For safety reasons, an assistant stayed with the horse (to ensure that it did not panic or get entangled in the ropes) but never interacted with the horse during the tests, remaining still and looking neither at the screen nor the horse, with the head down. Whether the assistant was standing on the left or the right of the horse was counterbalanced between horses. The experiment was filmed by two 4 K optic cameras placed in front of the horse on each side of the screen (Fig. 2). A thermal camera (FLIR T540) was placed in front of the horse on her left side, at the height of the horse's head, to record eye temperatures. The horses were equipped with a heart monitor system (Polar Equine RS800CX Science, Polar Oy, Finland).

Procedure

Habituation

The horse was taken from her stall and led to the testing area. Scenes of nature accompanied by bird songs were projected for at least 2 min, while the assistant monitored the horse's heart rate on the Polar watch. Once the horse had been calm (not neighing, pulling on the ropes with her head, nor trying to turn around or leave) and her heart rate had remained below 80 bpm for 30 s[13], the test phase began immediately. If this criterion was not met after ten minutes, the session ended, and a new session was scheduled for the following day. If this criterion was still not met after ten minutes in the second habituation session, the experiment was considered too stressful for the horse and she was excluded from the experiment. One horse was excluded from the experiment after two unsuccessful habituation sessions, all other horses went on to the test phase after the first habituation session.

Test

Immediately after the horse met the habituation criterion, videos of an actor saying a text with different emotions (see Stimuli) were projected on the screen for two minutes. For two horses, the test had to be interrupted due to lack of cooperation (pulling on the ropes, turning toward the door and trying to leave), and they were excluded from the experiment.

Behavioral and physiological analysis

Behavior

The 45 horses who participated in the test were included in these analyses. Videos of the tests were analyzed using BORIS[29] without sound. The coder could not see the projection screen in the videos or hear the voices, she was therefore blind to the condition. The time the horse spent looking at the screen with her right or left eye was measured. She was considered to be looking with her right eye, i.e., to have the image mainly in her right visual field, when her right eye could be seen from the left camera (her head turned toward her left). Similarly, she was considered to be looking with her left eye, i.e., to have the image mainly in her left visual field, when her left eye could be seen from the right camera (her head turned toward her right)[13,25]. Given the large monocular visual field of horses, and since horses never turned their head completely toward the back (opposed to the screen),

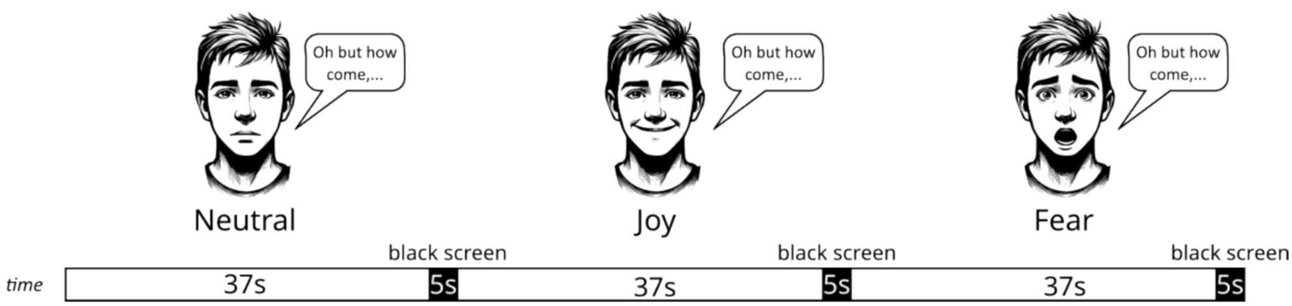

Fig. 1. Temporal sequence of stimuli. The order of the three emotions (neutral, joy and fear) was counterbalanced between horses. For a given horse, the three sections showed one same actor out of four possible actors (two males and two females).

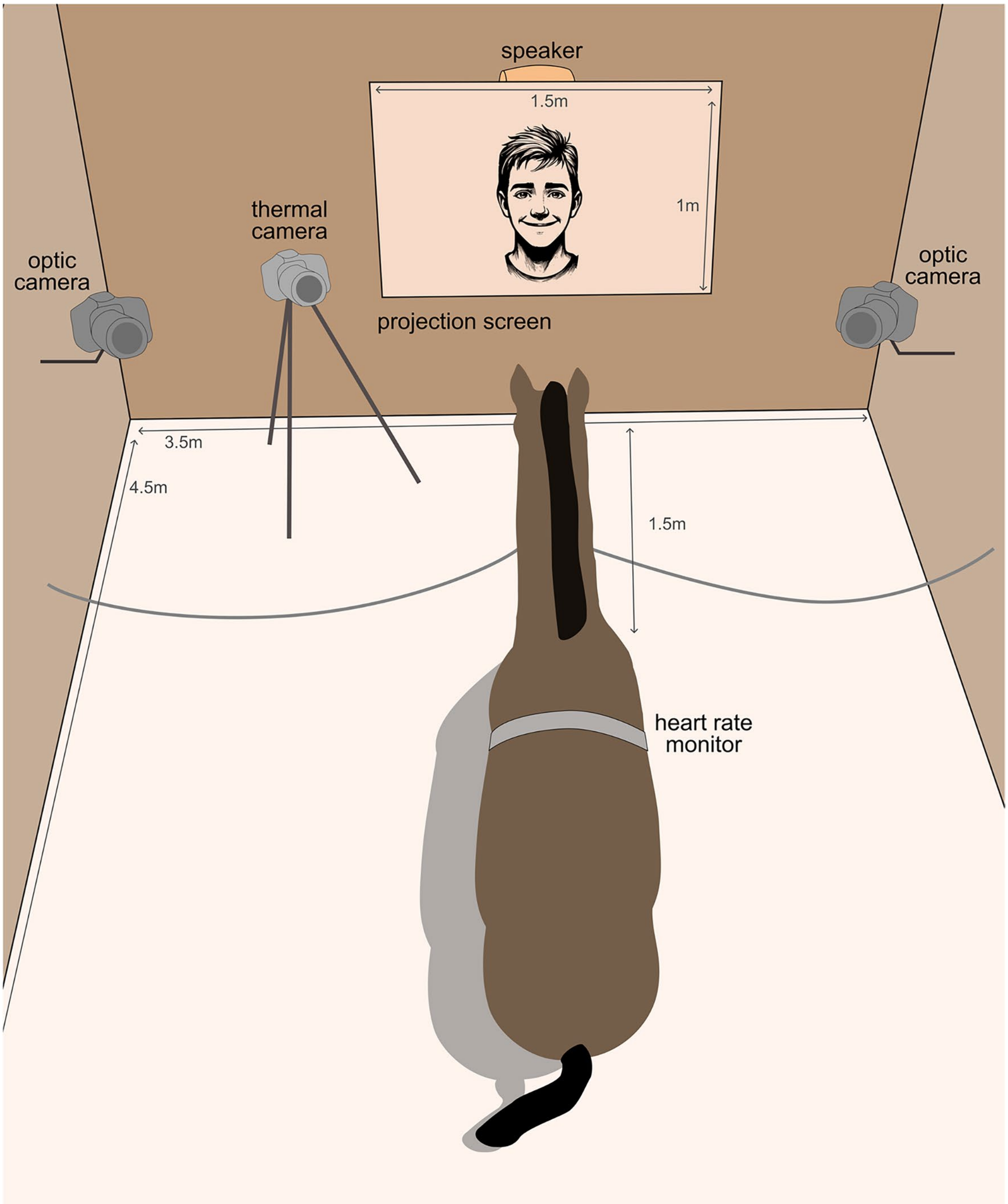

Fig. 2. Experimental setup.

the image was always in their visual field. For each section, we calculated a laterality index (I) to determine the propensity to use one eye more than the other (i.e., the propensity for the image to be in one of the visual hemifields rather than the other), it was defined as $I = R/(R + L)$, with R the time spent looking with the right eye and L the time spent looking with the left eye. Thus, it was equal to 0 if the horse only used her left eye to watch the section, 1 if she only used her right eye, and 0.5 if she used both her eyes equally. The time the horse spent in an alert position was also measured. It was defined as looking at the screen with both eyes (head facing the screen), with both ears forward and the neck held high. A second coder, also blind to the condition, reanalyzed 20% of the videos to assess the interobserver reliability of these two behaviors. Interclass Correlation Coefficients (ICC) were calculated, showing good to excellent reliabilities (ICC estimate and 95% interval: laterality index 0.93[0.85, 0.97], time spent in alert position 0.91[0.80, 0.97]).

Facial expressions were analyzed thanks to the Equine Facial Action Coding System (EquiFACS[30]). A certified coder, blind to the condition, noted the occurrences of all action units (AUs) and action descriptors (ADs). The AUs and ADs that represented more than 1% of the total occurrences of AUs and ADs were retained for the statistical analysis. They were AD1 (eye white increase), AD133 (blow), AD38 (nostril dilation), AU101 (inner brow raiser), AU145 (blink), AU26 (jaw drop), AU47 (half blink), EAD101 (ear forward) and EAD104 (ear rotator). Correlations between AUs were checked, revealing a strong correlation between EAD101 and EAD104. Therefore, only the number of occurrences of EAD101, representing the number of ear movements, was retained for the analysis.

Heart rate
Data for one horse were incomplete due to malfunction of the heart rate monitor. Thus, the 45 horses who participated in the test were included in this analysis, with data concerning the 3 conditions for 44 horses and data concerning one condition for one horse. RR data were extracted from the Polar recordings. A visual correction was applied to eliminate artifactual beats, as recommended in[31]. The mean and maximum heart rate were calculated for each stimuli section, the analyzer was blind to the condition.

Eye temperature
Due to technical difficulties with the thermal camera, thermal imaging was not saved for 7 horses. Thus, this analysis included 38 of the 45 horses who participated in the test. Thermal videos were analyzed using the FLIR Tools software, the analyzer was blind to the condition. Eye temperatures were measured before a stimulus section began (t = 0 s) and three times during each 37 s-long section (at t = 10 s, t = 20 s and t = 30 s). For each measurement, the maximum temperature in the area of the left eye was recorded thanks to the "Box" measuring tool (Fig. 3)[32,33]. Then, the corresponding variation in eye temperature was calculated by subtracting the temperature measured at the beginning of the section (t = 0 s) from the temperature measured at this time point (t = 10 s, t = 20 s or t = 30 s), to produce 3 data points of temperature variation per horse and per condition, corresponding to three time points in each video. For 20 out of the 342 time points of interest, the eye of the horse was not visible in the camera frame, resulting in some missing data (this concerned 11 horses, all 38 horses included in this analysis had at least one data point). Thus, this analysis produced 322 data points of temperature variation, concerning 38 horses.

Statistical analysis All statistical analysis were performed using R 4.3.1[34]. The significance threshold was set at $\alpha \leq 0.05$.

The design was a controlled experiment with repeated measures on individual horses (experimental units). We tested the influence of one fixed effect, the emotion, on several behavioral and physiological variables. Random factors were included: horse identity, identity of the actor in the stimulus, and order of presentation of the stimuli.

To test whether horses reacted differently to the emotions, we explored each variable with generalized linear mixed models (GLMM), using linear, Poisson, and generalized Poisson distributions as appropriate for the given variable (see Table 1). For each variable, a model was constructed to assess the effect of the emotion (joy, neutral or

Fig. 3. Example of eye temperature measurement. Maximum temperature in the area of the left eye was measured thanks to the "Box" measuring tool of the FLIR Tools software. Red triangle: pixel corresponding to the maximum temperature within the manually defined rectangle.

Type of variable	Response variable	Model family	Chi-square test		Df	Post-hoc tests		
General behavior	Looking laterality index	Gaussian (link = 'logit')	$\chi^2 = 7.11$	$p = 0.029$*	2	Joy-Neutral	t = 2.60	$p = 0.028$*
						Joy-Fear	t = 1.88	$p = 0.15$
						Neutral-Fear	t = − 1.01	$p = 0.57$
	Time spent in alert posture	Poisson	$\chi^2 = 11.24$	$p = 0.0036$**	2	Joy-Neutral	Z = 1.29	$p = 0.40$
						Joy-Fear	Z = − 2.03	$p = 0.10$
						Neutral-Fear	Z = − 3.29	$p = 0.0029$**
FACS	Eye white increase (AD1)	Poisson	$\chi^2 = 6.15$	$p = 0.046$*	2	Joy-Neutral	Z = 2.47	$p = 0.037$*
						Joy-Fear	Z = 0.93	$p = 0.62$
						Neutral-Fear	Z = − 1.54	$p = 0.27$
	Blow (AD133)	Poisson	$\chi^2 = 13.34$	$p = 0.0013$**	2	Joy-Neutral	Z = 1.775	$p = 0.18$
						Joy-Fear	Z = − 1.753	$p = 0.1856$
						Neutral-Fear	Z = − 3.643	$p < 0.001$***
	Inner brow raiser (AU101)	Poisson	$\chi^2 = 8.11$	$p = 0.017$*	2	Joy-Neutral	Z = 1.61	$p = 0.24$
						Joy-Fear	Z = − 1.24	$p = 0.43$
						Neutral-Fear	Z = − 2.85	$p = 0.012$*
	Ear movements	Gaussian	$\chi^2 = 20.86$	$p < 0.001$***	2	Joy-Neutral	t = 4.09	$p < 0.001$***
						Joy-Fear	t = 2.05	$p = 0.10$
						Neutral-Fear	t = − 2.51	$p = 0.035$*
Physiological variables	Mean heart rate	Poisson	$\chi^2 = 28.12$	$p < 0.001$***	2	Joy-Neutral	Z = 3.89	$p < 0.001$***
						Joy-Fear	Z = − 1.24	$p = 0.43$
						Neutral-Fear	Z = − 5.12	$p < 0.001$***
	Maximum heart rate	Poisson	$\chi^2 = 35.25$	$p < 0.001$***	2	Joy-Neutral	Z = 4.53	$p < 0.001$***
						Joy-Fear	Z = − 1.15	$p = 0.49$
						Neutral-Fear	Z = − 5.66	$p < 0.001$***
	Variation in eye temperature	Gaussian	$\chi^2 = 7.38$	$p = 0.025$*	2	Joy-Neutral	t = − 0.62	$p = 0.81$
						Joy-Fear	t = − 2.60	$p = 0.026$*
						Neutral-Fear	t = − 1.96	$p = 0.12$

Table 1. Statistical differences in variables according to the emotion for models that were significantly different from the null model. (°$p \leq .1$, *$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$, n = 45).

fear—fixed effect) on the behavioral or physiological parameter, and compared to the null model via likelihood-ratio (chi-square) test (Table S1). Horse identity and actor identity were added as random factors to account for individual variations. The number of the video Section (1, 2 or 3) was also added as a random factor to account for potential variations in horse behavior and physiology according to the order of presentation of the emotions. The general formula of the models was y ~ emotion + (1|horse_identity) + (1|actor_identity) + (1|video_section). For the variation in eye temperature, time was added in interaction with the emotion to assess the evolution of eye temperature along a video section. The model formula was temperature_variation ~ emotion:time + (1|horse_identity) + (1|actor_identity) + (1|video_section). This model was compared to a simpler model with only the emotion and to the null model in order to select the best version (Table S2).

Distributions, within-group variance and homoscedasticity of the residuals were checked for each model. A likelihood-ratio (chi-square) test was performed on models that explained data variability significantly better than the null model, to assess the influence of the emotion on the response variable. Post hoc tests based on Tukey's method were performed when necessary.

The functions used in R for these analyses were the following : *glmmTMB()* from the package *glmmTMB*[35] to create the GLMMs, *DHARMa*[36] package for residuals checking, *Anova()* from the package *car*[37] for chi-square tests, *emmeans()* from the package *emmeans*[38] for post-hoc tests. Figures were generated using the package *ggplot2*[39].

Results

Descriptive statistics and effect sizes for all variables are provided in Table S3.

Behavior

The looking laterality index, the time spent in alert posture, and the number of occurrences of FACS units AD1, AD133, AU101 and of ear movements varied significantly according to the emotion (Table 1). Post-hoc tests revealed that horses looked significantly more at the videos with their right eye when the video was of joy compared to when it was neutral, and they spent significantly more time in an alert posture when the video was of fear compared to when it was neutral (Fig. 4, Table 1). Concerning FACS, there were significantly more occurrences of eye white increase (AD1) and of ear movements when the video was of joy compared to when it was neutral, and significantly more occurrences of blowing (AD133), of inner brow raise (AU101) and of ear movements when the video was of fear compared to when it was neutral (Fig. 5, Table 1). The number of

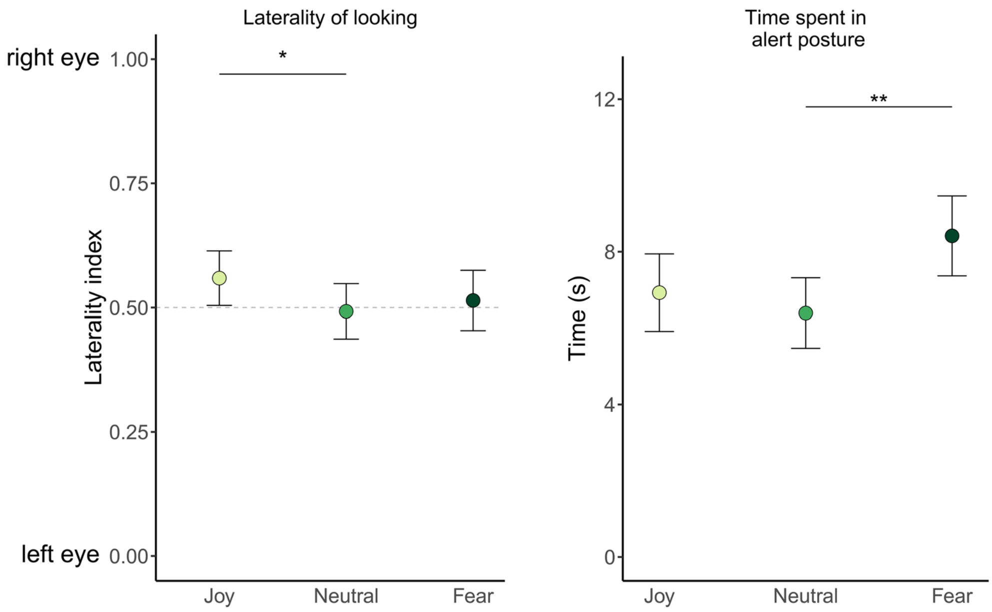

Fig. 4. Differences in horses' general behavior according to the emotion in the video. Means and standard errors. *$p \leq 0.05$, ** ≤ 0.01, n = 45.

occurrences of nostril dilations (AD38) and of half blinks (AU47) did not significantly vary according to the emotion (Table S1).

Physiology
The mean heart rate, maximum heart rate and variation in eye temperature varied significantly according to the emotion (Table 1 and Table S2). Post-hoc tests revealed that the mean heart rate and maximum heart rate were significantly higher when the video was of joy or fear compared to when it was neutral, and that the variation in eye temperature was significantly higher when the video was of fear than of joy (Fig. 6, Table 1).

Discussion
In this study, we examined the presence of emotional contagion of fear and joy from humans to horses based on auditory and visual cues, by measuring horses' physiological and behavioral reactions to videos of humans expressing fear, joy or a neutral expression. According to our hypothesis, we observed higher levels of arousal in horses when the video was of fear or joy compared to when it was neutral, and we also observed reactions specific to the joy video or to the fear video, which indicated a correspondence in emotional valence. Concerning arousal, horses' heart rates were higher and attained higher maxima when the video was of joy or fear (higher emotional arousal) than when it was neutral (lower emotional arousal), showing a correspondence in arousal between emitter and receiver, i.e., emotional contagion of arousal[27]. Concerning valence, horses spent more time in an alert posture when the video was of fear than when it was neutral, indicating a fear response[40,41] to videos of human fear. Similarly, we observed an increase in eye temperature in horses when they watched the fear videos, higher than their variation in eye temperature when they watched the joy or neutral videos. Increase in eye temperature has been validated in horses as an indicator of negative emotional valence[42–45] and more specifically as a physiological reaction of fear[33], supporting the idea of a fear response in horses watching videos of human fear in this study. In contrast, horses seemed to perceive videos of human joy as more positive than the neutral ones, as indicated by the difference in laterality bias. Indeed, bias for the right eye was higher in the joy than in the neutral condition, indicating that horses used their right eye more to watch the videos of joy than the neutral videos, relatively to their use of their left eye. As projections of optic nerves in the brain are mostly contralateral in mammals[46], this shows a higher prevalence of the left brain hemisphere to process human expressions of joy in horses compared to neutral expressions. In accordance with previous observations of laterality biases in domestic mammals[47], this indicates horses perceived videos of human joy more positively compared to neutral videos.

In this study we also observed differences in horses' facial expressions according to the emotions in the stimuli. During the fear videos, facial expressions included more occurrences of blowing (AD133) and raising the inner brow (AU101), and tended to include more ear movements (EAD101 and EAD104, which were correlated) than during the neutral videos. The AD133 EquiFACS code (blow) has not been previously identified in a specific context (google scholar search : "equifacs" + "AD133"), but blowing is often associated in horses with negative-valence situations such as encountering a fear-inducing object[48]. Similarly, raising the inner brow (AU101) has been associated with negative-valence situations like social isolation[49] or pain[50]. Thus, this facial expression is consistent with negative emotional valence. During the joy videos, facial expressions included more occurrences of eye white increase (AD1) and more ear movements than during the neutral videos. Although the observation

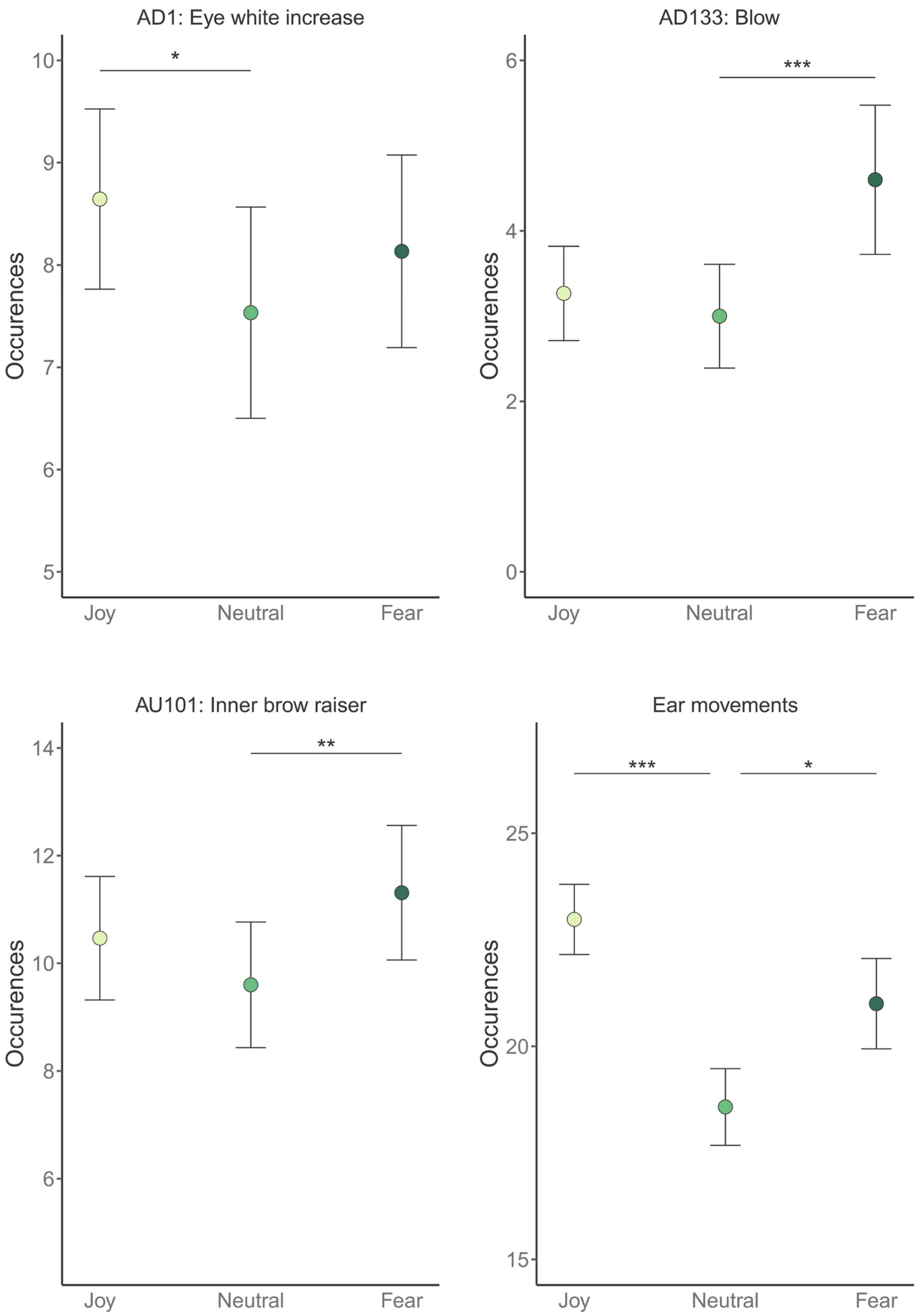

Fig. 5. Differences in horses' facial expressions according to the emotion in the video. Facial expressions were analysed thanks to the Equine Facial Action Coding System (EquiFACS) by a certified coder. Means and standard errors. °$p \leq 0.1$, *$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$, n = 45.

of eye white in horses has been observed in mildly stressful situations[41,51], AD1 as described by the EquiFACS method[30] corresponds to an increase in eye white, which could correspond to different emotional situations. AD1 (eye white increase) has been observed both in positive (positive reinforcement[52]) and negative situations (frustration[49,53]) and its signification may depend on its combination with other facial movements, but further research on this facial action is needed for better interpretation. Finally, the increase in ear movements, observed both during fear and joy videos, is compatible with a higher arousal in horses during these videos compared to neutral videos. The somewhat lower level of ear movements observed during fear videos compared to joy videos could be related to fear inducing a more frozen attitude, with the ears more often pointed forward rather than moving, in connection with the higher level of alert postures observed in the fear condition. To summarize,

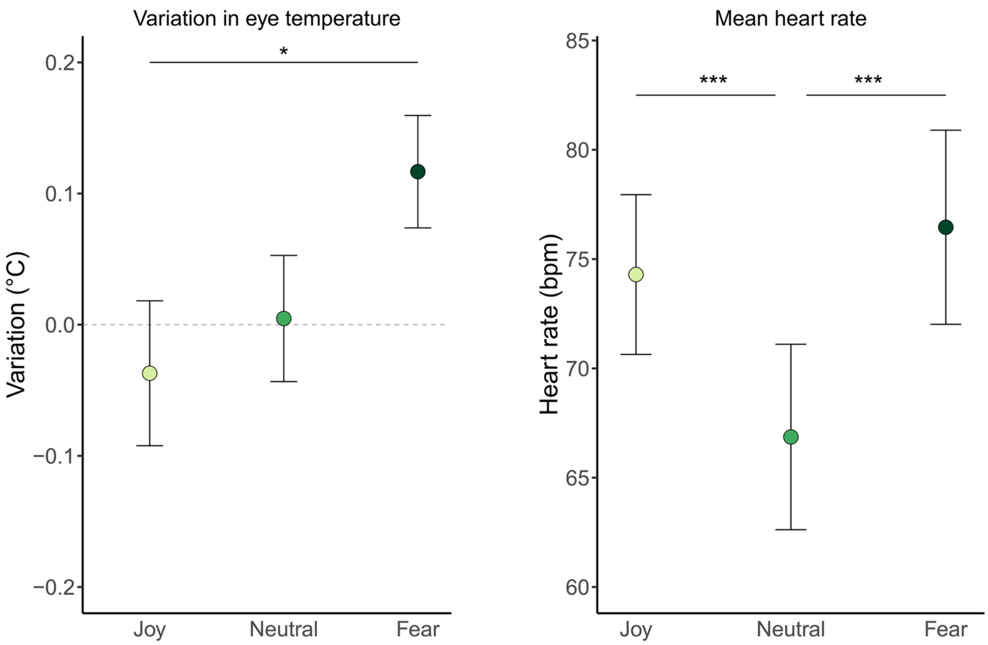

Fig. 6. Variation in horses' physiological parameters according to the emotion in the video. Means and standard errors. °$p \leq 0.1$, *$p \leq 0.05$, ***$p \leq 0.001$. Variation in eye temperature: n = 38, mean heart rate: n = 45.

in this experiment we observed facial expressions in horses suggesting higher arousal when watching human videos of fear or joy compared to neutral videos, and suggesting a more negative valence during the fear videos.

Overall, in this study we observed indications of emotional contagion of fear and joy from humans to horses through visual and vocal signals. These results are in accordance with previous studies on horses' perception of human emotions, which suggested a possible emotional contagion from humans to horses from visual and vocal cues of anger or joy[13,15,54]. It has also been shown that horses can react to human voices according to the valence of past interactions associated with this voice[55]. In the present study, horses saw videos of people that they had never heard or seen prior to the experiment, ensuring that the observed reactions could not have been influenced by any prior associations with these people. Thus, this study further extends the range of human emotions known to provoke physiological and behavioral reactions in horses to fear. In addition, here we observed that horses' reaction to human fear was not only congruent in arousal and valence, but seemed to correspond to a fear response in horses too (alert posture and cardio-vascular adaptations). Emotional contagion is one of the fundamental factors of empathy[27], and these results therefore suggest that a form of empathy may take place between humans and horses, and more broadly between individuals of different species. Such emotional communication between humans and domestic mammals could be linked to domestication, either as a consequence of artificial selection or as a factor in the election of species that underwent domestication[8,56]. Previous studies have highlighted that the way horses behave during interactions with humans can depend on their living conditions, on their age or on their relationship with humans[57,58]. These factors could also influence the process of emotional contagion between humans and horses and would be interesting to explore in future studies on this process.

The transmission of emotions between individuals of different species could result from an unconditioned response to specific features of vocalizations and facial expressions, or it may stem from a learned response[59]. Certain acoustic characteristics have been shown to activate the autonomic nervous system in conspecifics without previous exposure[59], suggesting that a similar unconditioned mechanism could contribute to emotional contagion between humans and horses through vocal signals. However, given the differences in facial structure between primates and domestic mammals, a learning process might better explain the responses to facial expressions observed in this experiment. Despite these differences, some facial actions, such as the inner brow raiser (AU101), are shared by humans and horses and have been linked to negative emotional states in both species[28,49,50]. Therefore, both hypotheses—unconditioned and learned responses—remain equally plausible with regard to our results. Further studies on emotional contagion between different species, particularly focusing on young individuals, could help clarify the developmental dynamics of this phenomenon.

Last, in this study we used concurrent visual and vocal signals, to ensure the stimuli were relevant to horses and to maximize the opportunity to observe emotional contagion. The relative importance of each sensory modality in this phenomenon could be better understood through studies using pictures alone or vocal playback alone, such as those previously conducted for joy and anger[10,60]. Cross-modal experiments could also help to determine whether horses associate human facial and vocal expressions of fear and joy, as they do for anger and joy or sadness and joy[13,54]. This could also inform whether the phenomenon of interspecific emotional contagion has to do with an automatic response or if a cognitive integration and recognition of emotional signals may also be involved.

Conclusion

In this study, we observed evidence of interspecific emotional contagion of fear and joy from humans to horses based on visual and vocal signals. Horses showed fear reactions with a heightened arousal and negative-valence emotional state in response to videos of human fear, and heightened arousal and positive-valence emotional state in response to videos of human joy, compared to neutral videos of humans. This suggests the possibility of a form of empathy between domestic mammals and humans.

Data availability

The datasets generated and analyzed during the current study are available in the Data INRAE repository : https://doi.org/https://doi.org/10.57745/Y50IJK.

Received: 8 January 2025; Accepted: 15 April 2025
Published online: 21 May 2025

References

1. Panksepp, J. Affective Neuroscience: The Foundations of Human and Animal Emotions. Affective neuroscience: The foundations of human and animal emotions. (Oxford University Press, New York, NY, US, (1998).
2. Pérez-Manrique, A. & Gomila, A. Emotional contagion in nonhuman animals: A review. *Wiley Interdiscip. Rev. Cogn. Sci.* **13**, e1560 (2022).
3. de Groot, J. H. B., Smeets, M. A. M., Kaldewaij, A., Duijndam, M. J. A. & Semin, G. R. Chemosignals communicate human emotions. *Psychol. Sci.* **23**, 1417–1424 (2012).
4. de Groot, J. H. B. et al. A sniff of happiness. *Psychol. Sci.* **26**, 684–700 (2015).
5. Reimert, I., Bolhuis, J. E., Kemp, B. & Rodenburg, T. B. Indicators of positive and negative emotions and emotional contagion in pigs. *Physiol. Behav.* **109**, 42–50 (2013).
6. Trösch, M. et al. Horses feel emotions when they watch positive and negative horse–human interactions in a video and transpose what they saw to real life. *Anim. Cogn.* **23**, 643–653 (2020).
7. Huber, A., Barber, A. L. A., Faragó, T., Müller, C. A. & Huber, L. Investigating emotional contagion in dogs (Canis familiaris) to emotional sounds of humans and conspecifics. *Anim. Cogn.* **20**, 703–715 (2017).
8. Jardat, P. & Lansade, L. Cognition and the human–animal relationship: a review of the sociocognitive skills of domestic mammals toward humans. *Anim. Cogn.* **25**, 369–384 (2022).
9. Galvan, M. & Vonk, J. Man's other best friend: domestic cats (F. silvestris catus) and their discrimination of human emotion cues. *Anim. Cogn.* **19**, 193–205 (2016).
10. Smith, A. V., Proops, L., Grounds, K., Wathan, J. & McComb, K. Functionally relevant responses to human facial expressions of emotion in the domestic horse (Equus caballus). *Biol. Lett.* **12**, 20150907 (2016).
11. Albuquerque, N., Guo, K., Wilkinson, A., Resende, B. & Mills, D. S. Mouth-licking by dogs as a response to emotional stimuli. *Behav. Process.* **146**, 42–45 (2018).
12. Nawroth, C., Albuquerque, N., Savalli, C., Single, M. S. & McElligott, A. G. Goats prefer positive human emotional facial expressions. *R Soc. Open Sci.* **5**, 180491 (2018).
13. Jardat, P. et al. Horses discriminate between human facial and vocal expressions of sadness and joy. *Anim. Cogn.* **26**, 1733–1742 (2023).
14. Jardat, P. et al. Horses can learn to identify joy and sadness against other basic emotions from human facial expressions. *Behav. Process.* **220**, 105081 (2024).
15. Jardat, P. et al. Pet-directed speech improves horses' attention toward humans. *Sci. Rep.* **12**, 4297 (2022).
16. Siniscalchi, M., D'Ingeo, S., Fornelli, S. & Quaranta, A. Lateralized behavior and cardiac activity of dogs in response to human emotional vocalizations. *Sci. Rep.* **8**, 77 (2018).
17. Siniscalchi, M., D'Ingeo, S. & Quaranta, A. Orienting asymmetries and physiological reactivity in dogs' response to human emotional faces. *Learn. Behav.* **46**, 574–585 (2018).
18. Baba, C., Kawai, M. & Takimoto-Inose, A. Are horses (Equus caballus) sensitive to human emotional cues?. *Animals* **9**, 630 (2019).
19. Jardat, P. et al. Horses discriminate human body odors between fear and joy contexts in a habituation-discrimination protocol. *Sci. Rep.* **13**, 3285 (2023).
20. Sabiniewicz, A., Tarnowska, K., Świątek, R., Sorokowski, P. & Laska, M. Olfactory-based interspecific recognition of human emotions: Horses (Equus ferus caballus) can recognize fear and happiness body odour from humans (Homo sapiens). *Appl. Anim. Behav. Sci.* **230**, 105072 (2020).
21. Boissy, A. Fear and fearfulness in animals. *Q. Rev. Biol.* **70**, 165–191 (1995).
22. Kim, A., Keum, S. & Shin, H.-S. Observational fear behavior in rodents as a model for empathy. *Genes Brain Behav.* **18**, e12521 (2019).
23. Fernandes Silva, P., Garcia de Leaniz, C. & Luchiari, A. C. Fear contagion in zebrafish: a behaviour affected by familiarity. Anim. Behav. **153**, 95–103 (2019).
24. Semin, G. R., Scandurra, A., Baragli, P., Lanatà, A. & D'Aniello, B. Inter- and intra-species communication of emotion: Chemosignals as the neglected medium. *Animals* **9**, 887 (2019).
25. Jardat, P. et al. Horses form cross-modal representations of adults and children. *Anim. Cogn.* **26**, 369–377 (2023).
26. Lansade, L. et al. Female horses spontaneously identify a photograph of their keeper, last seen six months previously. *Sci. Rep.* **10**, 6302 (2020).
27. Adriaense, J. E. C., Koski, S. E., Huber, L. & Lamm, C. Challenges in the comparative study of empathy and related phenomena in animals. *Neurosci. Biobehav. Rev.* **112**, 62–82 (2020).
28. Ekman, P. & Friesen, W. Facial Action Coding System: Manual. (Consulting Psychologists Press (1978).
29. Friard, O. & Gamba, M. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol. Evol.* **7**, 1325–1330 (2016).
30. Wathan, J., Burrows, A. M., Waller, B. M. & McComb, K. EquiFACS: The equine facial action coding system. *PLoS ONE* **10**, e0131738 (2015).
31. von Borell, E. et al. Heart rate variability as a measure of autonomic regulation of cardiac activity for assessing stress and welfare in farm animals—A review. *Physiol. Behav.* **92**, 293–316 (2007).
32. Hall, C., Burton, K., Maycock, E. & Wragg, E. A preliminary study into the use of infrared thermography as a means of assessing the horse's response to different training methods. *J. Vet. Behav.* **6**, 291–292 (2011).
33. Dai, F. et al. Validation of a fear test in sport horses using infrared thermography. *J. Vet. Behav.* **10**, 128–136 (2015).
34. R Core Team. R: A Language and Environment for Statistical Computing. (2021).
35. Brooks, M. E. et al. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **9**, 378–400 (2017).

36. Hartig, F. DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. (2021).
37. Fox, J. & Weisberg, S. An {R} Companion to applied regression. (Sage, Thousand Oaks {CA}, (2019).
38. Lenth, R. V. emmeans: Estimated marginal means, aka least-squares means. (2022).
39. Wickham, H. Ggplot2: Elegant graphics for data analysis. Springer International Publishing (2016).
40. Forkman, B., Boissy, A., Meunier-Salaün, M. C., Canali, E. & Jones, R. B. A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. *Physiol. Behav.* **92**, 340–374 (2007).
41. Lansade, L., Bouissou, M. F. & Erhard, H. W. Fearfulness in horses: A temperament trait stable across time and situations. *Appl. Anim. Behav. Sci.* **115**, 182–200 (2008).
42. McGreevy, P., Warren-Smith, A. & Guisard, Y. The effect of double bridles and jaw-clamping crank nosebands on temperature of eyes and facial skin of horses. *J. Vet. Behav.* **7**, 142–148 (2012).
43. Kim, S. M. & Cho, G. J. Validation of eye temperature assessed using infrared thermography as an indicator of welfare in horses. *Appl. Sci.* **11**(16), 7186. https://doi.org/10.3390/app11167186 (2021).
44. Valera, M. et al. Changes in eye temperature and stress assessment in horses during show jumping competitions. *J. Equine Vet. Sci.* **32**, 827–830 (2012).
45. Fenner, K., Yoon, S., White, P., Starling, M. & McGreevy, P. The effect of noseband tightening on horses' behavior, eye temperature, and cardiac responses. *PLoS ONE* **11**, 1–20 (2016).
46. Rogers, L. & Vallortigara, G. Lateralized Brain Functions: Methods in Human and Non-Human Species. vol. 122 (2017).
47. Siniscalchi, M., d'Ingeo, S., Quaranta, A., D'Ingeo, S. & Quaranta, A. Lateralized emotional functioning in domestic animals. *Appl. Anim. Behav. Sci.* **237**, 105282 (2021).
48. Stomp, M. et al. An unexpected acoustic indicator of positive emotions in horses. *PLoS ONE* **13**, e0197898 (2018).
49. Lundblad, J., Rashid, M., Rhodin, M. & Andersen, P. H. Effect of transportation and social isolation on facial expressions of healthy horses. *PLoS ONE* **16**, e0241532 (2021).
50. Gleerup, K. B., Forkman, B., Lindegaard, C. & Andersen, P. H. An equine pain face. *Vet. Anaesth. Analg.* **42**, 103–114 (2015).
51. Trindade, P. H. E. et al. Effect of work on body language of ranch horses in Brazil. *PLoS ONE* **15**, e0228130 (2020).
52. Carmo, L. G., Werner, L. C., Michelotto, P. V. & Daros, R. R. Horse behavior and facial movements in relation to food rewards. *PLoS ONE* **18**, e0286045 (2023).
53. Ricci-Bonot, C. & Mills, D. S. Recognising the facial expression of frustration in the horse during feeding period. *Appl. Anim. Behav. Sci.* **265**, 105966 (2023).
54. Trösch, M. et al. Horses categorize human emotions cross-modally based on facial expression and non-verbal vocalizations. *Animals* **9**, 862 (2019).
55. D'Ingeo, S. et al. Horses associate individual human voices with the valence of past interactions: A behavioural and electrophysiological study. *Sci. Rep.* **9**, 11568 (2019).
56. Ferreira, V. H. B., Lansade, L., Calandreau, L., Cunha, F. & Jensen, P. Are domesticated animals dumber than their wild relatives? A comprehensive review on the domestication effects on animal cognitive performance. Neurosci. Biobehav. Rev. **154**, (2023).
57. Liehrmann, O. et al. Multiple handlers, several owner changes and short relationship lengths affect horses' responses to novel object tests. *Appl. Anim. Behav. Sci.* **254**, 105709 (2022).
58. Liehrmann, O. et al. What drives horse success at following human-given cues? An investigation of handler familiarity and living conditions. *Anim. Cogn.* **26**, 1283–1294 (2023).
59. Briefer, E. F. Vocal contagion of emotions in non-human animals. *Proc. R. Soc. B Biol. Sci.* **285**, 20172783 (2018).
60. Smith, A. V. et al. Domestic horses (Equus caballus) discriminate between negative and positive human nonverbal vocalisations. *Sci. Rep.* **8**, 13052 (2018).

Acknowledgements
We would like to thank Laetitia Boichot from IFCE for lending the thermal camera and Léa Paglia for reanalyzing 20% of the videos. We thank the staff at the UEPAO (Unité Expérimentale de Physiologie Animale de l'Orfrasière) for technical assistance. We thank Gaelle Lefort for her help with the statistical analysis during the revision of the manuscript.

Author contributions
PJ: data curation, formal analysis, funding acquisition, investigation, methodology, writing—original draft; SY: methodology, validation, writing-review & editing; MR: methodology, validation, writing-review & editing; NTG: data curation, investigation, methodology; CP: data curation, investigation, methodology; FR: methodology, resources, validation; LC: conceptualization, project administration, resources, writing-review & editing; LL: conceptualization, funding acquisition, methodology, project administration, supervision, validation, writing-review & editing.

Competing interests
The authors declare no competing interests.

Additional information
Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-025-98794-3.

Correspondence and requests for materials should be addressed to P.J.