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Human emotional chemical cues collected in situations of disgust or sadness modulate horses' behaviour and physiology in a multimodal context

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Article

Keywords: Equus caballus, disgust, emotion, human-animal relationship, sadness

Posted Date: November 2nd, 2026

DOI: https://doi.org/10.21203/rs.3.rs-11219192/v1

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Additional Declarations: No competing interests reported.

Human emotional chemical cues collected in situations of disgust or sadness modulate horses' behaviour and physiology in a multimodal context

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Abstract

Human emotional chemical cues influence the behaviour and physiology of several domestic species, including dogs and horses. While previous studies have mainly focused on fear and happiness, less is known about sadness and disgust, which may convey distinct affective information. This study examined whether human chemical cues collected during sadness and disgust -two negatively valenced emotions differing in arousal and presumed adaptive function - could modulate horses' behavioural and physiological responses when presented with corresponding visual and auditory cues. Twenty-eight Welsh mares were exposed, while viewing emotion-matched facial expressions, to sweat samples collected from human donors during either neutral or emotional inductions (sadness or disgust). The two groups were tested twice, once with neutral chemical cues and once with emotional chemical cues. Compared with the neutral condition, emotional chemical cues altered horses' physiological and behavioural responses: sadness-related cues induced lower physiological arousal and calmer postures, whereas disgust-related cues elicited increased heart rate and movement. Despite their shared negative valence, sadness and disgust elicited opposite behavioural and physiological responses consistent with their typical arousal levels. These findings suggest that horses can discriminate between emotion-specific chemosensory cues. By providing the first evidence of horses' responses to human sadness- and disgust-related chemical cues, this study extends previous work beyond fear and highlights the role of olfactory cues in multimodal processing of emotional information across species.

Keywords

Equus caballus, disgust, emotion, human-animal relationship, sadness

Introduction

Chemical communication represents one of the most primitive modes of information exchange among living organisms. In humans, body odours contain chemical cues capable of signalling various affective states and inducing behavioural and physiological changes in receiving individuals [1, 2]. Several studies have shown that these human olfactory cues can cross species boundaries and influence the physiology or behaviour of domestic animals. For instance, dogs (*Canis familiaris*) and horses (*Equus caballus*) exposed to human odours collected in a fear-related emotional context display increased vigilance, avoidance, or elevated heart rate [3, 4, 5]. Horses are also able to discriminate between odours collected in a fear context and odours collected in a joyful context using a habituation–dishabituation paradigm [5]. To date, however, research on chemical communication of emotions between humans and animals has focused almost exclusively on fear, often using joy as a control, or comparing fear with a more "neutral" emotional state.

This emphasis raises a key question: is interspecific chemical communication truly specific to fear, or does it more broadly reflect the transmission of negative emotions, regardless of their specific emotional content? Emotions are commonly described along two main dimensions: valence, which ranges from positive (rewarding or pleasant) to negative (aversive or punishing), and arousal, which reflects the intensity of physiological and behavioural activation elicited by the emotional state [6, 7, 8]. It is essential to investigate additional emotional contexts, because phenomena interpreted as specific recognition of fear may instead reflect a more general discrimination between a highly arousing emotional state and a more neutral one, independently of the emotion's qualitative content. For example, a global increase in sweat production could be sufficient to generate such discrimination [9]. In this case, one might incorrectly conclude that animals detect human fear odours, whereas they would simply be responding to odours associated with high arousal rather than fear itself. It is therefore crucial to determine whether animals can identify chemical cues produced in other emotional contexts, particularly negative ones.

Among human negative-valence emotions, sadness constitutes a highly relevant candidate. First, it shares the same negative valence as fear, but differs in its level of arousal: sadness is typically associated with low arousal (in the absence of crying), whereas fear is characterised by high arousal [10]. If horses react to sadness despite its low arousal level, this would indicate that their discrimination does not rely solely on the intensity of the

emitter's emotional arousal. Second, one study has assigned specific social functions to sadness. Silent sadness without crying may play a calming or soothing role [11]. This proposed function is consistent with physiological responses typically associated with sadness in humans, such as decreased heart rate, reduced skin conductance, and more regular breathing patterns [12, 13]. Moreover, distinct olfactory signatures associated with sadness obtained from tear samples have been identified in humans [14, 15], making their detection by other species plausible. Some odours collected in sadness contexts have even been associated with decreased arousal in exposed human recipients [16]. Finally, visual and auditory cues associated with human sadness (facial expression and vocal prosody) are detected by horses [17]. For instance, horses can learn to identify joy and sadness among other basic emotions from human facial expressions displayed on a screen [17]. They can also match a sad voice to a sad facial expression in a multimodal paradigm. Furthermore, they exhibit specific behavioural and physiological responses when exposed to sad voices, such as reduced heart rate and lower activation compared to responses to joyful voices [17]—a result consistent with the proposed soothing function of sadness [10].

Another negative-valence emotion of interest is disgust, which is characterised by high arousal [18]. In many species, disgust is considered an adaptive emotion whose primary function is to help individuals to avoid potentially harmful or contaminated substances [19, 20, 21]. In horses, this may be particularly relevant because their digestive anatomy prevents vomiting: due to a unidirectional peristalsis and the position of the cardia — a muscular valve separating the stomach from the oesophagus — food cannot flow back from the stomach [22, 23]. Consequently, the ability to detect and respond to cues associated with disgust may contribute to avoiding ingestive hazards. For example, Jankunis and Whishaw [24] showed that horses have a distinctive facial expression of disgust, which potentially serves as social information for other horses. Moreover, several studies have highlighted that horses were able to distinguish disgust against neutral or sadness emotions thanks to visual cues such as human facial expressions [17, 25]. Beyond its role in individual protection, recognising disgust-related cues in conspecifics or heterospecifics may provide adaptive benefits by allowing individuals to avoid potentially contaminated environments or food sources without direct exposure. In humans, disgust is associated with distinct facial and olfactory cues [26, 27]. In humans, exposure to disgust-related chemical cues has been shown to elicit behavioural patterns consistent with sensory rejection and avoidance, including reduced exploratory sampling of the environment, suggesting an increased motivational state oriented toward

contamination avoidance [26]. Similarly, Vrana [28] reported autonomic activation during disgust elicitation, including heart rate modulation consistent with higher arousal negative states. At a broader psychophysiological level, disgust has also been associated with autonomic responses indicative of higher arousal compared to low-arousal negative states such as sadness, including heart rate modulation during emotion elicitation [28]. To our knowledge, no study has yet investigated whether animals can detect and respond to chemical cues potentially associated with sadness and disgust. It remains unknown whether they can discriminate human olfactory cues collected in a sadness and disgust context, and whether such cues elicit specific functional reactions, as demonstrated for fear.

Horses are a relevant model for addressing these questions as this species possess a highly developed sense of smell, supported by a strongly convoluted olfactory bulb [29, 30]. Olfaction plays an essential role in social recognition and intraspecific interactions [31, 32]. Horses also display advanced socio-cognitive abilities toward humans: they recognize human faces in photographs and retain these memories for several months [33, 34], can interpret some human actions as goal-directed [35], discriminate positive and negative human facial and vocal expressions [36, 37, 38, 39], and integrate emotional information across modalities-including fear, anger, joy, and, as shown above, sadness [17, 40, 41, 42]. These multimodal capacities extend to olfaction: several studies have shown that horses discriminate human body odours collected in fear and joy contexts [4, 43], and that these odours modulate their behaviour and physiology. Notably, odours associated with fear can induce responses consistent with this emotion, such as increased vigilance or elevated heart rate, particularly when a threatening stimulus is presented simultaneously [5], an effect that parallels what has been observed in humans exposed to anxiety- or fear-related olfactory cues [44, 45, 46].

The main objective is to examine whether human chemical cues collected in a sadness and disgust context can induce a functional response coherent with the proposed soothing nature of sadness, whereas chemical cues collected in a disgust context are expected to promote increased behavioural and physiological activation, potentially expressed as behavioural avoidance, in line with the adaptive function of disgust in preventing contact with potentially harmful stimuli. Given the multimodal nature of emotional communication [47], we investigated the interaction of olfactory cues with visual and auditory signals associated with human sadness and disgust, to determine whether olfactory cues amplify horses' responses to this emotion.

To address these objectives, our study comprises an experiment examining the behavioural and physiological responses of horses to these odours while they are simultaneously exposed to videos of sad and disgusted facial expressions, and comparing these responses with those observed when horses are exposed to a neutral odour.

We predicted that human odours collected in a sadness context would induce lower agitation, reflected by a decreased time spent moving, a more relaxed posture (reflected by a lower neck position), and a decreased heart rate compared with neutral odours, in accordance with the presumed soothing function of this emotion and with previous findings obtained using visual and auditory cues. Conversely, we predicted that chemical cues collected from humans in a disgust context would induce greater agitation, reflected by increased movement, a more tense posture (reflected by a higher neck position), and an increased heart rate compared with neutral odours.

Methods

Ethical statement

All experimental procedures were conducted in accordance with the ethical standards for the treatment of animals in behavioural research and teaching (in compliance with the ARRIVE guidelines). The experimental design was approved by the local Animal Ethics Committee of INRAE Val-de-Loire (CEEA VdL, Nouzilly, France, authorization number CE19-2022-1511-2). All procedures complied with the European Directive 2010/63/EU on the protection of animals used for scientific purposes. No anesthesia or euthanasia was performed during the study. The horses remained in their usual housing conditions throughout the study. For each experimental session, they were temporarily brought to the experimental room for the experimental procedures and subsequently returned to their usual housing. At the end of the study, all horses remained in their usual housing. Human participants who donated sweat samples gave their informed consent prior to participation. All procedures involving human participants were carried out in accordance with relevant ethical guidelines and regulations. The experimental protocol was approved by the Research Ethics Committee for Research Projects (CEPR INRAE, CIRAD, IFREMER, IRD; authorization no. CEPR48). All data were anonymized prior to analysis. Informed consent for the publication of the identifiable individuals' images in Fig. 3 in an online open-access publication was obtained prior to submission of the manuscript. We confirm that the necessary consent was obtained in accordance with the journal's requirements

Horses

The study involved 28 adult Welsh mares (*Equus caballus*), with an average age of 8.46 ± 2.60 years (mean ± standard deviation) and all at least 4 years old, raised and housed at the Animal Physiology Experimental Unit (UEPAO, 37380 Nouzilly, France, https://doi.org/10.15454/1.5573896321728955E12), INRAe (National Institute for Agricultural and Environmental Research). These horses lived in groups in outdoor paddocks, with free access to shelter, fodder and water.

Human odour collection

Axillary sweat collection

Collection took place in December 2024. Participants included 43 male and female volunteers (25 for sadness: 7 males and 18 females, and 18 for disgust: 6 males and 12 females) who responded to an advertisement posted on social media and on posters in public places. Human odours emitted in contexts of sadness and disgust were collected using a method similar to that described in the study by Jardat et al. [42]. Axillary sweat odours were collected while viewing videos eliciting different emotions: sadness and disgust. Participants had to comply with dietary restrictions such as not consuming spices, garlic, or onions. They also had to use hygiene products provided by the experimenters and refrain from wearing perfume for 48 hours prior to the experiment in order to minimize contamination of sweat odours by other odorous compounds. While watching the films, the participants wore cotton pads under their armpits (7.5 × 7.5 cm, Euromedis, Neuilly-sous-Clermont, France) and a cotton T-shirt provided by the experimenters, which had been washed in clean water at 40°C.

Film selection

The videos selected for the conditions of sadness and disgust consisted of film clips and videos found on the internet . Each film lasted 20 minutes, and three-quarters of the selected clips were taken from the literature on emotion perception. In previous studies, these film clips were selected for their ability to elicit the targeted

emotions [48]. The remaining quarter was selected by the research team after confirming with six independent participants that the images elicited the intended emotion. A total of two film screening sessions were organized (one per emotion). The films presented conveyed the emotions of sadness and disgust (see Supplementary Note S1 for the list of films). At the end of each film, the cotton pads were placed in airtight bags and stored in a freezer at −80°C until they were presented to the horses. In addition to the odour pads, the same procedure was done for the sterile cotton pads to be used as neutral odours (control).

Questionnaires

After watching, participants completed two questionnaires, one confirming their compliance with dietary and hygiene guidelines, and another one where they rated on 7-point Likert scales (1: not at all - 7: very strongly) the extent to which they felt angry, scared, happy, sad, disgusted, neutral, surprised, calm, and amused during the different sessions [49]. Then, these samples were sorted to ensure their relevance to the study.

The samples selected were those from participants who stated that they had complied with hygiene precautions and dietary restrictions, and who felt the emotion corresponding to the film they watched and those who experienced this emotion intensely enough (score > 4/7). Seven samples (5 for the sadness condition and 2 for the disgust condition) were excluded from the study as they did not encounter the criteria. Among the remaining samples, the odour pads associated with the strongest target emotional responses, based on the self-reported emotional scores, were selected for the experiment. Specifically, among the 20 eligible sadness samples, the 15 samples with the highest sadness scores were retained to match the number of horses included in the experiment. Similarly, among the 16 eligible disgust samples, the 13 samples with the highest disgust scores were retained.

Production of emotional videos

The visual and auditory stimuli presented to the horses consisted of 2-minute videos. As in Jardat et al. [5], these videos showed an actor repeating a text in one of the following emotions: sadness and disgust. The text was: "Oh, but how is that possible, I've never seen that before. Oh no, that's not possible! Wait, really, are you sure? No, I don't believe it, it's not possible." This text was chosen because it could express intense positive or negative

emotions. A two-minute sequence included eight 15-second repetitions during which the actor recited the text in one of the emotions. The people appearing in the videos were four men and four women, with only their head and shoulders visible. The emotions conveyed in the videos were evaluated using a questionnaire by 20 people not participating in the experiment, confirming that the emotions expressed by the actors corresponded to sadness and disgust. The sound intensity of each video was equalized using Audacity (v3.7.1) to ensure equivalent sound levels across all stimuli.

Experimental set-up

The test area was a stall (3.5 × 4.5 m), the horse was tied in the centre of the stall with two loose lunges, facing a projection screen (2 × 1.6 m) onto which the videos were projected (Figure 1). The faces that appeared on the screen were approximately twice the size of a real human face. The sound was broadcast through a speaker (Ultimate Ears Megaboom 3) placed just behind the centre of the screen. The sound intensity was between 60 and 70 dB at the location of the horse's head. The horse was positioned 1.5 m from the screen. For safety reasons, an experimenter remained with the horse to ensure that it did not panic, but did not interact with her during the video projection. The experimenter remained motionless, without looking at either the screen or the horse, and kept her face turned toward the ground (see also section “Measures taken to prevent odour contamination”). Two 4K cameras (Sony FDR-AX43A) were placed in front of the horse, on either side of the screen, in order to analyse the animal's behaviour later. An overhead camera was placed behind the horse. It was connected via Wi-Fi to a tablet, allowing a second assistant outside the stall to monitor the progress of the experiment. A heart rate monitor continuously measured the horse's heart rate (HR) (Polar Equine RS800CX Science, Polar Oy, Finland). The horses were clipped where the device's sensors were located (i.e., girth and withers on the left) to allow for accurate HR measurement.

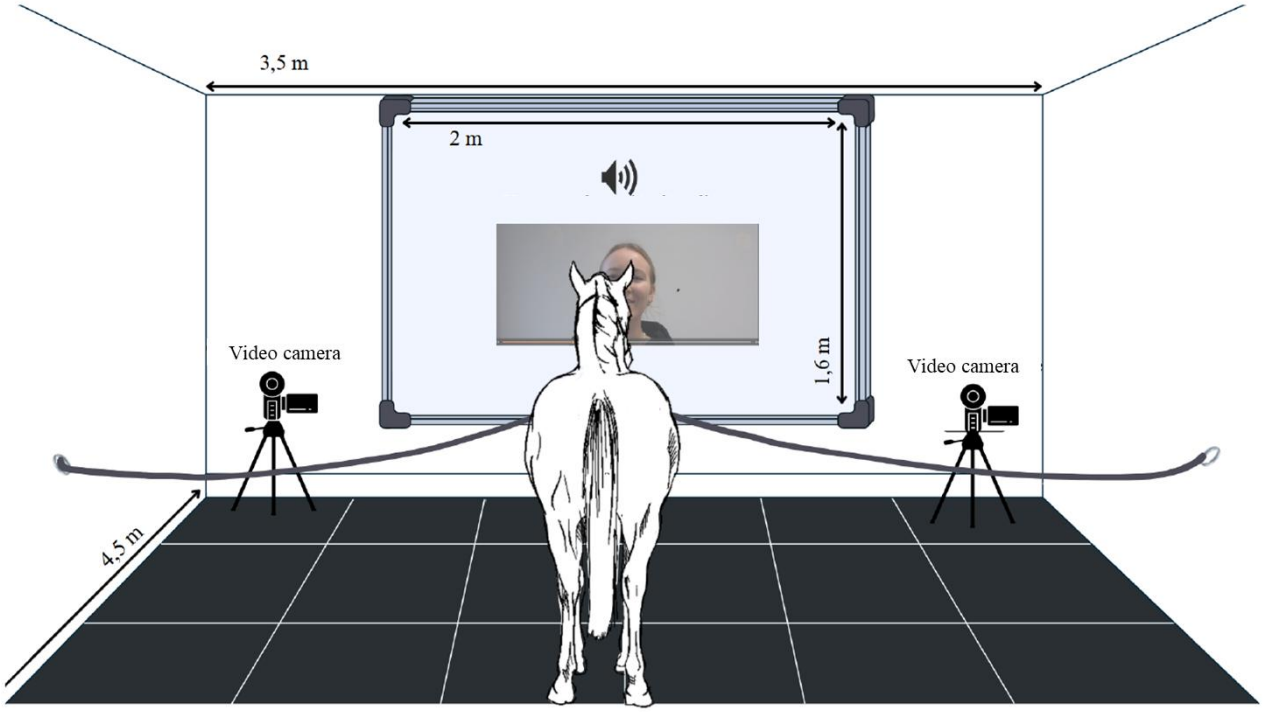


Figure 1. Experimental set-up. The horse is placed in the centre of the stall and watches the facial expression video while wearing the odour exposure mask.

Odour exposure mask

To expose the horses to odours, single-use Lycra masks were used. Inside the mask, two pads were attached with clips so that they were positioned in front of the horse's nostrils (Figure 2). The horses could breathe normally through the device. The masks were made from disposable tights (never worn before) that had been rinsed with clean water. The pads were thawed at room temperature (≈10°C) in airtight bags ten minutes before use. Each horse was presented with either two sterile pads for the neutral group (one pad for each nostril) or two pads from a participant who had watched a film evoking one of the emotions (sadness and disgust).

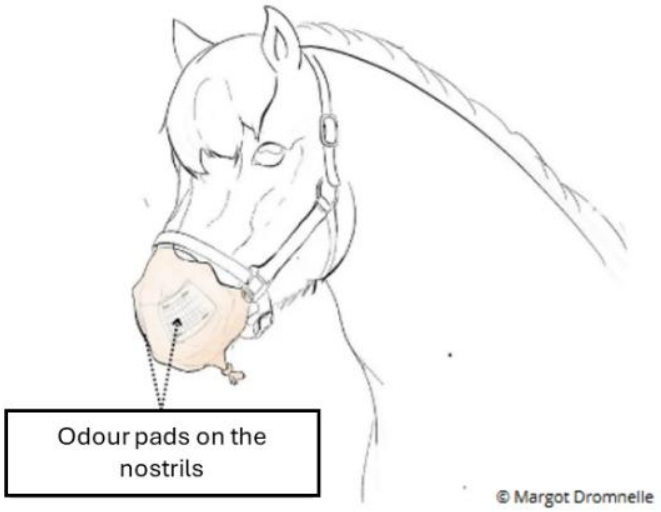


Figure 2. Lycra mask used to expose the horses to the odours.

Experimental procedure

Horses were divided into two groups, one exposed to the videos of sadness (n = 15 horses) and another exposed to the videos of disgust (n = 13 horses, Figure 3). The horses were assigned to a group based on the homogeneity of average ages between groups. The two groups were tested twice, once with the neutral odour and once with the emotional odour condition (sadness and disgust). At the same time as they were exposed to the odours (neutral or emotional), the horses watched videos of human facial expressions corresponding to the emotions (sadness and disgust). For a same horse, the test sessions were spaced one week apart. The order of presentation of the two conditions was counterbalanced between horses. Each horse was randomly assigned to one of the actors featured in the video (a total of 4 actors were used in the recordings - see below). Thus, in both conditions, the horse viewed the same actor displaying a given emotion.

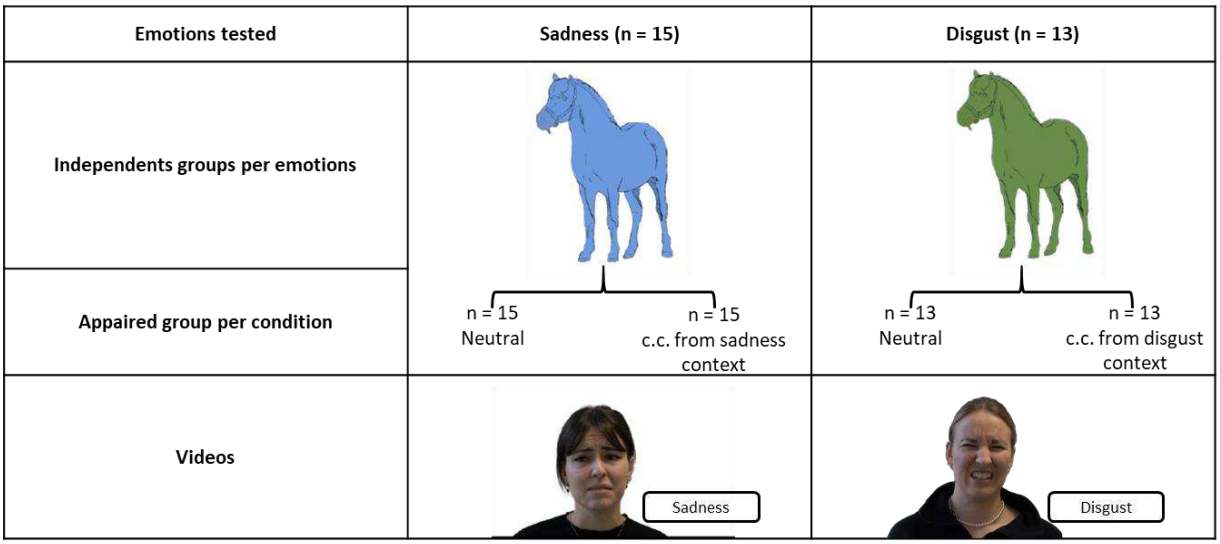


Figure 3. Experimental procedure (Note: c.c. = chemical cues).

Video projection test

Habituation

During the habituation phase, the video projector showed a film of a nature scene with bird sounds. After at least one minute, when the horse's heart rate had stabilized below 80 beats per minute (bpm) for one minute, the test phase began [5]; otherwise, the habituation phase continued until the heart rate criterion was met. If this criterion was not met after ten minutes, a new habituation phase was scheduled for the following day. If the criterion was still not met after ten minutes during the second habituation session, the experiment was considered too stressful for the horse, which was then excluded from the study. Horses that reared during the habituation phase were also excluded from the study for safety reason.

Placing the mask and showing videos of facial expressions

After wiping the horse's nostrils with absorbent paper, the mask containing the scent pads was placed over the horse's nostrils [50]. Only the experimenter in charge of preparing the masks knew the nature of the samples (sadness, disgust or neutral); the experimenter present in the stall with the horse (known from the horse) remained unaware of this information. Once the horse was centrally in front of the screen, the mask in place,

the projection of the emotional videos began, for two minutes. Four horses were stopped during the first video projection as they reared (one in the 'Disgust' group and three in the 'Sadness' group).

Measures taken to prevent odour contamination

Throughout the tests, the odour samples were handled exclusively with disposable gloves. In order to limit the spread of their own body odour, the experimenters did not wear any perfume during the entire experiment. They wore disposable gloves, a mask, shoe covers, and a clean coverall, which they changed between each horse. Between horses, the heart rate monitor strap was rinsed, as were the lunge lines used to secure the horses in the stall. Faeces were removed, and the stall was thoroughly cleaned with a water jet after each trial. The mask was discarded after each use.

Behavioural analysis

The videos of the tests were analysed using BORIS [51] by a blind experimenter, i.e., without knowing the nature of the treatment to which the animal was exposed. The behavioural measurements taken during the video projection test included the position of the neck: high (i.e., above the withers) and low (i.e., between the underside of the withers and the chest); and the amount of time spent moving, i.e., as soon as the horse lifted more than one limb.

Physiological analysis

Heart rate was measured using a heart rate monitor throughout the tests. We measured the minimum and maximum heart rates as well as the mean heart rate. The variation in heart rate in beats per minute between the last five seconds and the first five seconds of each test was calculated as the variation in HR. The data was cleaned using the following algorithm: for each data point, if the difference with the previous point was greater than 35 bpm, the data was not considered sufficiently reliable and the horse was excluded from the HR data [52]. Following this procedure, only one individual in the disgust condition was excluded for this analysis.

Statistical analysis

All statistical analyses were performed using R 4.4.3 [53] and graphs were generated using the *ggplot2* package [54]. For each variable, a model was constructed to assess the effect of the emotion odour (sadness and disgust) compared to a neutral odour on the horses' behaviour and physiology. We compared these two conditions using a generalized linear mixed model (GLMM), parameterized with a Tweedie family for high and low neck postures and movements. The mean HR, maximum and minimum HR were parameterised with a Gamma family, and the variation in HR with a Gaussian family. This analysis was performed using the *glmmTMB* package (v1.1-30, [55]). The model allowed for pseudo-replications due to the pairing of each individual by emotion, taking the paired individuals as a random factor but also the order of passage (the first or second week of testing). The results of the model were studied using a Type II ANOVA, using the *Anova()* function of the *car* package (v3.1-3, [56]). The distributions, intra-group variance, and homoscedasticity of the residuals were verified using the *DHARMa* package [57]. The significance threshold was set at P-values ≤ 0.05 and trends were considered based on P-values ≤ 0.1.

Results

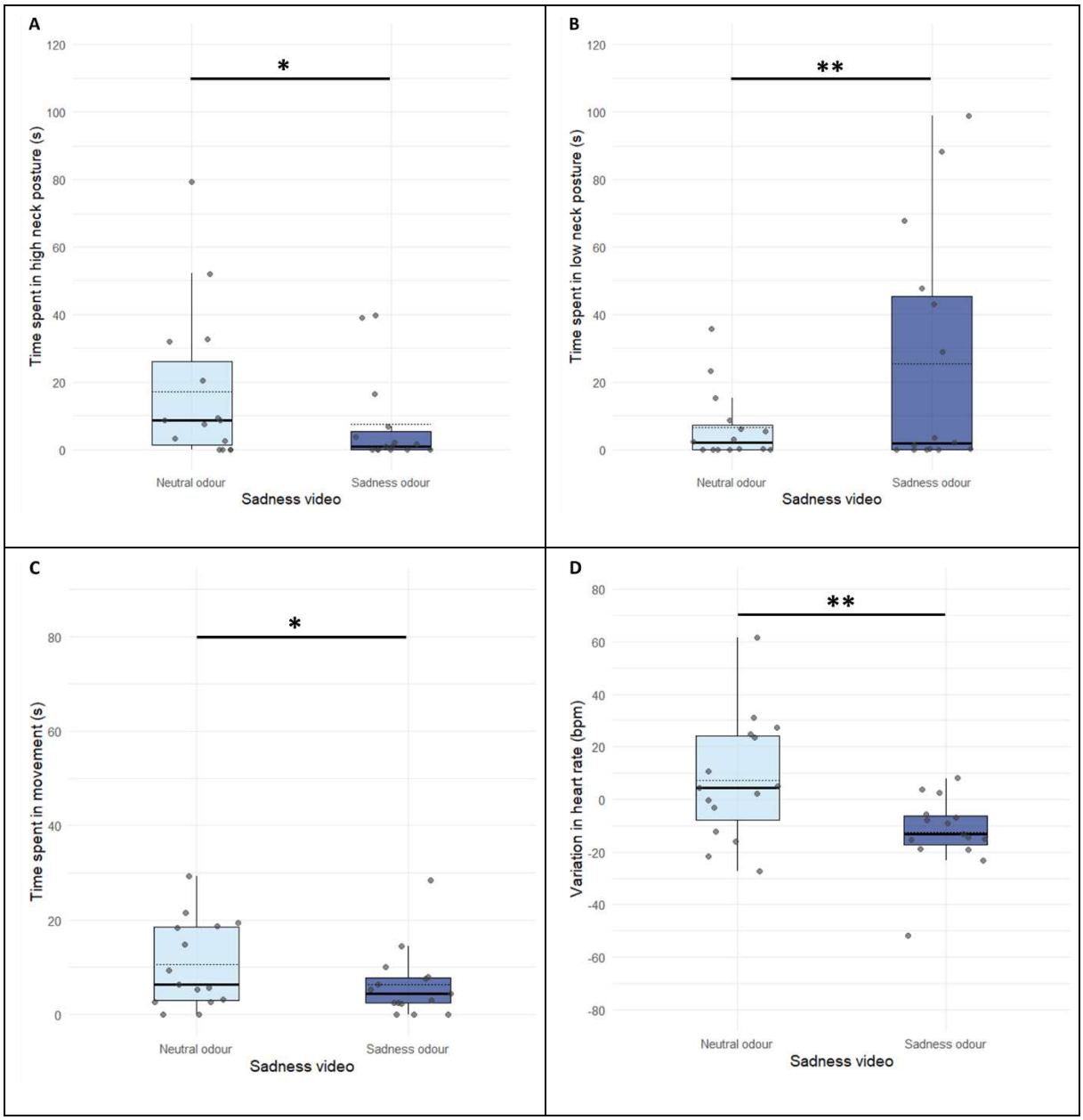
All the results are expressed in Mean ± S.E.M.

Sadness condition

Horses spent significantly less time in a high neck posture in the presence of chemical cues collected during the sadness context compared to neutral ones (neutral: 17.11 ± 5.96 s; sadness: 7.39 ± 3.53 s; $\chi^2(1) = 4.88$, P-value = 0.027; Figure 4A). At the opposite, they adopted a low neck posture significantly longer in the presence of chemical cues collected during the sadness context compared to neutral one (neutral: 6.61 ± 2.71 s; sadness: 25.41 ± 9.12 s; $\chi^2(1) = 7.46$, P-value = 0.006; Figure 4B). They also moved less when exposed to chemical cues collected during the sadness context compared to neutral one (neutral: 10.47 ± 2.35 s; sadness: 6.30 ± 1.89 s; $\chi^2(1) = 5.34$, P-value = 0.021; Figure 4C).

The variation in heart rate between the start and end of the test was significantly lower in the presence of chemical cues collected during the sadness context compared to neutral one (neutral: 7.32 ± 6.04; sadness: -

12.47 ± 3.65; $\chi^2(1) = 8.42$, P-value = 0.004; Figure 4D). The mean heart rate was not significantly different in the presence of chemical cues collected during sadness context than in the presence of neutral one (neutral: 72.75 ± 7.56 bpm; sadness: 69.81 ± 5.37 bpm; $\chi^2(1) = 0.30$, P-value = 0.585; Figure 4E). There was no significant difference in maximum (neutral: 94.93 ± 10.37 bpm; sadness: 96.40 ± 9.31 bpm; $\chi^2(1) = 0.01$, P-value = 0.905) and minimum heart rate between the conditions implying chemical cues collected during the sadness context and neutral one (neutral: 53.87 ± 3.61 bpm; sadness: 53.60 ± 3.96 bpm; $\chi^2(1) = 0.30$, P-value = 0.582; Figure 4F).



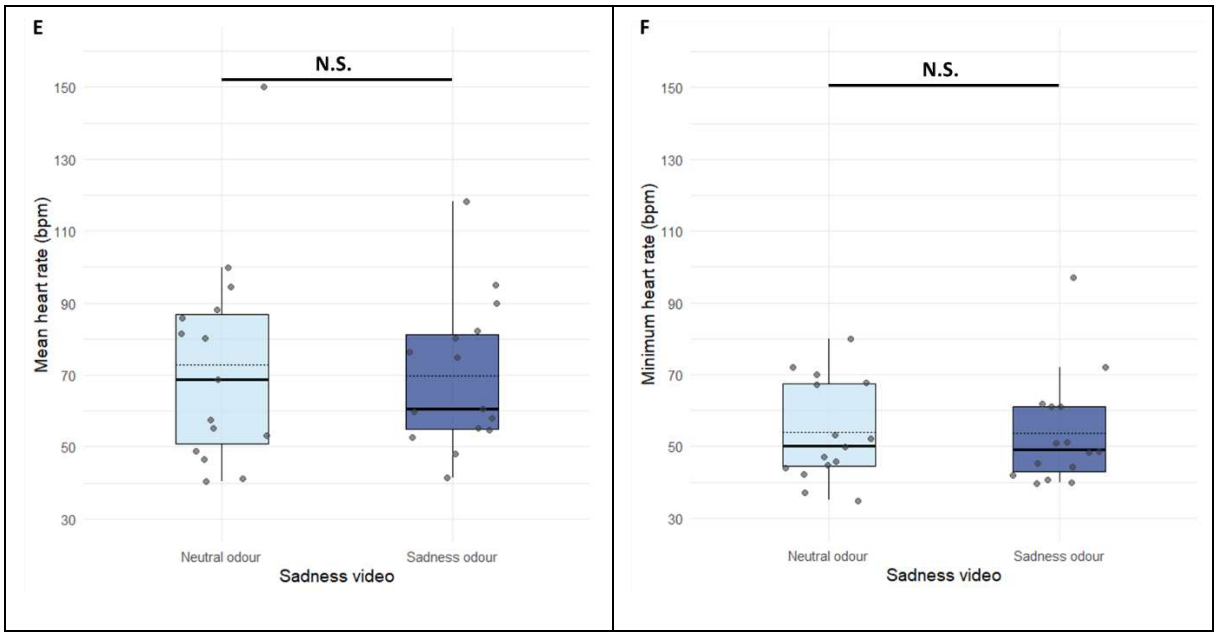


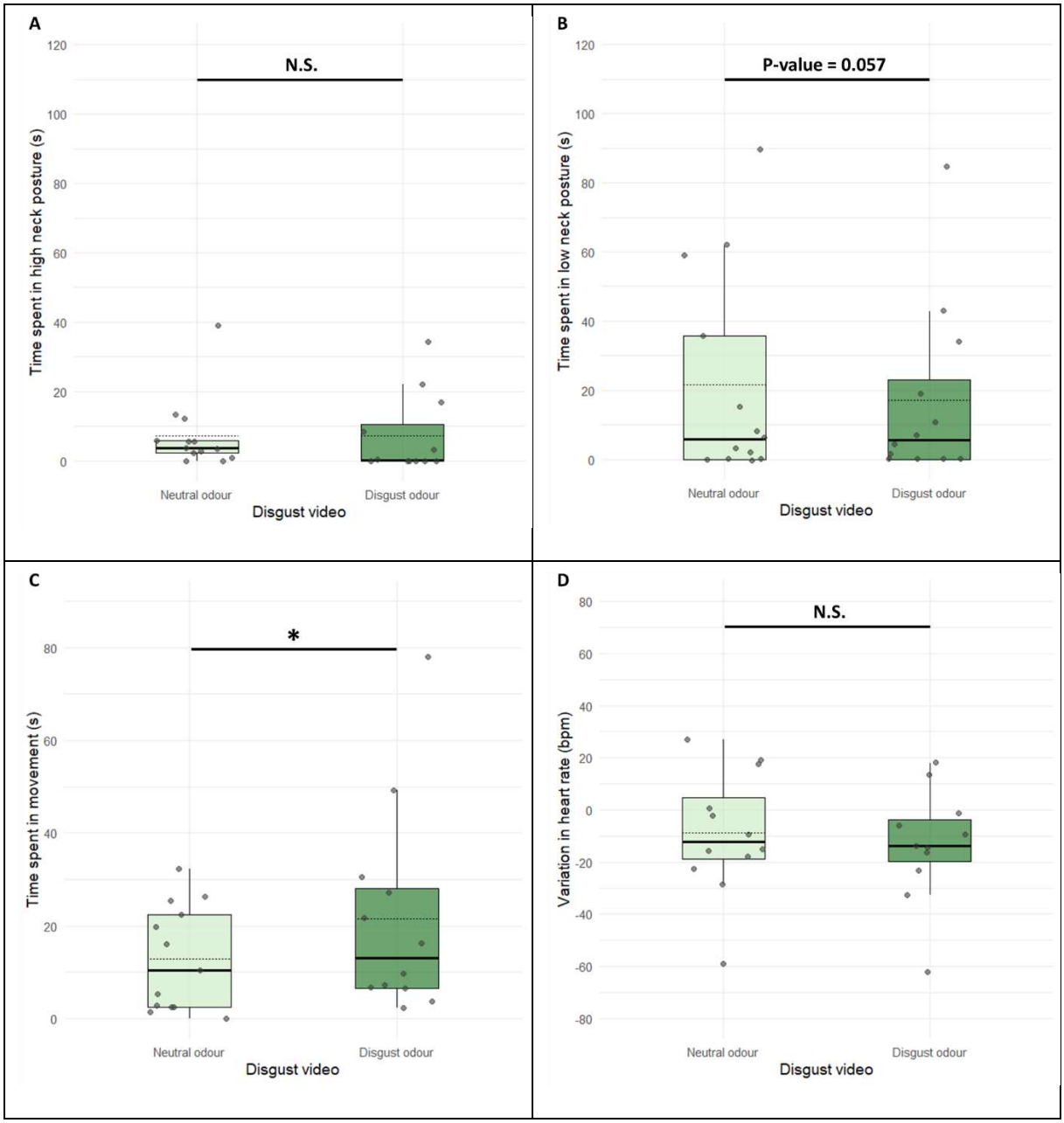
*Figure 4: Effects of sadness-related chemical cues on posture, activity, and heart rate during video projection. Time spent A. with a high neck posture, B. with a low neck posture, C. moving, D. variation in heart rate, E. mean heart rate and F. minimum heart rate, while watching videos, depending on the condition: neutral versus chemical cues collected during sadness context (named on the graphics 'sadness odour'). The dots represent individuals; the boxes indicate the median (solid line) and the first and third quartiles (box limits). The whiskers extend to extreme values not exceeding 1.5 times the interquartile range. The dotted line indicates the mean. (Note: ** P-value < 0.01; * P-value < 0.05).*

Disgust condition

There was no significant difference concerning the time spent with a high neck posture in the presence of chemical cues collected during the disgust context and neutral one (neutral: 7.27 ± 2.88 s; disgust: 7.13 ± 3.28 s; $\chi^2(1) = 0.31$, P-value = 0.575; Figure 5A). However, there was a tendency for horses to adopt a low neck posture for a shorter period of time in the presence of chemical cues collected during the disgust context compared to neutral one (neutral: 21.63 ± 8.35 s; disgust: 17.05 ± 7.39 s; $\chi^2(1) = 3.64$, P-value = 0.057; Figure 5B). Moreover, horses moved significantly longer in the presence of chemical cues collected during the disgust context compared to neutral one (neutral: 12.82 ± 3.14 s; disgust: 21.57 ± 6.51 s; $\chi^2(1) = 4.00$, P-value = 0.046; Figure 5C).

The variation in heart rate between the start and end of the test was not significantly different in the presence of chemical cues collected in the disgust context compared to neutral one (neutral: - 8.88 ± 6.84; disgust: - 13.45

± 6.60; $\chi^2(1) = 0.24$, P-value = 0.628; Figure 5D). However, the mean heart rate was significantly higher in the presence of chemical cues collected during the disgust context compared to neutral one (neutral: 76.43 ± 6.17 bpm; disgust: 87.30 ± 10.49 bpm; $\chi^2(1) = 4.23$, P-value = 0.040; Figure 5E). There was no significant difference for the maximum heart rate between chemical cues collected during the disgust context and neutral one (neutral: 102.67 ± 7.56 bpm; disgust: 112.18 ± 13.22 bpm; $\chi^2(1) = 1.17$, P-value = 0.279). However, the minimum heart rate was significantly higher in the presence of chemical cues collected during the disgust context compared to neutral one (neutral: 57.42 ± 4.14 bpm; disgust: 68.82 ± 7.60 bpm; $\chi^2(1) = 7.24$, P-value = 0.007; Figure 5F).



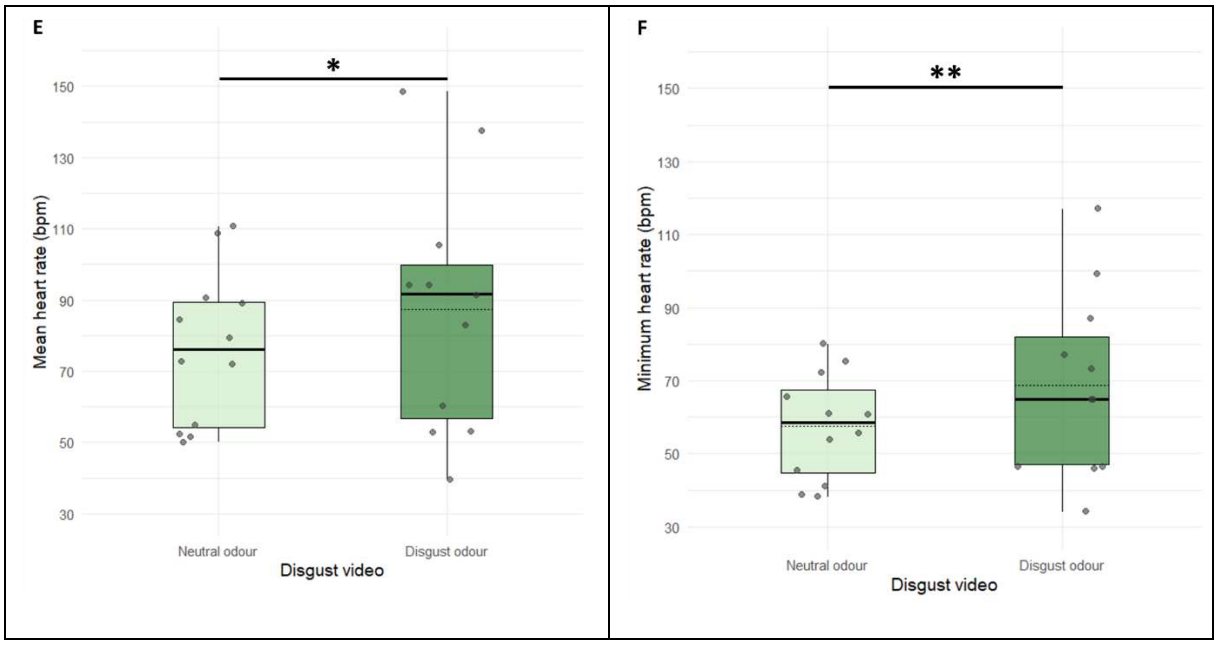


*Figure 5: Effects of disgust-related chemical cues on posture, activity, and heart rate during video projection. Time spent A. with a high neck posture, B. with a low neck posture, C. moving, D. variation in heart rate, E. mean heart rate and F. minimum heart rate, while watching videos, depending on the condition: neutral versus chemical cues collected during disgust context (named on the graphics 'disgust odour'). The dots represent individuals; the boxes indicate the median (solid line) and the first and third quartiles (box limits). The whiskers extend to extreme values not exceeding 1.5 times the interquartile range. The dotted line indicates the mean. (Note: ** P-value < 0.01; * P-value < 0.05).*

Discussion

The aim of this study was to test the behavioural and physiological impact of human emotional odours (sadness and disgust) when human visual and auditory modalities associated with the same emotion were present in horses. Our main finding is that human odours of sadness and disgust elicited specific behavioural and physiological patterns in this multimodal context: sadness was associated with lower levels of behavioural and physiological arousal, whereas disgust elicited higher levels of activation. Such contrasting effects suggest that horses discriminate between emotion-specific chemosensory cues rather than simply responding to the presence of a negative human emotional cue. The congruence between olfactory, visual and auditory emotional cues may have facilitated emotional processing in horses, as congruent multisensory information generally promotes more efficient and robust perceptual processing [58]. Such cross-modal integration could explain why emotional odours elicited measurable responses even in the presence of simultaneous audiovisual information. Specifically,

horses were calmer and maintained a low-neck posture for longer in the presence of chemical cues collected in a sadness context while watching a video displaying human facial expressions of sadness. Furthermore, their heart rate decreased more in the presence of the chemical cues collected during sadness than in the neutral odour condition. Conversely, when exposed to the chemical cues collected during disgust while watching the video of human disgust, the horses moved around more and exhibited a higher mean heart rate compared to the neutral odour condition. Previous studies have primarily focused on fear-related cues, making the present findings particularly noteworthy as they demonstrate that horses respond to emotional chemical cues linked to emotions that have received little to no attention in the animal literature.

During the viewing of videos depicting sadness, exposure to the scent of human sadness led to a significant increase in the time spent in a low-neck posture compared with the neutral scent. This result supports our hypothesis that horses exhibit a low level of arousal when exposed to the scent of sadness.

The horse's body tension reveals its state of arousal. This tension can be manifested through the positioning of the neck: a high neck indicates a high state of arousal, while a low neck is associated with muscle relaxation, which can indicate either a low state of arousal [59]. The low-neck posture may be associated with a low-intensity internal state, and thus with a state consistent with the dimensional characteristics of sadness, i.e. a low-arousal emotion with negative valence [8]. This interpretation is supported by the physiological data, which showed a greater decrease in heart rate during the test when horses were exposed to the chemical cues collected during the sadness context compared to the neutral odour. Changes in heart rate can result either from increased stimulation of the sympathetic nervous system or from decreased stimulation of the parasympathetic nervous system, both of which are influenced by the horse’s level of arousal [60]. In this case, the decrease in heart rate observed in the presence of the chemical cues collected during sadness context suggests reduced autonomic nervous system activity. This finding is consistent with evidence that human emotional tears, considered as sadness-related chemical cues, can induce behavioural and physiological changes associated with reduced arousal in human receivers [16]. While these effects have been demonstrated in an intraspecific context, our results suggest that similar emotional information may be perceived across species, as horses displayed behavioural and physiological responses consistent with a low-arousal state when exposed to human sadness-related chemical cues. Similarly, a decrease in heart rate has previously been observed in horses exposed to

403 human voices expressing sadness compared to cheerful voices [43]. If horses respond to auditory signals of
404 sadness, the effects induced by sadness-related odours could be additive to, or interact synergistically with,
405 auditory cues. The overall response elicited by these different modalities could therefore be amplified compared
406 to the perception of a single modality [47].
407
408 Whilst watching the disgust video, the horses moved around more and exhibited a higher mean heart rate when
409 exposed to the chemical cues collected during the disgust context compared to the neutral odour. They also
410 tended to adopt a less relaxed posture in the presence of the chemical cues collected during the disgust context.
411 These findings support our hypothesis that odours of disgust induce greater arousal in horses when they are
412 exposed to videos depicting disgust.
413 These findings are consistent with the literature on horses' perception of disgust. Baba et al. [25] demonstrated
414 that both gaze-tracking frequency and total gaze duration decreased in response to human facial expressions of
415 disgust compared to neutral expressions, suggesting that horses tend to avoid faces expressing disgust. Similarly,
416 in the present study, the odour of disgust appeared to trigger avoidance-related behaviours. Furthermore, both
417 minimum and mean heart rate were higher in the presence of the chemical cues collected during the disgust
418 context compared to the neutral ones. The increase in heart rate may reflect greater agitation in horses exposed
419 to the aversive odour.
420 Disgust is thought to have evolved as a mechanism to reduce the risk of disease and is associated with
421 behavioural, cognitive, and physiological responses that enable animals to avoid parasites, pathogens, and toxins
422 [61]. It is therefore possible that the horses moved around more and exhibited a higher mean heart rate because
423 the aversive odour induced a stress response. As suggested for sadness, the perception of disgust-related odours
424 may amplify responses triggered by other sensory modalities conveying disgust [47]. In humans, Zheng et al. [62]
425 reported that exposure to human body odours collected during a disgust context influenced decision-making
426 processes, including food choices, with participants showing a tendency to select healthier food options over
427 junk food.
428
429 Interestingly, the behavioural and physiological responses observed in horses appear to reflect the dimensional
430 characteristics typically associated with these emotions in humans. Sadness is generally characterised by
431 negative valence and low arousal, whereas disgust is associated with negative valence but higher arousal [8]. In

the present study, sadness-related odours were associated with calmer postures and reduced heart rate, while disgust-related odours elicited increased movement and higher heart rate. These findings therefore suggest that horses may respond not only to the valence of human emotional cues, but also to their level of arousal. These results highlight the ability of horses to adapt their behaviour in response to the emotions displayed by humans. These findings therefore suggest that horses may respond not only to the negative valence of human emotional cues, but also to differences in their level of arousal. Because both sadness and disgust are negatively valenced emotions but differ in terms of arousal, the contrasting behavioural and physiological responses observed here are unlikely to be explained by emotional valence alone. Instead, they suggest that horses extract information beyond emotional valence from human chemical cues, allowing them to differentiate between distinct negative emotional states. This interpretation is consistent with the dimensional framework of emotions, in which valence and arousal represent two complementary components underlying emotional experience [8]. The ability to discriminate between emotions sharing the same valence but differing in arousal may be particularly relevant in interspecific interactions, as these emotional states can signal different social or environmental contexts and therefore require different behavioural responses. Such sensitivity would enable horses to adjust their behaviour more appropriately to the emotional state of humans, contributing to more flexible and adaptive human–horse interactions.

Several limitations should nevertheless be considered when interpreting these findings. First, the animal sample included only female Welsh horses. Although breed and sex have not previously been identified as major factors influencing horse–human interactions or olfactory perception [4, 31, 36, 37, 40, 41], the present findings should be generalised with caution until they are replicated in a more diverse population including stallions, geldings, and other breeds. In addition, age may also influence horses' olfactory perception and exploratory behaviour. Rørvang et al. [63] reported age-related differences in olfactory investigation behaviours, suggesting that olfactory abilities or prior olfactory experience may change throughout life in horses. Although the horses included in the present study were neither particularly young nor old (mean ± standard deviation: 8.46 ± 2.60 years), future studies including a wider age range would help determine whether age influences sensitivity to human emotional odours.

An aspect to consider in future research is the multimodal nature of the experimental design. In the present study, horses were exposed to emotional audiovisual stimuli paired either with a congruent emotional chemical

cue or with a neutral one, allowing the contribution of emotional chemical cues to be examined within a controlled audiovisual context. This approach was designed to investigate olfactory influences under conditions in which emotional information was simultaneously conveyed through visual and auditory cues. At the same time, because visual and auditory cues were presented together, the respective contribution of these modalities and their potential interactions with olfactory information could not be examined separately. Future studies could therefore build on the present findings by manipulating the sensory modalities more systematically, for example by comparing neutral audiovisual stimuli with unimodal emotional presentations (visual, auditory, or olfactory alone). Such approaches could help determine whether emotional chemical cues elicit behavioural and physiological responses in their own right, or whether they primarily modulate responses to emotional information conveyed through other sensory modalities. Interestingly, the contribution of individual modalities may also depend on the emotional category considered; for instance, previous work has examined horses' responses to sadness conveyed through facial expressions or vocalisations separately [64]. These approaches could provide a more comprehensive understanding of how emotional information is integrated across sensory modalities in horses.

Beyond the responses observed, identifying the chemical compounds involved represents a crucial step towards understanding the mechanisms underlying interspecific emotional communication. Recent work suggests that emotional body odours may be characterised by distinct chemical fingerprints, with differences in classes of volatile compounds such as aldehydes, ketones, esters and cyclic molecules across emotional states, although the specific compounds responsible for emotional communication remain unknown [2, 65]. It also remains unclear why horses are sensitive to these human emotional cues. This ability may reflect olfactory mechanisms conserved across mammals, stemming from a common ancestor and the sharing of certain chemical compounds or olfactory receptors. Alternatively, it may have been reinforced through the domestication process and the long history of close coexistence between horses and humans. Future research will be necessary to disentangle these hypotheses.

The present findings may contribute to a better understanding of the subtle mechanisms involved in human–horse interactions. Previous studies had already demonstrated that horses can respond to human fear-related cues, particularly through behavioural and physiological changes associated with heightened arousal [50]. The

present study extends these observations to other negative emotions, namely sadness and disgust, suggesting that horses may also perceive and respond to human emotional chemical cues beyond fear alone. By showing that horses react behaviourally and physiologically to sadness- and disgust-related odours, this study supports the idea that chemosensory cues may participate in the transmission of emotional information between species. In practical contexts such as horse management, training, or animal-assisted interventions, human emotional states could therefore influence horses in ways that are not always consciously perceived by handlers. Taking these processes into account may help improve both horse welfare and the quality of human–horse relationships. Future research could investigate whether repeated exposure to human emotional chemical cues affects horses' emotional regulation, or sensitivity to humans over time.

In conclusion, this study demonstrates, for the first time in horses, that human emotional odours can modulate behavioural and physiological responses in a multimodal emotional context combining visual, auditory, and olfactory cues. Importantly, whereas previous research on the interspecific perception of human chemical cues has focused primarily on fear-related cues, the present study extends this work to two emotions that have received little to no attention in animals: sadness and disgust. Horses displayed distinct behavioural and physiological responses to sadness- and disgust-related chemical cues, with sadness inducing lower activity and heart rate, and disgust eliciting increased activation. These contrasting patterns suggest that horses discriminate between emotional chemical cues rather than simply responding to the negative valence of human emotions, consistent with differences in the arousal associated with these emotional states. These findings indicate that chemical cues influence horses' processing of human emotional signals in a multimodal context. More broadly, this study emphasises the potential role of olfactory cues in shaping everyday human–horse interactions and opens new perspectives for understanding how emotions may be transmitted across species boundaries.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Acknowledgements

We would like to thank the UEPAO Equine team for their help and support during the data collection process. We also thank all the volunteers who generously provided their odour samples for this study.

Funding

LL discloses support for the research of this work from the Agence Nationale de la Recherche (ANR AAPG2023, CES 20: Biology of animals, photosynthetic organisms and microorganisms, project EMODOUR, grant ANR-23-CE20-0033).

Author contributions

Conceptualisation: L.L. Methodology development: L.L. Data collection: M.D., J.L., F.C., J.C., J.P. and F.R. Project administration: L.L. Data validation and analysis: C.R.B. Writing of the manuscript: C.R.B. Commenting on and editing the manuscript: C.R.B., A.D., I.L., X.B., P.J., V.H.B.F., L.C., and L.L.

Additional information

Competing interests

The authors declare no competing interests.

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