



Research

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Animal behaviour

Functionally relevant responses to human facial expressions of emotion in the domestic horse (*Equus caballus*)

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Whether non-human animals can recognize human signals, including emotions, has both scientific and applied importance, and is particularly relevant for domesticated species. This study presents the first evidence of horses' abilities to spontaneously discriminate between positive (happy) and negative (angry) human facial expressions in photographs. Our results showed that the angry faces induced responses indicative of a functional understanding of the stimuli: horses displayed a left-gaze bias (a lateralization generally associated with stimuli perceived as negative) and a quicker increase in heart rate (HR) towards these photographs. Such lateralized responses towards human emotion have previously only been documented in dogs, and effects of facial expressions on HR have not been shown in any heterospecific studies. Alongside the insights that these findings provide into interspecific communication, they raise interesting questions about the generality and adaptiveness of emotional expression and perception across species.

1. Background

In many social species, emotions provide valuable social and environmental information and are likely to play a key role in facilitating group cohesion and functioning [1]. Since observing positive emotion elicits approach behaviour towards rewarding stimuli, while negative emotions promote avoidance of possible threats, responsiveness to emotion in others is potentially highly adaptive [2]. Perception of emotion across species may be challenging where considerable morphological variation divides signaller and receiver. To date, several species have been found to recognize human emotional expressions when presented with the full array of body cues, or after training to specifically match facial features associated with particular emotions (e.g. [3,4]). However, the extent to which facial expressions can be spontaneously discerned across species barriers has received surprisingly little attention (but see [5,6]). Here we use functionally relevant tests to explore this directly, in a paradigm that allows us to assess both the underlying cognitive and physiological mechanisms involved.

The occurrence of lateralized responses can provide an important means of evaluating how signals are processed cognitively [7,8]. The perceived emotional valence of stimuli can be determined through hemispheric biases, generally with right-hemispheric specialization for processing negatively valenced stimuli including agonistic encounters. Correspondingly, left-hemispheric specialization for positive environmental stimuli has also been reported, but there is contradictory evidence on the lateralization of responses to positive social situations [7]. The lateralized perception of heterospecific facial cues to emotion has only been documented in dogs, where 'angry' human facial expressions are viewed with a left-gaze bias, though no gaze bias is seen towards happy facial

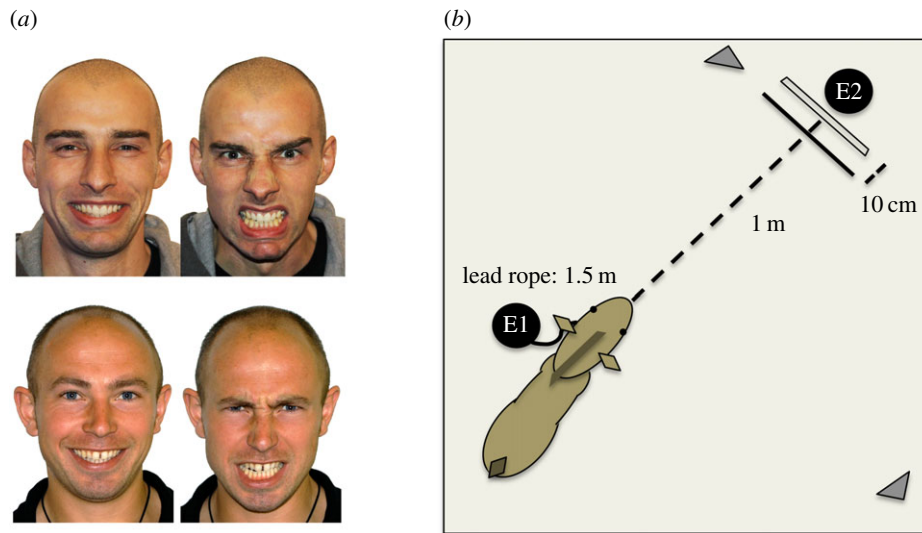


Figure 1. (a) Stimuli (L–R, positive, negative); (b) experimental set-up (E1 = experimenter 1 holding horse whilst facing away from stimulus, E2 = experimenter 2 behind board, holding stimulus; triangles represent cameras). See the electronic supplementary material for photograph of set-up. (Online version in colour.)

expressions [5]. Additionally, heart rate (HR) measures have the potential to provide objective insights into an animal's perception of external stimuli. In horses, HR correlates with behavioural indices of stress and fluctuates according to handler stress, demonstrating a potential physiological sensitivity to human affect [9].

Horses are an ideal model for research into interspecific communication of emotion, because they are able to both produce complex facial expressions [10] and perceive these in conspecifics [11], as well as being sensitive to human-given signals including facial cues [12]. Furthermore, lateralization measures are particularly appropriate for horses given their laterally placed eyes and their tendency towards lateralized behaviours [8]. This study examines whether horses spontaneously discriminate between and respond appropriately to positive (happy) and negative (angry) human facial expressions. Each horse was shown two photographs—one happy and one angry—across two trials, while its behavioural and physiological (HR) responses were measured. It was expected that negative stimuli would induce avoidance behaviour and a left-gaze bias, whereas positive stimuli would induce approach behaviour and either a right-gaze bias or no bias. Moreover, horses' HRs were expected to be higher, to increase faster and to require longer recovery periods in response to negative stimuli.

2. Material and methods

Horses were recruited from five riding/livery stables in Sussex and Surrey, UK, between April 2014 and February 2015. The final sample contained 28 horses in the behavioural analyses (21 geldings, seven mares; ages 4–23 years, $M = 15.46$, $s.d. = 5.25$), with a subset of 17 in the main HR analyses and 15 in the HR recovery analyses (see the electronic supplementary material). Stimuli were A3 (42×29.7 cm) laminated, high-quality colour photographs of two models mounted on an A1 poster board, each with one positive (happy) and one negative (angry) image (figure 1a). Facial expressions were validated using Facial Action Coding System (FACS) descriptives (see the electronic supplementary material).

Trials were conducted in stables by a team of female experimenters. Firstly, experimenter 1 held the horse on a loose lead rope for 4 min to obtain baseline HR measures, then moved the

horse into position and waited until the HR had returned to baseline. Experimenter 2 then entered the stable and presented the photographic stimuli in the horse's binocular field of vision. The top of the board was held at wither height to standardize placement of stimuli. Stimuli were held 1 m from the horse's nose for 10 s, then moved forwards by 10 cm and held for 10 s, then moved back to the original position and held for a final 10 s (figure 1b). HR measurements encompassed the test period plus approximately 5 s before and after stimulus presentation. During presentations, experimenter 1 stood at the horse's left shoulder facing away from the stimulus, with the horse held on a 1.5 m loose lead rope (allowing free movement within this length) while experimenter 2 crouched behind the stimuli board. HR was monitored for a final 4 min to assess recovery rates. Each horse saw both positive and negative expressions of either model 1 or model 2 at least two months apart, counterbalanced equally by emotion and model. HR was measured with a Polar Equine® RS800CX monitor and trials were recorded with Panasonic HC-X900 and HC-V720 digital camcorders. Behavioural responses (looking durations, approach and avoidance durations, and occurrences of stress-related behaviours: see the electronic supplementary material, table SI) were blind-coded from videos in .mov format on a Macbook Pro using Sportscode Gamebreaker Plus® 7.5.5 (www.sportstec.com) software. Experimenters were blind to the stimulus in 82% of trials and analyses showed no difference in subject responses according to this factor (see the electronic supplementary material tables SII and SIII). Ten out of 56 videos were double-coded by A.S. and K.G. and found to be reliable at or above $r = 0.85$, $p \leq 0.002$ (see the electronic supplementary material for statistics).

3. Results

(a) Behavioural responses

The number of horses turning initially to the left or right for each emotion was assessed using two-tailed binomial tests. For each subject, a laterality index (LI) for total looking time was calculated: $LI = (L - R)/(L + M + R)$, where L , M and R represent the length of time (s) spent looking left, middle and right, respectively. Positive scores indicate a left-gaze bias and negative scores a right-gaze bias. Deviations from binocular gaze (chance level: 0) were measured using one-sample t -tests (two-tailed).

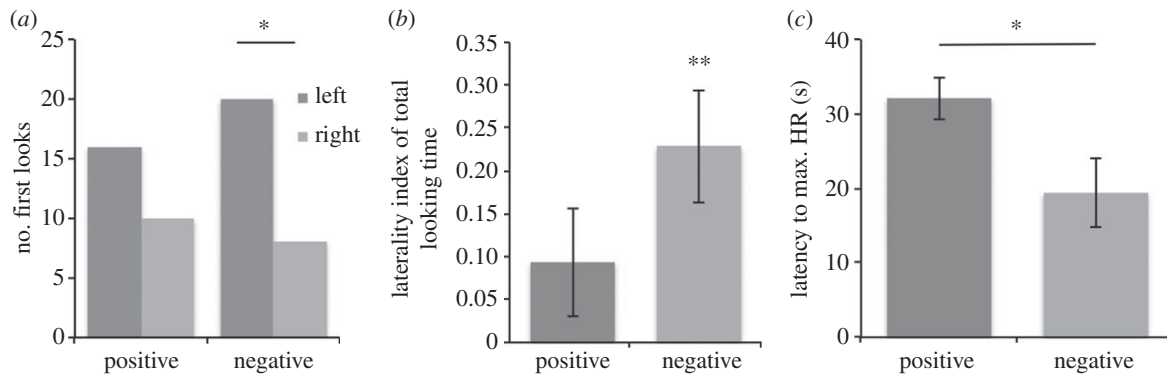


Figure 2. (a) Frequencies of first look direction by emotion; (b) mean laterality index by emotion (± 1 s.e.m.); (c) median time taken to reach maximum HR during test ($\pm 95\%$ CI). There were no significant differences in looking durations when the valences were directly compared, $t_{27} = -1.49$, $p = 0.15$ (paired-samples t -test, two-tailed). * $p > 0.05$, ** $p > 0.01$.

When viewing negative stimuli, more horses looked left for their first monocular look than right ($n = 28$, $K = 20$, $p = 0.036$). There was also a left-gaze bias in total looking time (laterality index) ($M = 0.23$, s.e.m. = 0.07), $t_{27} = 3.49$, $p = 0.002$. There were no laterality effects in responses to positive stimuli either in first monocular look ($n = 26$, $K = 16$, $p = 0.33$), or in total looking time ($M = 0.09$, s.e.m. = 0.063), $t_{27} = 1.48$, $p = 0.15$ (figure 2).

There were no significant differences in approach duration to positive versus negative stimuli (positive, Mdn = 0.48, CI ± 1.58 ; negative, Mdn = 0.00, CI ± 1.27), $z = -0.97$, $p = 0.33$, nor in avoidance duration (negative, Mdn = 2.9, CI ± 1.23 ; positive, Mdn = 1.14, CI ± 1.38), $z = -1.03$, $p = 0.30$ (Wilcoxon's tests, two-tailed). However, time spent looking left was positively correlated with time spent avoiding, $r = 0.37$, $p = 0.005$, but not time spent approaching, $r = -0.12$, $p = 0.37$, while time spent looking right was not correlated with avoidance, $r = -0.003$, $p = 0.99$, nor approach, $r = 0.16$, $p = 0.23$ (Spearman's ρ).

More stress-related behaviours were observed towards negative compared with positive stimuli; however, the number of incidences was relatively small and statistical analyses lacked power (see the electronic supplementary material for details).

(b) Heart rate

From the start of the test phase, the horses' HRs rose significantly faster when exposed to negative (Mdn = 19.4, CI ± 6.50) compared with positive (Mdn = 32.1, CI ± 4.01) stimuli, $z = -2.20$, $p = 0.028$ (figure 2; Wilcoxon's test, two-tailed). However, horses' average HR change between baseline and test, absolute maximum HR, and recovery time were not significantly affected by emotion (HR change: $z = -0.54$, $p = 0.59$; maximum HR: $z = -0.26$, $p = 0.80$; recovery time: $z = -1.22$, $p = 0.22$, Wilcoxon's tests, two-tailed; see the electronic supplementary material table SIV). Finally, the mean HR difference between test and baseline was positively correlated with the laterality index, $r = 0.34$, $p = 0.047$, and avoidance time, $r = 0.58$, $p > 0.001$ (Spearman's ρ).

4. Discussion

The behavioural and physiological results reported here support the hypothesis that horses are able to recognize and respond in a functionally relevant way to heterospecific

(human) facial expressions of anger. Horses demonstrated right-hemispheric biases towards angry stimuli (preferentially viewing images with the left eye), which were positively correlated with both avoidance duration and mean increase in HR; further, horses displayed a faster overall increase in HR to angry compared with happy stimuli. There were also non-significant trends to perform more stress-related behaviours towards angry stimuli. These findings raise interesting questions about the nature of emotional expression recognition, including the relative roles of learning and innate skills in its development.

There are numerous possible explanations for the emergence of horses' abilities to discriminate particular human facial expressions. Horses may have adapted a pre-existing (ancestral) ability to respond appropriately to the negative emotional expressions of conspecifics and, throughout their coevolution with humans, transferred this ability onto a morphologically different species. Alternatively, individuals may have to learn to interpret human expressions during their lifetime experience with humans. In support of the latter argument, familiarity is found to be a significant factor in dogs' recognition of human expressions; they perform better when faced with their owners [13] or with people of the same gender as their owners [4], suggesting that lifetime experience has a significant role in shaping this ability. To elucidate the evolutionary and ontogenetic mechanisms involved, the responses of species and individuals with varying degrees of human exposure should be compared.

Horses' right-hemispheric bias towards negative human facial expressions was expected on the basis of previous literature [7,8] and is also observed in dogs [5]. However, the lack of a lateralized response to positive expressions in our study is more difficult to interpret. This is also seen in dogs and may be because positive stimuli are less salient. The recognition of negative stimuli has particular functional relevance, as it allows individuals to anticipate potential negative consequences (e.g. rough handling, punishment). Alternatively, in this study, horses may not perceive either stimulus as overtly positive owing to the unfamiliarity of the humans depicted in stimuli and of the experimental set-up. It is also notable that in our experiments, the photographic stimuli were of two unfamiliar males. The generality of our findings could be further investigated through future studies into the particular effects of identity, familiarity, age and gender on abilities to discriminate a range of emotional expressions.

5. Conclusion

Here we report the first evidence of horses' abilities to spontaneously discriminate, both behaviourally and physiologically, between positive and negative human facial expressions, and the first evidence of heterospecific facial expressions of emotion affecting a species' HR. This raises intriguing questions about the flexibility and adaptability of emotional perception in this context, the potential role of experience, and the possibility of a generalizable, conserved and widespread ability to read emotional cues across species.

Ethics. This research adheres to the Association for the Study of Animal Behaviour (ASAB) guidelines and was approved by the University of Sussex Ethical Review Committee (ERC), reference number: Non-ASPA 3—January 14. Written consent to publish was obtained from both models presented in the stimuli (figure 1a).

Data accessibility. Raw data have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.2m6t6>.

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