



Research

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Animal behaviour

A horse's eye view: size and shape discrimination compared with other mammals

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Mammals have adapted to a variety of natural environments from underwater to aerial and these different adaptations have affected their specific perceptive and cognitive abilities. This study used a computer-controlled touchscreen system to examine the visual discrimination abilities of horses, particularly regarding size and shape, and compared the results with those from chimpanzee, human and dolphin studies. Horses were able to discriminate a difference of 14% in circle size but showed worse discrimination thresholds than chimpanzees and humans; these differences cannot be explained by visual acuity. Furthermore, the present findings indicate that all species use length cues rather than area cues to discriminate size. In terms of shape discrimination, horses exhibited perceptual similarities among shapes with curvatures, vertical/horizontal lines and diagonal lines, and the relative contributions of each feature to perceptual similarity in horses differed from those for chimpanzees, humans and dolphins. Horses pay more attention to local components than to global shapes.

1. Introduction

Currently, there are more than 5400 species of mammals on Earth [1]. Although the visual modality is dominant in some mammal species, the specific environmental adaptations of each type of mammal have had a significant influence on their visual perception and cognition. Visual perception and cognition have been intensively examined in primate species, but not so many studies have investigated this topic in other mammals. Recently, however, there has been an increase in the investigation of social intelligence in non-primate mammals such as dogs, elephants and horses [2–4]. To evaluate these studies within the framework of comparative cognitive science more appropriately, the basic abilities of these mammals to perceive their surrounding worlds need to be clarified. For example, horses have adapted to terrestrial environments by developing a very wide visual field owing to the lateral location of their eyes, and these anatomical characteristics may have affected their visual perception abilities. However, only a few studies have investigated visual perception in horses [5–8], and many issues remain to be addressed [8]. In this study, a computer-controlled touchscreen system was introduced to horses to investigate the visual size discrimination and shape perception abilities of these animals; the results were compared with those of other mammals that have adapted to different environments, including chimpanzees, humans and dolphins [9].

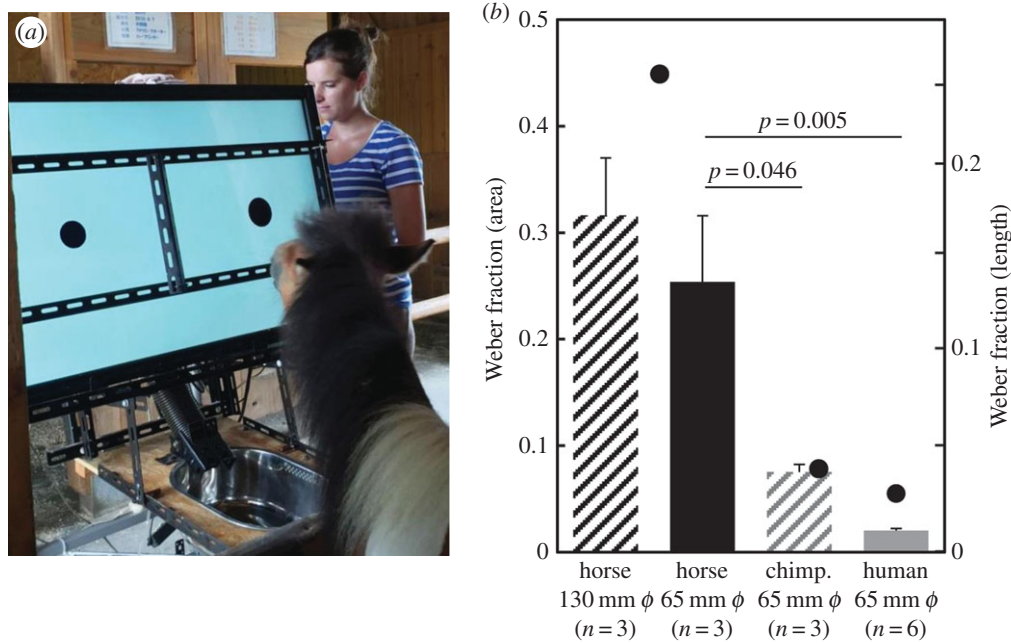


Figure 1. (a) A female horse, Nemo, performs the size discrimination task. (b) Mean Weber fractions for each species. Error bars show the standard deviations and the black circles show the Weber fractions for line lengths from previous studies [6,11,12]. (Online version in colour.)

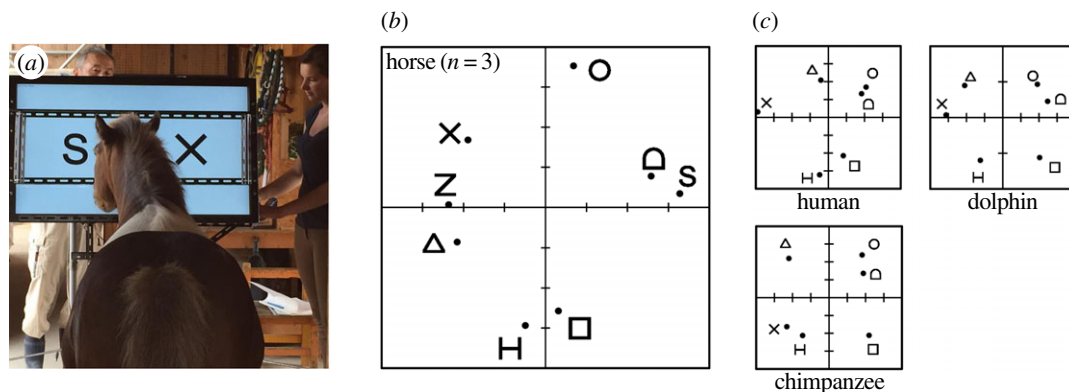


Figure 2. (a) A female horse, Ponyo, performs the shape discrimination task. (b) Two-dimensional solutions of the MDS for the horses. (c) Two-dimensional solutions of the MDS for humans, chimpanzees and bottlenose dolphins based on data from previous studies [9]. (Online version in colour.)

2. Methods

A detailed description of the methods and results of this study is provided in the electronic supplementary material.

(a) Participants

Three domestic horses (pony, *Equus caballus*) in a horse-riding facility participated in the present experiments. Three chimpanzees (*Pan troglodytes*) participated in previous experiments [9]. The chimpanzees lived with a social group of 13 individuals (including themselves) indoors and in an environmentally enriched outdoor compound (770 m²) at the Primate Research Institute at Kyoto University (KUPRI) in Japan [10]. Six adults with normal or corrected-to-normal vision participated in the human experiments.

(b) Apparatus

The horses were introduced to a 42-inch LCD touchscreen monitor installed on a portable stand. On each experimental day, the stand was set in front of the horse stalls (figures 1a and 2a) at a viewing distance of approximately 30–40 cm. All equipment and experimental procedures were controlled by a laptop personal computer (PC). The chimpanzees performed the experimental

procedures in an experimental booth that included a 17-inch LCD touchscreen monitor that was controlled by a PC. The human experiments were also conducted in this booth.

(c) Size discrimination

After completing a pre-training period, each horse performed a task that required discrimination of the sizes of black circles. Each session consisted of 12 trials in which the horses were required to touch the larger of two circles (figure 1a). Using a modified version of the up–down method, the discrimination threshold (difference limen, DL) for the circle sizes was assessed [13]. Based on session-based accuracy measures, the size of the smaller circle was changed from session to session by maintaining the accuracy rate at 70.8%, and the data from the 12 criterial sessions in which performance was stable were used to calculate the DL. Additionally, the horses were given two sets of standard circles with different diameter lengths (130 and 65 mm). The DL values were calculated based on the area and length differences between the two stimuli. The three chimpanzees performed the circle size discrimination task (standard = 65 mm) using the same testing procedure. The human participants completed a single session of 100 trials using the modified up–down method but, unlike for horses and chimpanzees, the DL was calculated based on trial-by-trial accuracy.

(d) Shape discrimination

The horses also performed a shape discrimination task using eight geometrical shapes (figure 2*a,b*). They were initially trained to discriminate between O (positive stimulus) and X (negative stimulus) and then they were given test pairs of stimuli in which the negative stimulus was replaced with another stimulus session by session. Each test pair was repeated for four sessions, and then the baseline pair was changed. There were seven baseline–test pairs in which the X was always the negative stimulus of the baseline pairs. Based on the accuracy data for all 28 pairs, multidimensional scaling (MDS) analyses were conducted to visualize the perceptual similarities in the two-dimensional space. To compare the data from the horses with those of the other species, the perceptual similarity data from the chimpanzees, humans and bottlenose dolphins obtained previously [9] were reanalysed. Of the nine stimuli used in this study, the six stimuli that were common to the tasks for all the species in both studies were used to conduct MDS analyses to obtain the two-dimensional solutions for each species.

3. Results and discussion

(a) Size discrimination

Figure 1*b* depicts the mean Weber fractions based on area and diameter length (DL divided by standard size) for each species. The DL of the horses was significantly worse than those of the chimpanzees and humans (statistical significance tests based on 10 000 bootstrap samples; horse versus chimpanzee, $p = 0.046$; horse versus human, $p = 0.005$; correction based on the false discovery rate set at 0.05). One possible reason for the high DL of the horses might be their visual acuity. The best reported visual acuity for horses is 23.3 cycles per degree [5], indicating that a horse can discriminate a difference of 0.15 mm from a viewing distance of 40 cm. However, the Weber fraction based on diameter length was 0.137 for the second set of experiments, which was much worse than expected based on the reported visual acuity of horses. It is also possible that there are differences in performance and motivational levels among the species. As shown in figure 1*b*, the Weber fractions of the horses were better for the second set of experiments than for the first set, which suggests that if they were trained for a longer period with more sessions the DL values would have been much lower.

To examine whether area or length was more critical for the discrimination, the Weber fractions for length were compared with those from previous studies that investigated the discrimination of line lengths among various species [6,11,12]. The estimated fractions for length from these studies are plotted in figure 1*b* as filled black circles. The data from chimpanzees and humans in this study can be more readily explained by the DLs based on length rather than area. Overall, this study found that all three species relied on diameter length rather than on area to discriminate the circles.

(b) Shape discrimination

Based on the MDS results, the horses performed similarly to each other (intra-class correlation coefficient, $ICC_{2,3} = 0.783$, $p < 0.001$; figure 2*b*). The spatial distance of the stimuli in the two-dimensional space of figure 2*b* depicts the perceptual similarities. There were three distinct perceptual categories for the horses: shapes with curvature, shapes made of only vertical and horizontal lines, and shapes including diagonal lines. Figure 2*c* depicts the MDS results of previous studies

[9]; the data for the four different species were moderately similar to each other and the ICC was significantly above 0 ($ICC_{2,4} = 0.565$, $p = 0.019$).

In general, the horses showed similar tendencies to the other species, but more detailed analyses revealed several differences among the species. To evaluate the species differences in perceptual categorization, the relative contributions of specific features to the perceptual similarities were further analysed [9]. Each shape contained various elementary features and, of these, six were selected for the analyses: vertical/horizontal line, curvature, diagonal line, closure, right angle and open end. Using the error-rate data from the horses in the present experiment and the data from previous experiments investigating dolphins, chimpanzees and humans, the standardized similarities of the shapes that shared each feature were calculated and compared among the species. Significance tests based on 10 000 bootstrap samples conducted for each feature category revealed that shapes with open ends (e.g. X and H) were more closely categorized by chimpanzees than by humans ($p < 0.001$) and horses ($p = 0.015$), shapes with diagonal lines (e.g. X, Z and triangle) were perceived as more similar by horses than by chimpanzees ($p = 0.008$) and humans ($p = 0.026$), shapes with right angles were less closely categorized by horses ($p = 0.031$) than by chimpanzees and humans ($p = 0.027$), and closed shapes (e.g. O, D, square and triangle) were less closely categorized by horses than by humans ($p = 0.002$, all p -values were corrected based on the false recovery rate). Additionally, the present findings suggest that the horses had a tendency to pay more attention to local components than global shapes, which is consistent with previous studies of nonhuman animals [14–16].

4. Conclusion

To the best of our knowledge, this study is the first to investigate horse perception and cognition using a touchscreen system and to demonstrate successfully the utility of this system for this particular species. This study assessed the ability of horses to discriminate sizes and shapes and compared these results with those from previous studies for other mammals that have adapted to different environments. The results clearly show both similarities and differences among the species, such as more reliance on local features in horses. We need to further investigate those similarities and differences from the standpoint of phylogenetic constraints and adaptation to specific environments, such as spatial anisotropy of visual perception and cognition. In this study, we tested only three ponies, thus we need to test more ponies to verify the generality of our results. Furthermore, it is highly plausible that there are some differences in visual perception and cognition among horse breeds. Using the present experimental settings, it will be further possible to compare these findings directly with those for other horse breeds as well as those for other species.

Ethics. The experimental procedures used to assess the horses and chimpanzees in this study were approved by the Animal Welfare and Animal Care Committee of KUPRI and by the Animal Research Committee of Kyoto University (no. 2015-134 and no. 2015-044). All procedures adhered to the Japanese Act on the Welfare and Management of Animals. The experimental procedure for humans was approved by the Human Research Ethics Committee of KUPRI (no. 2015-05). Informed consent was obtained from all human participants prior to experiments.

Data accessibility. All supplementary data are available on Dryad.

Authors' contributions. M.T., C.P. and T.M. conceived and designed the experiments, and M.T., K.K., S.N. and F.C. performed the experiments. M.T. and F.C. analysed the data, M.T. wrote the manuscript. All authors approved the final version and agreed to be accountable for all aspects of the work.

Competing interests. The authors declare that they have no competing interests.

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