Faculty of Science and Engineering

School of Biological and Marine Sciences

2023-03-02

# Do you see what I see? Testing horses' ability to recognise real-life objects from 2D computer projections

# Kappel, Sarah

https://pearl.plymouth.ac.uk/handle/10026.1/21003

10.1007/s10071-023-01761-6 Animal Cognition Springer Science and Business Media LLC

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

- 1 Do you see what I see? Testing horses' ability to recognise real-life objects from 2D computer projections
- 2 Sarah Kappel<sup>1</sup>, Marco A Ramirez Montes De Oca<sup>2</sup>, Sarah Collins<sup>1</sup>, Katherine Herborn<sup>1</sup>, Mike Mendl<sup>2</sup> and Carole
- 3 Fureix<sup>1,2</sup>
- 4 <sup>1</sup>University of Plymouth, School of Biological and Marine Sciences, Portland Square, Drake Circus, Plymouth,
- 5 PL4 8AA, UK
- 6 <sup>2</sup>University of Bristol, Bristol Veterinary School, Langford house, BS40 5DU Langford, UK
- 7 Corresponding author: Sarah Kappel sarah.kappel@plymouth.ac.uk
- 8

# 9 Abstract

10 The use of 2-dimensional representations (e.g. photographs or digital images) of real-life physical objects has 11 been an important tool in studies of animal cognition. Horses are reported to recognise objects and individuals 12 (conspecifics and humans) from printed photographs, but it is unclear whether image recognition is also true for 13 digital images, e.g. computer projections. We expected that horses trained to discriminate between two real-life 14 objects would show the same learnt response to digital images of these objects indicating that the images were 15 perceived as objects, or representations of such. Riding-school horses (N=27) learnt to touch one of two objects 16 (target object counterbalanced between horses) to instantly receive a food reward. After discrimination learning 17 (three consecutive sessions of 8/10 correct trials), horses were immediately tested with on-screen images of the 18 objects over 10 image trials interspersed with five real object trials. At first image presentation, all but two horses 19 spontaneously responded to the images with the learnt behaviour by contacting one of the two images, but the 20 number of horses touching the correct image was not different from chance (14/27 horses, p>0.05). Only one 21 horse touched the correct image above chance level across 10 image trials. (9/10 correct responses, p = 0.021). 22 Our findings thus question whether horses recognise real-life objects from digital images. We discuss how 23 methodological factors and individual differences (*i.e.* age, welfare state) might have influenced animals' response 24 to the images, and the importance of validating the suitability of stimuli of this kind for cognitive studies in horses.

25

26 Keywords: image recognition, horse cognition, individual cognitive performance, equines

# 27 1. Introduction

28 Visual 2-dimensional representations (e.g. printed photos, digital images, silhouettes, videos) are used as 29 substitutes for real-life objects, or individuals, in cognition studies of non-human animals, including horses. 30 Screen-displayed visuals are of advantage in research as stimulus timing and presentation of identical stimuli can 31 be repeatedly presented to the same or to different subject animals (D'Eath 1998). However, scientific evidence 32 of object-image recognition in animals is not always consistent (reviewed in Fagot 2000; Bovet and Vauclair 33 2000; Weisman and Spetch 2010). This might be because pictures designed for the human eye may not result in 34 the same sensory experiences in other species with different functional visual systems (Fagot and Parron 2010; 35 Weisman and Spetch 2010). Moreover, how images are perceived and cognitively processed is not fully 36 understood for most animal species (Fagot 2000; Fagot et al. 2010). For instance, Fagot et al. (2010) proposed 37 that animals could 'read' images using different processing modes. In a mode of confusion, images and their real-38 life exemplars are perceived and treated as functionally and physically the same thing. Conversely, in a mode of 39 independence, images could be perceived as different from their referents without making an association between 40 objects and their images. In a processing mode of equivalence, images are understood as representations of their 41 referents (i.e. images are used as referential cues for real-life objects, Fagot 2000; Fagot et al. 2010).

42 A variety of factors, including cognitive limitations or experience with images, could influence which processing 43 mode is deployed by animals and ultimately lead to differences in how images are treated by humans and other 44 animal species (Fagot and Parron 2010). Therefore, the suitability of artificial representations (*e.g.* digital images, 45 videos) for animal studies is likely to depend on the purpose of the stimuli. For instance, if images are used to 46 imitate real stimuli in behavioural experiments, animals need to respond to images in a comparable way to how 47 they respond to real stimuli (D'Eath 1998).

Investigating image recognition is challenging because pictures can never be identical to their 3D referents given the lack of dimensionality, depth cues and olfactory characteristics, which results in substantial sensory differences between objects and their 2D imitations (Bovet and Vauclair 2000; Aust and Huber 2006). Prior to image processing, the perceptual abilities of the viewer also need to be considered, for instance, whether an animal is able to identify an object from an image despite the lack of depth cues or additional cues (*e.g.* reflectance of photographic surface, Fagot and Parron 2010).

54 Unlike in humans, the visual field of horses is mainly monocular (*i.e.* visual input is received from just one eye,
55 (Waring 2003). Binocular vision allowing depth perception is only possible within a relative small area in front
56 of the horses' head (55°- 65°; Hughes 1977) extending downwards along the midsagittal plane (the vertical axis

57 dividing the head in left/right) at approximately 75°, enabling horses to view the ground in front of them with 58 both eyes (Duke-Elder 1958). A blind spot interrupts the almost panoramic visual field in front of the horses' 59 forehead (Waring 2003). In addition, visual acuity is much poorer in horses compared to most other terrestrial 60 mammals (Rørvang et al. 2020). Horses have dichromatic vision resulting in similar colour perception to humans 61 affected by red-green blindness (Hanggi et al. 2007). However, equine vision is highly adapted to low-light 62 conditions with a high ratio of rods to cones and a reflecting tapetum lucidum enabling scotopic vision (*i.e.* ability 63 to see under low light conditions) superior to that of humans (Hanggi and Ingersoll 2009a). Given these visual 64 differences, it appears that humans and horses see the world differently (Saslow 2002). This raises the question 65 of whether artificial stimuli such as digital images generated through computer projections are suitable 66 representations of real-life objects for horses and other ungulate species sharing these traits (e.g. cattle, goats, 67 sheep; Jacobs et al. 1998). Hence, further validation whether horses recognise the content of digital stimuli is 68 necessary.

69 Generally, two different experimental approaches are applied to test image recognition in animals (reviewed in 70 Bovet and Vauclair 2000; Weisman and Spetch 2010). For one, animals' spontaneous responses to artificial 71 representations of biologically relevant stimuli (e.g. photos of food, prey, predator or conspecifics) is tested as an 72 indication of direct transfer (i.e. images are treated as the same as objects). In this case, the same adaptive 73 behaviour is provoked by the artificial representations as if the real referent was present (Bovet and Vauclair 2000; 74 Weisman and Spetch 2010). A study in sheep, another ungulate species, found that animals respond to the image 75 of a sheep with species-specific social behaviour (e.g. sniffing of the anogenital region and the head) and the sheep 76 image appears to have fear-reducing effects on socially isolated sheep comparable to the presence of real 77 conspecifics (Vandenheede and Bouissou 1994). Interestingly, a human image did not result in the same fear 78 response as elicited by a real human, suggesting that different stimuli types may be processed differently by sheep 79 (*i.e.* sheep image possibly confused with a real sheep whereas the human images was not treated as a substitute; 80 Vandenheede and Bouissou 1994). Horses also respond to 2D and 3D horse imitations (photograph, life-size 81 model) with sniffing behaviour near the head and flank areas corresponding to their natural approach of 82 conspecifics, while an incomplete horse drawing and a dog image were not approached (Grzimek 1943). These 83 observations might suggest that horses are able to recognise conspecifics based on specific cues, such as social 84 cues conveyed by a near-realistic 3D model and photograph but not a drawing. However, approach and sniffing 85 behaviours are also associated with exploration meaning that using explorative responses as outcome measures is 86 not specific to image recognition alone and could result from other motivations, such as gathering novel

87 information. Similar reasoning may apply to other studies that use spontaneous approach behaviours to indicate
88 image recognition in horses (*e.g.* Smith et al. 2016; Wathan et al. 2016). Physiological changes (mean heart rate)
89 measured alongside horse behaviour were interpreted by the authors as support for horses' ability to differentiate
90 between emotional stimuli, although cross-validation through multiple physiological measure (*e.g.* HRV indices
91 to infer autonomic response; von Borell et al. 2007) could have strengthened these findings even more.

92 An alternative to the above-described adaptive behaviour responses is studying animals' ability to transfer 93 acquired (operant) responses associated with real life objects to their pictorial representations (Bovet and Vauclair 94 2000). For example, Cabe (1976) trained pigeons to discriminate between two solid objects (one rectangular block 95 and a cross) by pecking the rewarded stimulus. The birds spontaneously transferred the learnt discrimination rule 96 when the objects were replaced by pictorial representations (e.g. black-and-white photographs, white-on-black 97 silhouettes) demonstrating that pigeons are able to recognise objects from images (Cabe 1976). Using a similar 98 approach, Hanggi (2001) reported that, after multiple presentations, horses (N=2) were able to transfer a learnt 99 behaviour (contact object with nose for food) from real objects (various toys varying in colour, shape and size) to 100 their pictures, indicating image recognition. However, the ability to categorise images does not automatically 101 provide evidence of representational insight (i.e. the subject understands what the image stands for; Aust and 102 Huber 2006). The horses might have learnt to discriminate between the images during repeated testing, e.g. based 103 on invariant features between images (e.g. colour, shapes, or distribution of light/dark patterns) unrelated to the 104 real objects. According to the author, this explanation seems unlikely given the large number and diversity of 105 objects tested (Hanggi 2001). However, the same two horses were previously reported to understand shared 106 characteristics between stimuli (pattern rules; (Hanggi 1999), indicating their ability of categorisation learning, 107 which one animal was reported to still remember several years later (Hanggi and Ingersoll 2009b).

108 Experimental biases and ambiguity of outcome measures can further hamper the validity of image recognition 109 evidence. For instance, it has been reported that horses can recognise humans from images because they were not 110 only able to differentiate between happy and angry human faces, but also appear to possess emotional memory 111 (Proops et al. 2018). Horses were described as reacting "appropriately" following the theory of emotional 112 lateralisation (*i.e.* left-eye bias for humans with angry faces and more time engaging in stress-related displacement 113 behaviours) when encountering the real human hours after they had seen a photo of the same person displaying 114 an angry face. Another study suggested that horses have the ability to cross-modally recognise the emotional states 115 of familiar caretakers and stranger when presented with on-screen image of human faces and voice recordings 116 (Nakamura et al. 2018). However, due to experimental limitations (e.g. in Proops et al. (2018), horses were kept 117 in different conditions between tests, non-specificity of response behaviours (e.g. scratching, floor sniffing; these 118 activities that are also expressed in other contexts (Waring 2003)) and statistical weakness (e.g. no control 119 conditions), the robustness of these findings has been questioned (Amici 2019). Moreover, inferring evidence of 120 recognition from emotional responses might not be straightforward in absence of control (*i.e.* non-emotional) 121 comparisons. Hence, it is possible that the horses' response could have been associated with image-inherited cues 122 unrelated to the emotional image content (e.g. image colours, brightness or contrast). The study by Lansade et al. 123 (2020a) reduced experimental biases by training horses first to reliably select a screen image showing one of four 124 human faces instead of images of objects (novel objects differing on each trial), thereby priming horses to respond 125 to content-specific information. The horses significantly discriminated between the familiar faces and a novel 126 face. When a photo of the horses' keeper replaced the training faces, the animals again selected the keeper image 127 at above chance level suggesting that the keepers' faces were also identified as familiar. Alternatively, the keeper 128 images might have been more similar to each of the training images than the novel images. In a follow-up study using on-screen images, Lansade et al. (2020b) controlled for this and found that horses can reliably select familiar 129 130 faces paired against unfamiliar faces, despite removing photo colour, external cues (hairstyle), or facial features 131 (eyes).

132 Overall, given a variety of experimental difficulties in this area, there is still a need for further evidence of the 133 ability of horses to recognise the content of screen images and their relationship with real-life objects. The 134 motivation of this study was therefore to test if horses spontaneously respond to digital images of two real-life 135 objects, which they had previously learnt to discriminate. We predicted that horses would touch the images of the 136 correct (rewarded) object at a level above chance if they recognised the images as real objects or representations 137 of such. We only tested horses' transfer ability from real-life objects to on-screen images, and not the reverse (i.e. 138 training horses with images to test discrimination with their real-life counterparts), to gain evidence that digital 139 images are suitable stimuli for cognitive tests in this species. For this, we developed relative simple and practical 140 testing approach. For the same reason, we only used two real-life objects.

Animals' performance in cognitive tests can be influenced by individual characteristics, including personality (Carere and Locurto 2011; Dougherty and Guillette 2018), learning speed, and motivation to engage in the task (reviewed in Rowe and Healy 2014). In horses, age (Krueger et al. 2014), sex (Murphy et al. 2004), but also emotional state (Christensen et al. 2012; Valenchon et al. 2013), and welfare status (reviewed in Hausberger et al. 2019) have been identified as sources of individual variation in cognitive performance. Therefore, we tested each horse in a total of 10 trials and assessed the effects of intrinsic (*i.e.* age, welfare score) and experimental factors
(*e.g.* type of target, trial order, facility) on horses' performance.

148

#### 149 2. Methods

# 150 2.1. Ethical statement

This study was approved by the Animal Welfare and Ethical Review Body of the University of Plymouth (ETHICS-41-2020). The experimental procedure complied with the UK Animals (Scientific Procedures) Act 1986 (ASPA) and followed the ARRIVE guidelines 2.0. The horses belonged to two UK riding schools who consented the use of their animals. Housing, care and health check was provided by the riding schools. The animals remained at their home facility at the end of the study, except one horse that was relocated during our data collection for reasons not related to this study. Horses that did not learn the object discrimination in stage 1 were excluded from the object recognition test in stage 2.

158

# 159 2.2. Animals and housing

160 In total, 36 horses of mixed breeds from two UK riding schools (yard A: N=17, mean  $\pm$  SD age 10.6  $\pm$  2.5 years; 161 yard B: N=19, 16.6  $\pm$  6.5 years, of which three animals did not complete training at this yard as one was relocated 162 and two became aggressive towards nearby conspecifics during training) were trained in an object discrimination 163 test (ODT, stage 1). All horses that completed stage 1 (*i.e.* discrimination between the real objects; N=28) were 164 tested in the on-screen object recognition test (ORT, stage 2). However, one horse was scared of the test setup and 165 was therefore excluded from testing, resulting in a total of 27 horses (16 from yard A of which 6 were females, 11 from yard B of which 4 were females) used in the ORT. The horses were used in riding lessons approx. 3-7h 166 per week. In both facilities, horses were kept in single stalls, or tie-stalls, with full, or limited visual/physical 167 168 contact to conspecifics during daytime (details of horses in Supplementary Information, Table 1). All horses had 169 pasture access (in stable groups) at night and/or during parts of the day. Hay provision was restricted (i.e. facilities 170 adjusted hay allowance based on body weight), and horses received an additional adjusted diet (at yard B, brand 171 Thunderbrook Equestrian), or not (at yard A where horses were "on a diet" due to the lowered workload associated 172 with COVID-19 restrictions). Water was freely accessible through automatic troughs in yard A and provided with 173 water buckets in yard B.

174

175 *2.3.* Experimental design

176 The experimental design consisted of two stages summarised in Fig. 1. In stage 1, the horses were trained to 177 discriminate between two real objects by touching the rewarded (target) object with their muzzle in order to 178 receive a food reward before their spontaneous response to on-screen images was tested in stage 2.

- 179
- 180

# 2.3.1. Object discrimination – stage 1

181 All horses were first trained inside their stall by a single familiar person (experimenter SK) to respond to the real 182 objects and discriminate between the target (rewarded) and an unrewarded object. The horses were able to move 183 around freely (although six horses at yard B were tethered as they were kept in tie-stalls). Two objects (kong<sup>TM</sup>: 184 red dog toy, Ø 10cm, length 16cm; ring: doughnut-shaped dog toy, Ø 20cm, depth 4cm, with dark and light blue 185 stripes, see Fig. 1) used as target objects were mounted onto a 50 cm wooden stick to facilitate the presentation of 186 the objects in different positions and at distance to the experimenter. Which object a horse received as *target* 187 (rewarded object) was pseudo-randomly allocated, ensuring that the numbers of horses trained with the same 188 target was evenly distributed across yards. As only horses that completed ODT and learnt the discrimination 189 within the 5 training sessions were used in ORT, the final number of horses tested in ORT with the ring and 190 kong<sup>TM</sup> as target object was 11 and 16, respectively.

191 The first training step consisted of shaping horses' **response to the target object** using instrumental conditioning. 192 The experimenter moved toward the horses' shoulder (whichever side that was most accessible) hiding the target 193 behind her back. Standing at the shoulder height, she then slowly moved the object into view for the horse and 194 held the target at approx. 20-30cm from the horses' muzzle (approx. 1.0 - 1.2m above the ground depending on 195 horses' height). The horse could voluntarily move towards the object and contact with the object was never forced. 196 Upon the first voluntary contact, the horse was instantly rewarded with a piece of carrot retrieved from a treat bag 197 attached to the experimenter's waist at her back. At the same time, the target was moved behind the experimenter's 198 back. Within 5s of rewarding the horse, the same motion of moving the target near the horses' muzzle was repeated 199 and the horse was instantly rewarded upon voluntary contact. All contacts with the object only (regardless of 200 where on the object and with which part of the muzzle) were rewarded. The target training was repeated for 10 201 consecutive trials. The experimenter then left the stall to refill the treat bag again with 10 pieces of carrots and 202 repeated this training step so that each horse received a total of 20 single target trials.

After a 2-min break, 10 single target trials were conducted again to remind the horses of the correct (familiar)
target before a second unfamiliar object was introduced. The experimenter followed the same procedure as before
to present the objects, except that now two objects were shown to the horses simultaneously for object

206 **discrimination** training (**ODT**, see Fig.1A). For this, the experimenter moved both objects simultaneously from 207 behind her back to in front of the horses' head holding each object by its handle in one hand at approx. 1.0-1.2m 208 above the ground and with objects separated approx. 0.4-0.6m. If horses touched the unrewarded object, the 209 objects were shortly moved behind the experimenter's back for 5s time-out before starting a new trial. If the 210 unrewarded object was consecutively touched over three trials, the experimenter only presented the target to the 211 horse (to remind it of the target, and guarantee that the horse received a reward and maintained motivation). The 212 number of these *forced* trials was not recorded as this occurred rarely. If a horse did not touch any objects within 213 30s, this response was regarded as incorrect, and a new trial was started. On each trial, the experimenter slightly 214 altered her position relative to the horse, in which location and side, from the horses' perspective, the objects were 215 shown, and alternated the hand used to reward the horse. These changes were done to avoid the horses develop 216 side biases, or learning by association which object to contact relative to the handler (e.g. always chose object in 217 experimenter's left hand). In addition, the side of object presentation was pseudo-randomly selected by the 218 experimenter with the same object never being presented on the same side more than twice during consecutively. 219 Depending on horse availability, each horse received a maximum of two ODT training sessions per day, each 220 comprising four trial blocks and 10 discrimination trials per block with 2min breaks between each block. Horses 221 were trained over a maximum of five sessions (equal to 200 discrimination trials in total), and with a maximum 222 of three days between sessions. Training of three horses at yard 2 was interrupted due to COVID-19 restrictions 223 and resumed 6 months later starting from ODT. For these horses, only trials conducted after the break were 224 included in the data analysis. Learning criterion (LC) required to move to stage 2 (testing) was defined as 225 performing eight or more correct responses per trial block over three consecutive trial blocks. The eight horses 226 that did not reach LC within five training sessions were not tested in stage 2.

227



# 2.3.2. Object recognition test - stage 2

Stage 2 consisted of the on-screen object **recognition** test (**ORT**) and was divided into three steps (see Fig.1B).
Pre-tests conducted in the horses' stall (step 1) and the test arena (step 2) using the real objects serving as verification of reliable discrimination performance before the horses were tested with images in the screen test (step 3).

233

**234** *2.3.2.1. Pre-test in stall* 

235 The horses first received 10 single target trials conducted by the experimenter in the horses' home stalls. A second 236 unfamiliar handler (MR) then entered the horses' stall alongside the experimenter to take hold of the lead rope, 237 hence mimicking the handler's presence later in the test stage. The handler stood next to the horses' left shoulder, 238 with his back turned to the horse and wearing noise-cancelling headphones to remain blinded to which of the two 239 objects was the target. The experimenter presented the two objects for 10 trials as done in the ODT, except that 240 the objects were now always presented in front of the horses' head at approx. 1–1.5m height, *i.e.* at similar position 241 as to where the images replacing the real object would later occur in the screen test. The handler's role was to 242 reward the horse as indicated by the experimenter (saying her name to indicate an incorrect response, or the 243 handlers' name to indicate a correct response) whilst remaining blind to the correct target to avoid any conscious 244 or unconscious signalling from the handler (*i.e.* 'clever Hans effects', Pfungst and Rahn 1911) during later stages 245 of testing. If the horse performed  $\geq 8$  correct responses out of 10 in the pre-test, it was immediately taken to the 246 test area for the screen test. Horses that did not perform as such were re-tested in the same manner after a break 247 (of varied duration for practical reasons, e.g. horse availability).

- 248
- 249

# 2.3.2.2. Pre-screen test (PST)

250 The horse was led into the test area (familiar indoor riding arena) where a back-projection polyvinyl chloride 251 screen (1.6m W x 2.5m H) was set up. A multi-coloured pole (normally used as training item and familiar to the 252 horse) serving as visual marker was placed on the ground directly in front of the screen at approx. 50cm distance 253 to indicate the position of the horse during testing. The horse was habituated to the screen (first turned off, then 254 turned on not showing any images) and test equipment until it stood calmly in front of the screen. The screen was 255 then turned off again and the handler positioned himself approx. 1m away from the ground pole by the horses' 256 left shoulder, turning his back towards the screen (position allowing him to stay blind to the images to be shown 257 in the next phase). The experimenter stood in front of the horse (between the ground pole and screen) towards the 258 right side of its head. She retrieved the real objects from a bucket and conducted 10 ODT trials following the same 259 procedure as during the pre-test in stall (i.e. the experimenter presented the objects and indicated to the blinded 260 handler when to give deliver the reward). This was done to test if the horse still discriminated between the real 261 objects in this different context (arena rather than stall). After five trials, the experiment briefly moved behind the

screen (out of view from the horse<sup>1</sup>) to habituate the horse to her movement and absence. After five seconds, she
 returned to her original position in front of the screen and conducted five more trials.

If the horse performed  $\geq 8$  correct responses out of 10, the experimenter stepped behind the screen to start the screen test. If the horse performed below this level, it was led around the arena for approx. 2min and the prescreen test was repeated. In total, horses received a maximum of six pre-screen tests, with a maximum of three daily (number derived from pilot observations where one horse needed six pre-screen tests to move to the screen test). All horses performed at the required criterion within six pre-screen tests.

- 269
- 270

#### 2.3.2.3. Screen test

271 In preparation for the screen test, each object was photographed three times using a Fujifilm X-T100 digital 272 camera (focal lens 23mm). Images were edited to remove the background so that only the object and wooden 273 handle were visible in the final images (see Fig.1). Three versions of computer presentations (Microsoft 274 PowerPoint) were created, each consisting of 10 stimulus slides. Each slide contained one image of each object 275 side-by side on white background. Within the three presentations, the location of target images was balanced (50% 276 left) and pseudo-randomised so that the target object was shown no more than twice in a row on the same side. 277 The order and side of images varied between the three presentations to control for order effects. Additionally, the 278 images were randomly rotated around their horizontal plane to change the position of the wooden handle. Later 279 on screen, the images were shown approx. 1.1-1.2m above the ground and at 0.5-0.7m distance from each other. 280 Each stimulus slide was preceded by a white blank slide, except for the slides prior to stimulus slides 4, 7 and 9, 281 which were black, indicating the points in the test at which real object trials were to be conducted (later described). 282 Each horse was tested with only one out of the three presentations (equally spread across tested horses). Which 283 presentation was projected was unknown to the experimenter at the time of testing, ensuring blindness to the target 284 location (since the only slide she saw when starting playing the presentation was a blank slide).

The screen test started immediately following the pre-screen test. The images were broadcasted from a laptop (Lenovo ThinkPad 13) *via* a LCD-projector (HITACHI CP-WX3030WN) placed at approx. 2.5m distance behind the screen. Standing next to the laptop, the experimenter used a remote control to start the slide show and advance the slides (thereby moving as little as possible to avoid any distracting noise). The first slide was blank but the experimenter advanced to the first stimulus slide as soon as the horses' head was straight in front of the screen

<sup>&</sup>lt;sup>1</sup> but the experimenter could observe the horse *via* a web cam connected to a computer (Lenovo ideapad) serving as monitor

290 (monitored via the web cam allowing to see the horse and the screen content). As soon as the horse contacted one 291 of the images, the stimulus slide was immediately advanced to the next blank slide. At the same time, the 292 experimenter indicated to the blind handler whether a reward should be delivered. A trial commenced as soon as 293 the horses' head was straight in front of the screen again resulting in variable inter-trial intervals. The stimulus 294 slides advanced automatically to the next blank slide after 20s if no contact was made. In case the horse moved 295 away from the screen immediately after trial onset (approx. within <2s after stimulus onset), the presentation was 296 moved to the previous blank slide and the trial repeated as soon as the horses' head was back in a straight position 297 in front of the screen.

298 In total, 10 trials with images were conducted, interspersed with real object trials (where the experimenter returned 299 to her position by the horse). Two object trials were conducted after image trial 3 and 6, and one object trial was 300 conducted after image trial 8 (i.e. five objects trials in total conducted during the screen test). The real object trials 301 were conducted as per the pre-screen test procedure, to remind the horses of the properties of the real objects, and to test whether they were still motivated to touch the objects, even if the images were not touched. To avoid that 302 303 horses learnt to respond to the images when contacting the correct picture, a partial rewarding schedule was 304 applied during the screen test (first and every third correct contact with the target image rewarded). Horses were 305 always rewarded if they contacted the correct object on real object trials. Following the last stimulus trial (trial 306 15), all horses received one last target trial (single object, not included in results) to ensure that all animals ended 307 the testing with a positive experience. Horse behaviour was recorded throughout with three GoPro cameras (Hero 308 3+), and number of correct responses later extracted from the videos. A second naïve coder analysed 30% of the 309 screen test videos, which were selected at random (using Excel random number generator and choosing the first 310 8 videos after sorting in ascending order). Inter-observer reliability (Cohen's kappa) for coding the response 311 behaviours was very high (0.94).

312

313 Fig.1 Experimental design A) 2-step objects discrimination training (ODT). Horses first learnt to contact a single 314 rewarded object (target) with their muzzle to receive food. A second (unrewarded) object was subsequently added 315 and horses trained to discriminate between both until it touched the correct object on  $\geq 8$  trials/10 over 3 316 consecutive 10-trials blocks. B) 3-step object recognition test (ORT). A pre-screen test was first conducted in the horse's stall. When  $\geq 8$  correct responses were performed, the horse was moved to the test arena (illustrated as 317 rectangle with dashed lines) and re-tested in a pre-screen test to ensure it performed reliably in the new 318 319 environment. When  $\geq 8$  correct responses were performed, the horse was immediately tested with images on the screen (indicated by rectangle with solid black lines). During the screen test, the horse was presented with the real 320 321 objects on five trials interspersed between the 10 image trials to test whether it was still motivated to touch the 322 objects, even if the images were not touched

323

**324** 2.4. Welfare assessment

Previous studies have suggested that welfare status can cause great individual variation in cognitive performance (reviewed in Hausberger et al. 2019). We therefore tested the effect of welfare condition, i.e. the level of provided environmental resources (*e.g.* stall space, pasture access), social factors (*e.g.* ability and stability of social contact) and animal-based measurements (including health indicators, workload, abnormal behaviour), putatively contributing to good horse welfare on learning ability and test performance.

The welfare assessment protocol was developed as part of another study (Kappel et al. *in prep*). Details to the protocol are provided in the Supplementary Information (Table 2). Briefly, for each factor, non-weighted numerical scores were given (0-1 indicating absence/presence of resource) and all scores combined to calculate an overall welfare score (maximum score was 20 with higher scores reflecting better welfare conditions).

334

#### **335** 2.5. Statistical analysis

Horses' responses to the objects/images were extracted from footage and coded as "correct" if the horses touched
the rewarded object/image, and "wrong" if the unrewarded object/image or if neither object/image was touched.
Hence, responses in trials where horses did not react to the stimuli were counted as "wrong" outcome.
Furthermore, the location (left/right) of the target image was recorded to assess side effects.

340 Data were analysed in R (R Core team 2021). Age and the welfare scores of horses between the yards were 341 compared using Wilcoxon rank sum tests. The number of trial blocks needed to reach learning criterion in ODT 342 was assessed as a measure of learning ability and followed a normal distribution (Shapiro- Wilk's test, p=0.09). 343 Thus the effect of fixed factors (*i.e.* yard, target) and covariates (*i.e.* age, welfare score) on learning ability were 344 assessed by fitting generalised linear models (glm() function with Gaussian distribution in lme4 package, Bates 345 et al.). Predictor covariance was check with the vif() function from the car package (Fox and Weisberg 2019), 346 which indicate that age co-varied with the other fixed factors (vif=7.08). The effect of age on learning ability was 347 therefore separately analysed using Pearson correlation test. Sex was not used as fixed factor given the unbalanced 348 number of females (n=10) and males (n=17) in the final sample of horses.

Indication of recognition ability at group level was assessed by measuring whether the number of horses responding correctly and incorrectly on trial 1 of the screen test was significantly different from random using a Chi-square test. To test if the proportion of correct responses performed at group level in each of the ORT tests (*i.e.* pre-test, pre-screen test and screen test) was better than chance, one-sample Wilcoxon tests were used. Whether proportions of correct responses differed between trials following real object trial and trials following image trial was tested with a Chi-square test. Likewise, we tested the effect of reward delivery (i.e. received orwithheld upon correct image contact) on subsequent trial performance using a Chi-square test.

356 Individual performance (correct/wrong response) during the 10 image trials was modelled using generalised linear

357 mixed models (GLMMs; glmer() function in lme4 package, binomial family) with target type (kong<sup>TM</sup>/ring), target

358 side (left/right), and trial order (after object/not after object) as categorical fixed factors, age and welfare score as

- 359 covariates, and horse ID as random factor. P-values were exacted via the anova() function from the car package
- and reported as significant for  $p \le 0.05$  and as trends for p < 0.1.
- 361

#### 362 **3. Results**

- **363** 3.1. Learning ability during object discrimination training
- In total, 27 horses (16 out of 17 at yard A, 11 out of 16 at yard B) learnt to discriminate between the two objects.
- 365 Overall, horses needed 11 trial blocks (median, Q1-Q3=7-15) to reach learning criterion. Learning ability was

predicted by target and yard, with horses from yard B (vs yard A) and those trained with the ring (vs with the

367 kong<sup>TM</sup>) needing more trials, but by not welfare level (see Table 1 for model estimates). Pearson correlation test

indicated a significant positive correlation between learning ability and age ( $t_{25}$ =4.09,  $r^2$ =0.63, p=0.0003). Horses

from yard A were significantly younger (mean±SD, 10.6±2.51; W=3950, p<0.0001) and had significantly lower</li>
welfare scores (14.1±1.30, W=4400, p<0.0001) than horses from yard B (age: 14.8±5.7, welfare score:</li>

- **371** 15.5±1.73).
- 372

Table 1 Estimated regression parameters from the GLM model. Learning ability (dependent variable) predicted
 by welfare score, yard and target type with information to the comparator category in square brackets. P-values
 ≤0.05 are highlighted in bold

Predictors	Estimates	Confidence Interval	P-value	
(Intercept)	1.08	0.98 - 1.20	0.146	
welfare score	1	1.00 - 1.01	0.326	
yard [B]	0.97	0.94 - 0.99	0.008	
target [ring]	0.96	0.94 - 0.99	0.005	
Observations	27			
$\mathbb{R}^2$	0.454			

377

378

379 3.2. Objects Recognition Test

380

3.2.1. Image recognition at first presentation

- When the horses were first presented with the images, 92.6 % of the horses (25/27) spontaneously reacted to the images as trained, *i.e.* by contacting one of the two objects' images with their nose. However, the number of horses responding correctly by touching the target image (n=14) was not significantly different from the number of horses responding incorrectly (combining the 11 horses that contacted the image of the unrewarded object, and the 2 horses that did not contact the screen at all;  $X_{1}^{2}=0.03$ , p=0.8).
- 386
- 387

# 3.2.2. Performance during the different stages of the ORT

388 Fig.2 shows the proportion of correct responses during the pre-test (PT) and pre-screen test (PST) leading up to 389 the screen test. Since all horses needed to perform at least 8 out of 10 responses in the PT to move on to the PST, 390 and in the PST to be tested with the images on screen (which all horses did, although some animals were re-tested 391 in PST, see Table 3 in Supplementary Information), the effect of fixed factors (*i.e.* target, age, welfare score) on 392 individual performance in the PT and PST tests was not further analysed. At group level, horses performed 393 significantly better than chance (50%, V=36585, p<0.0001, see Fig.2) in PT, PST (as required) and on object 394 trials, but significantly below this threshold during image trials (V=7340, p<0.0001). 395 Considering individual performance over the 10 image trials, one horse performed above chance level by selecting 396 the correct target images 9 times (p=0.021). Other horses (N=3) always contacted the correct image when making 397 contact with the screen, but failed to touch the images on other trials (two horses did not touch the screen on four 398 trials, one on two trials), and therefore were not considered to perform better than chance (6/10 and 8/10 correct, 399 both p>0.1). An overview of individuals' performance when omitting trials where horses did not make any image 400 contacts is provided in the Supplementary Information Table 4.

401

402 Fig. 2 Proportion of correct responses during each step of the object recognition test (ORT). The results of the 403 screen test are shown separately for the 10 images trials ('screen test (images)') and 5 real objects trials 404 interspersed between image trials ('screen test (object)'). Dashed line indicates 50 % correct (chance level 405 performance) against which group level performance was tested (one-sample Wilcoxon test, \*\*\* p<0.0001 (note that performance above chance level during PT and PST was required for the horses to move the screen test). 406 407 Horses significantly performed below the 50 % threshold during screen test with images. Lines across boxplots 408 show individual performances throughout the stages of the ORT. One horse touched the correct images 409 significantly above chance level during screen test (images); data for this individual is indicated as bold line 410

- 411
- 3.2.3. Factors influencing response to the images

412 Horses' response to the images (*i.e.* correct/wrong) was predicted by the type of preceding trial (p<0.001, model

413 estimates shown in Table 2). Horses were more likely to respond correctly in trials following real object trials

414 than in trials following images trials ( $X^{2}_{1}$ =8.45, p=0.004), although the proportion of horses touching the correct

415 image was only 51.8% (Fig.3). Overall, horses did not make any image contacts on 144 trials (53.3%), whereas

416 horses always approached the real-objects.

- 417 Whether horses received a reward upon correct image contact or reward was (unexpectedly) withheld during a
- 418 preceding image trial had no significant effect on horses' performance ( $X_2^2=0.268$ , p=0.874). However, images
- 419 on the right side more like to result in correct responses than when the target was shown on the left ( $X_{1}^{2}=3.85$ ,
- 420 p=0.05, model estimates in Table 2).
- 421

Fig. 3 Proportion of horses out of the 27 horses responding correctly or incorrectly depending on whether the
 preceding trial was refreshed with objects (yes) or not (no). More horses performed correctly than incorrectly
 when the preceding trial was refreshed with objects (p=0.004)

425

426 **Table 2** Model estimates of GLMM with response as binary dependent variable (correct/wrong) and predictors 427 with comparator information in square brackets. P-values  $\leq 0.05$  are highlighted in bold

428

Predictors	Odds Ratios	Confidence Interval	P-Value
(Intercept)	0.24	0.00 - 47.44	0.6
Yard [B]	2.12	0.60 - 7.51	0.246
Age	1.09	0.94 - 1.27	0.254
Welfare score	1.06	0.76 - 1.48	0.716
Side [R]	1.79	1.00 - 3.19	0.05
Target [ring]	0.54	0.17 - 1.74	0.304
AfterObject [yes]	0.33	0.18 - 0.61	<0.001
Learning ability	1.01	0.87 - 1.19	0.869
Marginal R2 / Conditional R2	0.174 / 0.347		

429

#### 430 **4.** Discussion

431 This study investigated if horses can recognise real-life objects from on-screen images. The majority of horses 432 initially reacted to images with the conditioned response (*i.e.* touching the target with their muzzle for food), but 433 the number of horses touching the correct image was not significantly different from the number of horses 434 contacting the wrong image. Therefore, performance at group level did not suggest that the horses recognised the 435 real objects from their 2D representations shown on-screen. However, we found that more correct responses being 436 performed on image trials following real object trials, suggesting that horses' reactions to the images was not 437 completely random. In fact, one horse selected the correct images at a level significantly above chance when tested 438 repeatedly over 10 images trials, suggesting that this individual recognised the images either as the real object 439 (confusion mode) or as a representation of it (equivalence mode; Fagot et al. 2010). 440 Previous studies have reported that horses are able to recognise other individuals from photographs (Smith et al.

441 2016; Wathan et al. 2016; Proops et al. 2018; Lansade et al. 2020a, b). As presented in the introduction, the validity

442 of existing evidence might be hampered by experimental limitations (see Amici (2019) for discussion of Proops 443 et al. (2018). Moreover, discrimination ability is not automatic proof of recognition (Aust and Huber 2006), and 444 alternative mechanisms such as learning, categorisation (i.e. of biologically relevant objects such as food), or 445 habituation might also influence animals' responses to repeated presentation with images (reviewed in Bovet and 446 Vauclair 2000). Here we tested if horses would spontaneously respond to on-screen images with the same learnt 447 response that they were trained to make to real objects, using a relative low number of test trials and partial reward 448 delivery to avoid learning. In contrast to previous reports, our horses failed to recognise the objects from images, 449 except for one individual. Several aspects need to be considered to put our findings in context with previous 450 findings.

451 When exposed to the images for the first time, all but two horses spontaneously responded to the images with the 452 conditioned response, suggesting the horses made some association between images and objects since the stimuli 453 provoked the learnt behaviour. We trained the horses to express their choice by contacting the target with their 454 muzzle, because this conditioned behaviour is commonly used in horses tested in two-choice discrimination tests 455 (e.g. Flannery 1997; Hanggi 2001, 2003; Lansade et al. 2020a, b). In retrospect, we question the suitability of this 456 behaviour as conditioned response. Horses naturally use their nose to explore unfamiliar items to gather 457 olfactory/tactile information whilst inspecting novel objects (De Boyer Des Roches et al. 2008). Therefore, the 458 horses might have contacted the images to explore the items rather than performing a conditioned behaviour. This 459 might explain why we found no significant preference for either image at first presentation (trial 1). Utilising 460 stimulus specific adaptive responses as done in studies in other species (e.g. grasping behaviour in marmosets (Oh 461 et al. 2019), eating attempts of banana images in gorillas (Parron et al. 2008), or shaping behaviours distinctively 462 different from normal horse behaviour (e.g. level pressing; Dougherty and Lewis 1991) could avoid this problem 463 of ambiguity.

464 Intriguingly, horses were nevertheless more likely to make correct responses to the images following real object 465 trials than following image trials. Maybe responding to the real objects before seeing the images somehow 466 facilitated horses' ability to transfer between the stimuli, despite perceptual differences (e.g. lack of depth cues), 467 for instance by matching them based on relational sameness (e.g. shape). In fact, Flannery (1997) observed that 468 horses have the capacity to learn higher-order discriminations based on relation between stimuli, such as geometric 469 shapes. It could be that horses initially confused objects and images (*i.e.* seeing both as the same), but once they 470 made physical contact with the images, the mismatch in sensory feedback (e.g. olfactory/tactile feedback) between 471 the familiar object and images resulted in independent processing of both as completely different items. Moreover,

cross-modal differences (*i.e.* looks like target but does not smell/feel like target), might have stopped the horses
from touching the images. Horses use cross-modal (visual/olfactory and auditory information) sensory input to
recognise individuals (*e.g.* horses (Proops et al. 2009); humans (Lampe and Andre 2012; Proops et al. 2013)), but
whether this is also true for identifying (familiar) objects has not been tested yet.

476 In addition, other experimental limitations might have influenced our findings. Work by one other group used 477 digital stimuli (computer screens (Lansade et al. 2020a, b) and projections (Trösch et al. 2019, 2020)) which is 478 why we anticipated that this type of visual information would be suitable for the purpose of our study. However, image quality and differences in colour perception of the images resulting from the use of the LCD projector 479 480 (images generated from a light signal comprised of red, blue and green components but horses cannot perceive 481 red/green colours) may have contributed to sensory image impressions different in horses to those generated by 482 the real object, and to what humans see in digital images. Besides, the equine eye is adapted to dim light conditions 483 and scattered light (e.g. from a bright light source such as a projector) can lead to loss of resolution (Hebel 1976). 484 One may wonder whether the close distance to the screen might have hindered our horses' ability to clearly see 485 the items in front of them given the blind spot directly in front of their forehead and limited visual acuity in close 486 proximity (Hebel 1976; Timney and Macuda 2001, reviewed in (Rørvang et al. 2020). Our setup seems appropriate 487 since others reported that horses successfully learn to discriminate between symbols of difference shapes and 488 sizes, and photographs, when standing directly ( $\leq$ 50 cm) in front of a screen and contacting the stimuli with their 489 muzzle (Gabor and Gerken 2012; Tomonaga et al. 2015). Varying the blinded handler position (always positioned 490 on the left-hand side for practical reasons) should be considered for future work, since we found that targets 491 presented on the right side were more likely to result in correct responses. The spatial relationship between cue, 492 reward and response influences discrimination learning (Miller and Murphy 1964; Hothersall et al. 2010), which 493 might explain why target location tended to affect performance.

494 Maybe our results do not support previous reports of image recognition in horses because of the type of stimuli 495 we used. From an adaptive perspective, processing visual cues of biological relevance is highly important, and 496 images representing biologically relevant stimuli (e.g. prey, conspecifics, predators) are instrumental in studies of 497 animal picture recognition where animals' spontaneous (initial) response to pictorial cues is tested (Bovet and 498 Vauclair 2000). For instance, (Kendrick et al. 1996) observed that sheep were much faster in learning to 499 discriminate between images of conspecifics (familiar or unfamiliar) than between geometrical shape 500 discrimination cues, possibly because sheep seem to cognitively process information associated with social 501 familiarity (i.e. facial features of conspecifics) more efficiently than non-social cues. It seems probable that

502 specialised sensory processing of social cues is also relevant to horses, since they show a range of postural and 503 facial expressions for social communication (Waring 2003; Wathan et al. 2015), and understand visual cues from 504 humans (Proops and McComb 2010). It seems therefore possible that equine studies using images of conspecifics 505 (Wathan et al. 2016) or humans (Smith et al. 2016; Proops et al. 2018; Lansade et al. 2020b, a) tap into different 506 sensory processing levels than when objects images are used. We chose real-life objects instead of images of 507 conspecifics as this allowed us to train and test horses' response more easily under controlled conditions (i.e. 508 excluding variation within the test stimuli). We also excluded food cues since disentangling animals' motivation 509 to respond to food cues when food rewards are provided during repeated testing might be difficult. Nevertheless, 510 we expected that the horses would pay attention to the on-screen stimuli if they perceive the images as equal to 511 the real objects given that they had learnt to associate these with food (*i.e.* a biologically relevant resource).

512 Digital images are increasingly applied in the study of horse cognition, but evidence that this species has the 513 ability to recognise the content of digital images is still sparse. Hence, we investigated how horses' spontaneously 514 respond to on-screen images of known objects and did not consider to test the reverse (i.e. whether horses' 515 recognise real-life objects from images). We do encourage future research to study this further (considering 516 cofounding factors discussed in the introduction regarding Hanggi et al., 2001), for instance, to understand what 517 stimulus characteristics (e.g. colour (Hangii and Ingersoll, 2007), shape, or size (Tomonaga et al., 2015; Hanggi 518 2003)) drive recognition as these could be easily manipulated in digital images. Here, we only used two real-life 519 objects distinctively differing in colour, shape and size (stimulus features horses can generally discriminate) as 520 using more items could have introduced more variability in individuals' responses making the interpretation of 521 findings more difficult. We therefore believe our findings that horses overall did not perform reliably enough to 522 suggest image recognition using two objects are of significance. However, we must acknowledge that our 523 observations may not be generalizable as the use of different objects could have led to different findings.

524 Only one out of 27 horses responded to the stimuli on screen above chance level suggesting that this individual 525 might have recognised the images as objects or representations of such. Rapid learning seems unlikely given the 526 experimental precautions we undertook. For example, we used partial reinforcement in the screen test to reduce 527 the possibility that horses would respond to image-related cues, *i.e.* exhibit the muzzle contact as new behaviour 528 specific to the images rather than touching them because they were recognise as a replacement of the objects. 529 Indeed, horses were not more likely to respond correctly to the images following images trials a reward was 530 delivered upon correct response than when reward was (unexpectedly) withheld. Likewise, horses were not more 531 likely to respond incorrectly following unrewarded trials. Still, learning cannot be completely excluded as partial

532 reinforcement reduces, but does not exclude, acquisition of a conditioned response compared to continuous 533 reinforcement (Gottlieb 2005; Amselme 2014). On the other hand, the performance of this particular horse might reflect a statistical Type I error (Pollard & Richardson 1987). Our study design does not allow us to draw 534 535 conclusions as to how this horse recognised the images (i.e. whether images and objects were seen as the same item (i.e. confused), the images seen as functional representations (equivalent) of the target or both processed 536 537 independently). Nevertheless, this finding is interesting as it highlights the importance of considering individual 538 variation in cognitive tests. In correspondence with other findings showing that older horses learn more slowly in 539 a social learning task (Krueger et al. 2014), we found that older horses needed more trial blocks to learn the 540 discrimination task, but we found no association between welfare level, learning ability and test performance. 541 Further study could investigate further inter-individual differences such as variations in personality or in 542 perceptual abilities on performance.

543

544 5. Conclusion

545 Only one of 27 horses responded to the images suggesting it might have recognised the images as objects or 546 representations of such, while all other horses apparently failed to do so. As a species, horses may possess the 547 basic capability to perceive the content of artificial visual stimuli such as digital image, but our findings indicate 548 that in horses unfamiliar with two-dimensional representations image recognition might not be an ability that can 549 be generalised across horses and testing situations. Instead, further research is warranted in order to understand 550 how horses perceive (at sensory level) and interpret (at cognitive level) images for the human eye, especially if 551 they are to be utilised as representations of real-life objects, as well as inter-individual variations in such abilities. 552 Until then, we do not know if humans and horses see eye to eye when viewing this type of artificial stimuli. 553

- 554 Acknowledgements:
- 555 We would like to thank the riding schools for the use of their animals and facilities. This project was founded by
- the University of Plymouth.

557

- 558 References:
- Amici F (2019) Memories of emotional expressions in horses. Learn Behav 47:191–192.
   https://doi.org/10.3758/s13420-018-0363-9
- Anselme P (2015) Incentive salience attribution under reward uncertainty: A Pavlovian model. Behavioural
   Processes 111:6–18. https://doi.org/10.1016/j.beproc.2014.10.016

- Aust U, Huber L (2006) Picture-object recognition in pigeons: Evidence of representational insight in a visual categorization task using a complementary information procedure. Journal of Experimental
   Psychology: Animal Behavior Processes 32:190–195. https://doi.org/10.1037/0097-7403.32.2.190
- Bates D, Maechler M, Bolker B, Walker S Fitting Linear Mixed-Effects Models Using lme4. Journal of
   Statistical Software 67:. https://doi.org/10.18637/jss.v067.i01
- Bovet D, Vauclair J (2000) Picture recognition in animals and humans. Behavioural Brain Research 109:143– 165. https://doi.org/10.1016/S0166-4328(00)00146-7
- 570 Cabe PA (1976) Transfer of discrimination from solid objects to pictures by pigeons: A test of theoretical
   571 models of pictorial perception. Perception & Psychophysics 19:545–550.
   572 https://doi.org/10.3758/BF03211224
- 573 Carere C, Locurto C (2011) Interaction between animal personality and animal cognition. Current Zoology
   574 57:491–498. https://doi.org/10.1093/czoolo/57.4.491
- 575 Christensen JW, Ahrendt LP, Lintrup R, et al (2012) Does learning performance in horses relate to fearfulness,
  576 baseline stress hormone, and social rank? Applied Animal Behaviour Science 140:44–52.
  577 https://doi.org/10.1016/j.applanim.2012.05.003
- 578 De Boyer Des Roches A, Richard-Yris M-A, Henry S, et al (2008) Laterality and emotions: Visual laterality in
   579 the domestic horse (Equus caballus) differs with objects' emotional value. Physiology & Behavior
   580 94:487–490. https://doi.org/10.1016/j.physbeh.2008.03.002
- 581 D'Eath RB (1998) Can video images imitate real stimuli in animal behaviour experiments? Biol Rev 73:267–
   582 292. https://doi.org/10.1017/S0006323198005179
- 583 Dougherty DM, Lewis P (1991) Stimulus Generalization, Discrimination Learning, and Peak Shift in Horses.
   584 Journal of the Experimental Analysis of Behavior 56:97–104. https://doi.org/10.1901/jeab.1991.56-97
- 585 Dougherty LR, Guillette LM (2018) Linking personality and cognition: a meta-analysis. Phil Trans R Soc B
   586 373:20170282. https://doi.org/10.1098/rstb.2017.0282
- 587 Duke-Elder S System of ophthalmology: vol. I. The eye in evolution. Henry Kimpton, London
- 588 Fagot J (2000) Picture Perception in Animals. Psychology Press, East Sussex
- Fagot J, Parron C (2010) Picture Perception in Birds: Perspective from Primatologists. CCBR 5:132–135.
   https://doi.org/10.3819/ccbr.2010.50007
- Fagot J, Thompson RKR, Parron C (2010) How to read a picture: Lessons from nonhuman primates.
   Proceedings of the National Academy of Sciences 107:519–520.
   https://doi.org/10.1073/pnas.0913577107
- Flannery B (1997) Relational discrimination learning in horses. Applied Animal Behaviour Science 54:267–
   280. https://doi.org/10.1016/S0168-1591(97)00006-3
- Fox J, Weisberg S (2019) An {R} Companion to Applied Regression. Version Third Edition. Sage, Thousand
   Oaks CA. URL https://socialsciences.mcmaster.ca/jfox/Books/Companion/
- 598 Gabor V, Gerken M (2012) Cognitive testing in horses using a computer based apparatus. Applied Animal
   599 Behaviour Science 139:242–250. https://doi.org/10.1016/j.applanim.2012.04.010
- Gottlieb DA (2004) Acquisition with partial and continuous reinforcement in pigeon autoshaping. Animal
   Learning & Behavior 32:321–334. https://doi.org/10.3758/BF03196031
- 602 Grzimek B (1943) Begrussung zweier Pferde: Das Erkennen von Phantomen und Bildern. 465–480

- Hanggi E (2001) Can horses recognize pictures? In: Proceedings of the third international conference of
   cognitive science, Beijing, China, pp 52–56
- Hanggi EB (1999) Categorization learning in horses (Equus caballus). Journal of Comparative Psychology
   113:243–252. https://doi.org/10.1037/0735-7036.113.3.243
- Hanggi EB (2003) Discrimination learning based on relative size concepts in horses (Equus caballus). Applied
   Animal Behaviour Science 83:201–213. https://doi.org/10.1016/S0168-1591(03)00136-9
- Hanggi EB, Ingersoll JF (2009a) Stimulus discrimination by horses under scotopic conditions. Behavioural
   Processes 82:45–50. https://doi.org/10.1016/j.beproc.2009.04.009
- Hanggi EB, Ingersoll JF (2009b) Long-term memory for categories and concepts in horses (Equus caballus).
   Anim Cogn 12:451–462. https://doi.org/10.1007/s10071-008-0205-9
- Hanggi EB, Ingersoll JF, Waggoner TL (2007) Color vision in horses (Equus caballus): Deficiencies identified
  using a pseudoisochromatic plate test. Journal of Comparative Psychology 121:65–72.
  https://doi.org/10.1037/0735-7036.121.1.65
- Hausberger M, Stomp M, Sankey C, et al (2019) Mutual interactions between cognition and welfare: The horse
  as an animal model. Neuroscience & Biobehavioral Reviews 107:540–559.
  https://doi.org/10.1016/j.neubiorev.2019.08.022
- Hebel R (1976) Distribution of retinal ganglion cells in five mammalian species (pig, sheep, ox, horse, dog).
   Anat Embryol 45–51
- Hothersall B, Gale EV, Harris P, Nicol CJ (2010) Cue use by foals (Equus caballus) in a discrimination learning
   task. Anim Cogn 13:63–74. https://doi.org/10.1007/s10071-009-0245-9
- Hughes A (1977) The Topography of Vision in Mammals of Contrasting Life Style: Comparative Optics and
   Retinal Organisation. In: Crescitelli F (ed) The Visual System in Vertebrates. Springer Berlin
   Heidelberg, Berlin, Heidelberg, pp 613–756
- Jacobs GH, Deegan JF, Neitz J (1998) Photopigment basis for dichromatic color vision in cows, goats, and
   sheep. Vis Neurosci 15:. https://doi.org/10.1017/S0952523898153154
- Kendrick KM, Atkins K, Hinton MR, et al (1996) Are faces special for sheep? Evidence from facial and object
   discrimination learning tests showing effects of inversion and social familiarity. Behavioural Processes
   38:19–35. https://doi.org/10.1016/0376-6357(96)00006-X
- Krueger K, Farmer K, Heinze J (2014) The effects of age, rank and neophobia on social learning in horses.
   Anim Cogn 17:645–655. https://doi.org/10.1007/s10071-013-0696-x
- Lampe JF, Andre J (2012) Cross-modal recognition of human individuals in domestic horses (Equus caballus).
   Anim Cogn 15:623–630. https://doi.org/10.1007/s10071-012-0490-1
- Lansade L, Colson V, Parias C, et al (2020a) Female horses spontaneously identify a photograph of their keeper,
  last seen six months previously. Sci Rep 10:6302. https://doi.org/10.1038/s41598-020-62940-w
- Lansade L, Colson V, Parias C, et al (2020b) Human Face Recognition in Horses: Data in Favor of a Holistic
   Process. Front Psychol 11:575808. https://doi.org/10.3389/fpsyg.2020.575808
- Miller RE, Murphy JV (1964) Influence of the spatial relationships between the cue, reward, and response in discrimination learning. Journal of Experimental Psychology 67:120–123.
   https://doi.org/10.1037/h0040113
- Murphy J, Waldmann T, Arkins S (2004) Sex differences in equine learning skills and visuo-spatial ability.
   Applied Animal Behaviour Science 87:119–130. https://doi.org/10.1016/j.applanim.2003.12.002

- Nakamura, K., Takimoto-Inose, A., & Hasegawa, T. (2018). Cross-modal perception of human emotion in
  domestic horses (Equus caballus). Scientific Reports, 8(1), 8660. https://doi.org/10.1038/s41598-01826892-6
- 647 Oh J, Šlipogor V, Fitch WT (2019) Artificial visual stimuli for animal experiments: An experimental evaluation
   648 in a prey capture context with common marmosets (Callithrix jacchus). Journal of Comparative
   649 Psychology 133:72–80. https://doi.org/10.1037/com0000129
- Parron C, Call J, Fagot J (2008) Behavioural responses to photographs by pictorially naïve baboons (Papio anubis), gorillas (Gorilla gorilla) and chimpanzees (Pan troglodytes). Behavioural Processes 78:351–
   357. https://doi.org/10.1016/j.beproc.2008.01.019
- Pfungst O, Rahn CL (1911) Clever Hans: the horse of Mr. Von Osten. A contribution to experimental animal
   and human psychology. Holt, Rineheart, and Winston, New York
- Pollard, P., & Richardson, J. T. (1987). On the probability of making Type I errors. Psychological Bulletin,
  102(1), 159–163. https://doi.org/10.1037/0033-2909.102.1.159
- Proops L, Grounds K, Smith AV, McComb K (2018) Animals Remember Previous Facial Expressions that
   Specific Humans Have Exhibited. Current Biology 28:1428-1432.e4.
   https://doi.org/10.1016/j.cub.2018.03.035
- Proops L, McComb K (2010) Attributing attention: the use of human-given cues by domestic horses (Equus caballus). Anim Cogn 13:197–205. https://doi.org/10.1007/s10071-009-0257-5
- Proops L, McComb K, Reby D (2009) Cross-modal individual recognition in domestic horses (*Equus caballus* ). PNAS 106:947–951. https://doi.org/10.1073/pnas.0809127105
- Proops L, Rayner J, Taylor AM, McComb K (2013) The Responses of Young Domestic Horses to Human Given Cues. PLoS One 8:e67000. https://doi.org/10.1371/journal.pone.0067000
- R Core team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rørvang MV, Nielsen BL, McLean AN (2020) Sensory Abilities of Horses and Their Importance for Equitation
   Science. Front Vet Sci 7:633. https://doi.org/10.3389/fvets.2020.00633
- 670 Rowe C, Healy SD (2014) Measuring variation in cognition. Behavioral Ecology 25:1287–1292.
   671 https://doi.org/10.1093/beheco/aru090
- 672 Saslow CA (2002) Understanding the perceptual world of horses. Applied Animal Behaviour Science 78:209–
   673 224. https://doi.org/10.1016/S0168-1591(02)00092-8
- 674 Smith AV, Proops L, Grounds K, et al (2016) Functionally relevant responses to human facial expressions of
  675 emotion in the domestic horse (*Equus caballus*). Biol Lett 12:20150907.
  676 https://doi.org/10.1098/rsbl.2015.0907
- Timney B, Macuda T (2001) Vision and hearing in horses. Journal of the American Veterinary Medical
   Association 218:1567–1574. https://doi.org/10.2460/javma.2001.218.1567
- Tomonaga M, Kumazaki K, Camus F, et al (2015) A horse's eye view: size and shape discrimination compared
  with other mammals. Biol Lett 11:20150701. https://doi.org/10.1098/rsbl.2015.0701
- Trösch, Cuzol, Parias, et al (2019) Horses Categorize Human Emotions Cross-Modally Based on Facial
   Expression and Non-Verbal Vocalizations. Animals 9:862. https://doi.org/10.3390/ani9110862
- Trösch M, Pellon S, Cuzol F, et al (2020) 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.
   https://doi.org/10.1007/s10071-020-01369-0

- Valenchon M, Lévy F, Prunier A, et al (2013) Stress Modulates Instrumental Learning Performances in Horses
   (Equus caballus) in Interaction with Temperament. PLOS ONE 8:e62324.
   https://doi.org/10.1371/journal.pone.0062324
- Vandenheede M, Bouissou MF (1994) Fear reactions of ewes to photographic images. Behavioural Processes
   32:17–28. https://doi.org/10.1016/0376-6357(94)90024-8
- von Borell E, Langbein J, Després G, et al (2007) Heart rate variability as a measure of autonomic regulation of
   cardiac activity for assessing stress and welfare in farm animals A review. Physiology & Behavior
   92:293–316. https://doi.org/10.1016/j.physbeh.2007.01.007
- 694 Waring GH (2003) Horse Behaviour, 2nd edn. Noyes Publications, New York
- Wathan J, Burrows AM, Waller BM, McComb K (2015) EquiFACS: The Equine Facial Action Coding System.
   PLoS ONE 10:e0131738. https://doi.org/10.1371/journal.pone.0131738
- Wathan J, Proops L, Grounds K, McComb K (2016) Horses discriminate between facial expressions of
   conspecifics. Sci Rep 6:38322. https://doi.org/10.1038/srep38322
- Weisman R, Spetch M (2010) Determining When Birds Perceive Correspondence Between Pictures and
   Objects: A Critique. CCBR 5:117–131. https://doi.org/10.3819/ccbr.2010.50006

701