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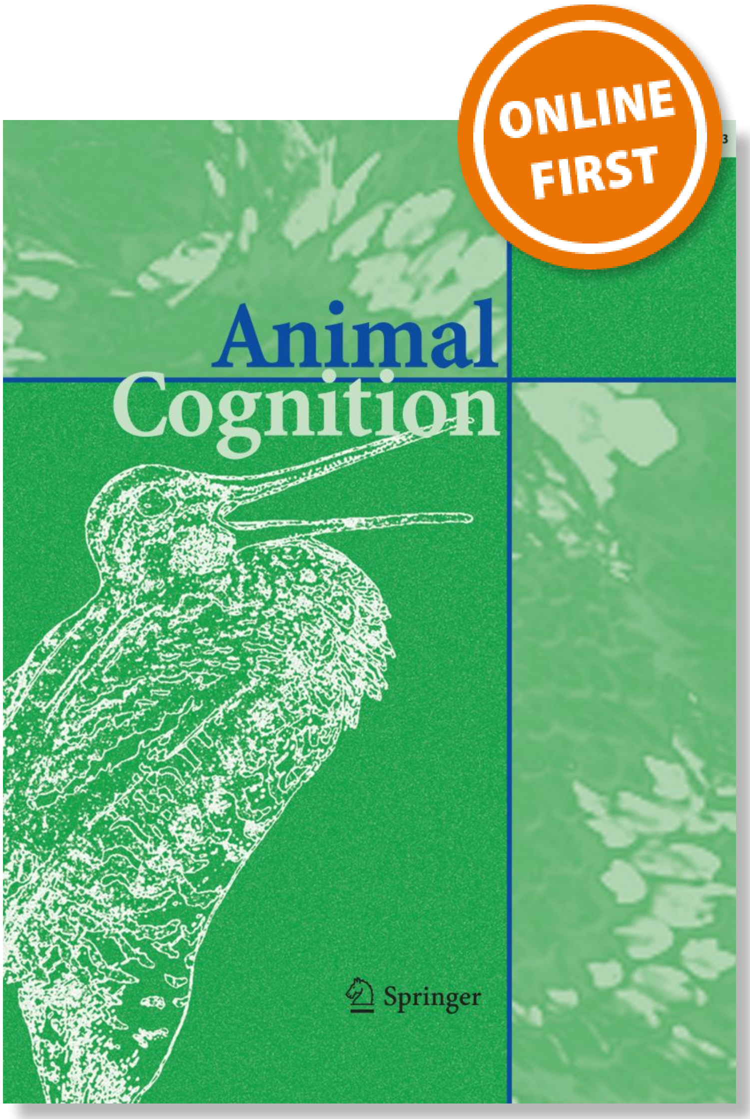

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ORIGINAL PAPER

How do horses (*Equus caballus*) learn from observing human action?

Kira Bernauer[1] · Hanna Kollross[1] · Aurelia Schuetz[2] · Kate Farmer[3] · Konstanze Krueger[1,4]

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Abstract

A previous study demonstrated that horses can learn socially from observing humans, but could not draw any conclusions about the social learning mechanisms. Here we develop this by showing horses four different human action sequences as demonstrations of how to press a button to open a feed box. We tested 68 horses aged between 3 and 12 years. 63 horses passed the habituation phase and were assigned either to the group Hand Demo ($N=13$) for which a kneeling person used a hand to press the button, Head Demo ($N=13$) for which a kneeling person used the head, Mixed Demo ($N=12$) for which a squatting person used both head and hand, Foot Demo ($N=12$) in which a standing person used a foot, or No Demo ($N=13$) in which horses did not receive a demonstration. 44 horses reached the learning criterion of opening the feeder twenty times consecutively, 40 of these were 75% of the Demo group horses and four horses were 31% of the No Demo group horses. Horses not reaching the learning criterion approached the human experimenters more often than those who did. Significantly more horses used their head to press the button no matter which demonstration they received. However, in the Foot Demo group four horses consistently preferred to use a hoof and two switched between hoof and head use. After the Mixed Demo the horses' actions were more diverse. The results indicate that only a few horses copy behaviours when learning socially from humans. A few may learn through observational conditioning, as some appeared to adapt to demonstrated actions in the course of reaching the learning criterion. Most horses learn socially through enhancement, using humans to learn where, and which aspect of a mechanism has to be manipulated, and by applying individual trial and error learning to reach their goal.

Keywords Copying · *Equus caballus* · Human demonstrator · Interspecies specific social learning · Social learning · Social enhancement

Introduction

Animals acquire new behaviours through individual and social learning. In individual learning, a change in the animals' behaviour is triggered by the experience of an individual animal (Rescorla 1982), while in social learning the animal is influenced by a second individuals behavioural, visual, olfactory, and/or auditory cues in such a way that it is more likely to learn (Hoppitt and Laland 2008). Individual and social learning may be used in combination to learn complex actions (Whalen et al. 2015; Leadbeater and Dawson 2017). Several mechanisms for social learning are under debate (Whiten et al. 2004; Hoppitt and Laland 2008). Firstly: 'Social facilitation' (Zajone 1965) in which the presence of a demonstrator may cause an animal to change its behaviour or 'Response facilitation' (Byrne 1994) in which the demonstrator performing an action may cause an animal to do the same. Secondly, 'Social enhancement' (Galef 1989) in which animals may be more likely to consume a

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certain food after being in contact with a demonstrator carrying cues of this food (Mersmann et al. 2011; Leadbeater and Dawson 2017), 'Stimulus enhancement' (Heyes 1994) in which animals may change their behaviour after being exposed to a particular stimulus by an observer's action, or 'Local enhancement' (Thorpe 1963) in which animals are more likely to visit or interact at a location after observing a demonstrator's action at this particular location. However, when the object to be manipulated is at a fixed location, local enhancement and stimulus enhancement are indistinguishable (Zentall 2006). Thirdly, social learning can occur through 'Observational conditioning' meaning positive or negative conditioning to an object, process or event through observing the outcome of repeated action sequences (Cook et al. 1985). Finally, animals may copy the behaviour of others as in 'Contextual imitation' (Byrne 2002) in which an animal may show a particular action in the same context in which it observed that behaviour, in 'Production imitation' (Byrne 2002) in which an animal displays a novel action or sequence not in its repertoire after observing the same action, or the animal emulates behaviours when it understands the demonstrator's goal from observing its action, but uses other actions to achieve it (Tomasello 1990; Whiten and Ham 1992; Custance et al. 1999).

Horses can learn socially from higher ranking, older conspecifics in their social group (Krueger and Heinze 2008; Krueger et al. 2014; Rørvang et al. 2015); Schuetz et al. (2017) showed that horses learn socially from familiar humans, but could not infer the social learning mechanisms. A mix of individual trial and error learning and social enhancement has been discussed as the primary mechanism, as but this has not been confirmed (Brubaker and Udell 2016).

Horses are well suited as subjects for the study of inter-species social learning from humans, as their domestication 3000–5000 years ago (Mills and McDonnell 2005) may have shaped their inter-species communication abilities. Similarly, dogs, with a domestication history of 15,000 years (Irving-Pease et al. 2019), are affected by human familiarity in their learning abilities (Topál et al. 1997), and learn socially from humans (Kubinyi et al. 2003; Pongrácz et al. 2001, 2004). Since Clever Hans, the "counting horse", was revealed to have "solved" mathematical tasks using human facial and body cues as signals for when to start and stop tapping his hoof (Pfungst 1907), it has been shown that domestic horses are able to use human pointing gestures to find food (Maros et al. 2008; Proops et al. 2010, 2013; Dorey et al. 2014) and that they orientate on the direction of human attention (Proops and McComb 2010; Sankey et al. 2011; Krueger et al. 2011). Horses distinguish between familiar and unfamiliar persons (Proops et al. 2009; Sankey et al. 2011; Proops and McComb 2012; Lamp and Andre 2012) and may not respond to a familiar command if it comes from an unfamiliar person (Sankey et al. 2011). They have expectations of human behaviour (Sankey et al. 2011), which may inhibit their performance under test conditions (Lesimple et al. 2012), and show referential communication when expressing their needs to humans, such as indicating whether a person should put on or take off a rug (Mejdell et al. 2016), or open a fence to allow access to food (Malavasi and Huber 2016). Horses generalise positive and negative experiences from one human to others (Sankey et al. 2011) and can infer emotional states from human photos (Smith et al. 2016) and human voices (d'Ingeo et al. 2019). They also know what humans may have seen, for example, whether they witnessed the hiding of food (Malavasi and Huber 2016; Ringhofer and Yamamoto 2017).

Here, we tested 68 horses of different sexes and breeds, aged between 3 and 12 years. We chose this age group as young horses demonstrated better learning performances in earlier studies (Nicol 2002; Krueger et al. 2014). The horses were tested on whether they would learn to open a novel feeding apparatus after observing a human demonstrator, and whether they would copy the demonstrated action sequence. They were semi-randomly assigned to five experimental groups, to receive a demonstration of one of four action sequences: pushing a button with the hand (Hand Demo), with the head (Head Demo), with the foot (Foot Demo), or with the hand and the head (Mixed Demo), or to receive no demonstration (No Demo). This study aims to evaluate (a) the action types and (b) the learning mechanism horses would apply to open a novel feeding apparatus.

Methods

Locations, study periods

The experiments were conducted between April 2016 and August 2018. We tested the horses in their home environments, as familiarity with the test area improves learning in domestic animals (Miklósi and Soproni 2006; Maros et al. 2008; Lovrovich et al. 2015). The horses were kept in different locations with different housing and management conditions (Table ESM_1), but all in line with German horse management guidelines. All the horses had at least 3–4 h turn-out in social groups each day. From April to June 2016 we used horses from 13 different locations close to Stuttgart, Germany, in April and May 2017 horses from 7 different locations close to Frankenthal, Germany, and in June and August 2017 horses from one location close to Luzern, Switzerland, and one location close to Vienna, Austria.

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Experimental groups and animals

The 68 horses included 22 ponies and 46 horses of various breeds, all aged between 2 and 14 years (Table ESM_1). They were semi-randomly distributed over 5 experimental groups with the demonstrations Hand Demo ($N=13$), Head Demo ($N=13$), Mixed Demo ($N=14$), Foot Demo ($N=13$), and No Demo ($N=15$) (for detail see: Experimenters and their tasks; Table ESM_1) so that the horses' age distribution in the groups was approximately similar. We chose horses with at least 3 months of basic "ground training" (Deutsche Reiterliche Vereinigung e.V. 2014) as domestic animals with basic training from humans may be better at reading human cues (Miklósi and Soproni 2006). All horses were mentally and physically sound and in good or very good feeding condition. During the 2 h before the habituation phase and before the experiments they were not trained and received only hay.

Experimental area and apparatus

We used lunging circles, riding arenas, or paddocks with sand, wood shavings or slip-proof paving. We fenced in experimental areas of 20 m^2, making sure that grass and other feed was out of the horses' reach (Fig. 1). The test feed eaten by humans and horses was pieces of carrot and apple at all the premises.

The experimental apparatus consisted of a feed box containing feed rewards and a separate button, which had to be pressed to open the feed box (Fig. ESM_2). The distance between the box and the button was 1 m, as learning can clearly be demonstrated if animals have to memorise a particular action for a couple seconds to achieve a goal a distance away (Heyes 1994; Shettleworth 1998; Healy and Jones 2002). The wooden feed box was 50 cm long, 50 cm wide, and 18 cm high, with a wooden lid. A removable plastic container for the feed was placed inside and cleaned after each test to avoid contamination. The button was 20 cm long, 20 cm wide, 11 cm high, and mounted on a 50 × 50 cm base plate. In contrast to the study of Schuetz

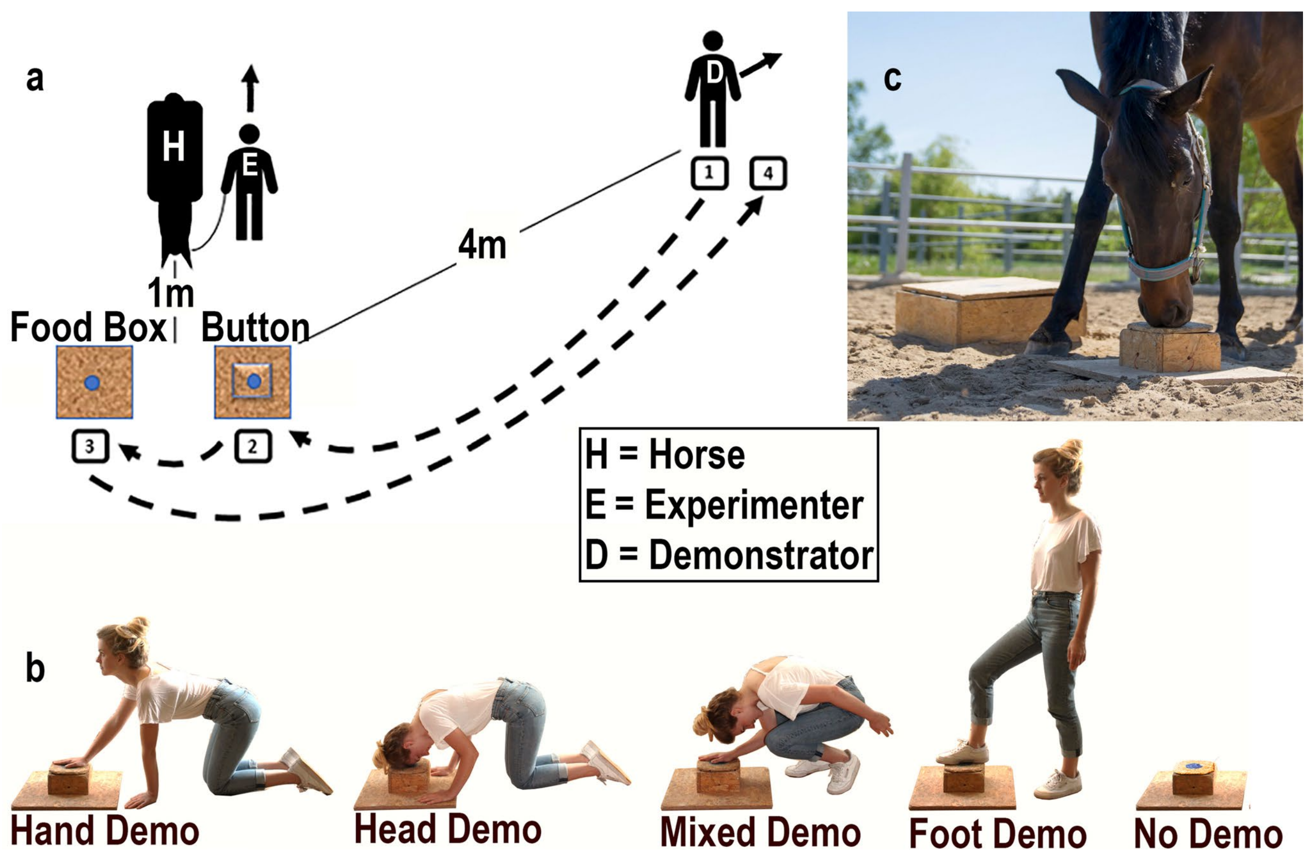

Fig. 1 Experimental procedure. **a** depicts the experimental set up in the demonstration phase, in which experimenter 1, the demonstrator (D) walks from the starting position (1) to the button (2), demonstrates one of the action sequences under **b** and walks to the feed box (3), eats a food item, returns to the starting position and remains there, facing away from the feed box. Demonstrators (D) of the No Demo situation remained at the starting position (1) with their back turned towards the horse. The experimenter 2 (E) keeps the horse on a loose rope while turning her back towards the experimental apparatus. **c** shows an observer horse, which pushes the button with its nose

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et al. (2017) the button was placed on the ground, so that it could be operated easily with the hoof. Although horses discriminate objects and colours best at ground level (Hall et al. 2003), we increased the visibility of the ground level button and the experimental apparatus by painting a blue dot (Carroll et al. 2001) with a diameter of 10 cm on top of the button and on the top of the feed box. Pressing the button activated a battery powered servomotor at the lid of the feed box. Within one second of activation the motor drew back a locking bar, so that a gas pressure spring opened the lid with a low-pitched clicking sound, which did not startle the horses (Fig. ESM_2).

Habituation phase

A maximum of ten habituation trials per horse were conducted on the first day. In this phase experimenter 1 touched the button and the feed box to spread potential scent marks equally (see "Experimenters and their tasks", below). The habituation criteria were reached when the horse approached the open feed box unprompted, and ate the food inside, twice in a row. Five horses were excluded from the test, because they did not feed from the box after the 10th habituation trial. The excluded horses were two horses from the Mixed Demo group ($N = 14$), one horse from the Foot Demo group ($N = 13$), and 2 horses from the No Demo group ($N = 15$). The remaining 63 test horses were $N = 13$ in the Hand Demo group, $N = 13$ in the Head Demo group, $N = 12$ in the Mixed Demo group, $N = 12$ in the Foot Demo group, and $N = 13$ in the No Demo group.

Experimenters and their tasks

Three experimenters participated, each with different tasks.

Experimenter 1 was the demonstrator (D; Fig. 1a). As horses learn from familiar persons (Schuetz et al. 2017), persons ($N = 55$) who had cared for the horse for at least 1 year were chosen. All were female. The persons demonstrated for their own horses which were randomly assigned to the demonstrations Hand Demo ($N = 13$), Head Demo ($N = 13$), Mixed Demo ($N = 12$), Foot Demo ($N = 12$), and No Demo ($N = 13$).

In the four demonstration groups the demonstrator (D) walked from the start to the button (about 4 m) and after passing the horse at its starting position called the horse's name during the second half of the walk to get its attention (Pongrácz et al. 2004). The demonstrators stopped at the button, facing the button in a 45° angle to the horse and a 45° angle to the button, so that the horse saw the demonstration clearly (Fig. 1b):

1. The demonstrators of the group Hand Demo knelt down on their hands and knees, lifted the right hand from the ground and pressed the button with the flat of the right hand.
2. The demonstrators of the group Head Demo knelt down on their hands and knees bent their arms and pressed the button with their heads.
3. The demonstrators of the group Mixed Demo squatted down, but remained on their feet, bent their body and head towards the button, then lifted their right hand from the ground and pressed the button with the flat of their right hand.
4. The demonstrators of the group Foot Demo stood at the button lifted their right foot from the ground and pressed the button with their foot.

The demonstrators of the group No Demo remained at the starting position with their back turned towards the horse.

After the demonstrator pressed the button, she waited for the feed box to fully open, then walked to the box, squatted down at the left side of the box so that the horses could see the procedure. She then took a piece of carrot or apple out of the box with her hand, and ate it within 5 s. She then closed the box, stood up, passed the horse at its starting position and returned to the demonstrator's start position, turning her back to the apparatus. The horse was then released by experimenter 2.

Experimenter 2 handled the horse (E; Fig. 1a) and was unknown to the horse. 17 different persons (16 women, one man) fulfilled the task at random assignment. Experimenter 2 led the horse to the start (Fig. 1), then stayed at the left shoulder of the horse, turning his/her back to the apparatus. S/he kept the horse on a loose rope, and did not touch the horse (Krueger et al. 2014) while it observed the demonstrator. Experimenter 2 released the horse at the starting position and led the horse back to the start after each trial.

In the No Demo group, if the horse did not open the box, experimenter 2 turned the horse away from the feeder and covered the horse's eyes with a hand, so that the feed could be removed from the box out of sight of the horse.

Experimenter 3 recorded the results, controlled the video camera, recorded the time, and refilled the box. One person recorded the groups Hand Demo and Head Demo, one person the groups Mixed Demo and Foot Demo, and a third person recorded the No Demo group. They placed themselves outside the experimental area, to the right of the apparatus, and turned away to about 135°. Refilling the feed box was done in full sight of the observing horse to reduce feature negative effects (Hopewell et al. 2010) which may lead some animals to assume that no food is left in the box.

Experimental procedure

The test horses received a maximum of 120 demonstrations, 10–20 per day, spread over 1–2 weeks, depending on their

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motivation (Krueger et al. 2014). To increase the motivation, horses were allowed to eat once from the box before the experiment started on each test day. If horses hesitated to approach the box, or if they kept approaching the experimental apparatus, but failed to push the button, they received a motivation feeding after the 10th trial on each test day.

The horse was positioned with its front feet 1 m away from the button to ensure it could closely observe the demonstration (Fig. 1a). The horse was then free to investigate the apparatus and attempt to open it for 3 min during each trial. After 3 min, experimenter 2 led the horse back to the start. When horses pressed the button (Fig. 1c) and opened the feed box they were allowed to eat the food inside.

Learning criteria were reached and the experiment finished when the horse opened the feed box 20 times in succession, ten trials with demonstration and ten without (Krueger et al. 2014). If a horse lost interest and did not touch the feeding apparatus (apart from one possible approach directly after a motivation feeding) or did not reach learning criteria within a total of 120 trials, the experiment was terminated for this particular horse. The button and/or the feed box was counted as touched when a horse nuzzled, licked, bit, or pushed it with its mouth, or when the horse pushed it with its hoof or tilted the button and its base plate with the hoof. Touches were counted whether the touch activated the opening of the feed box and were recorded on paper, and the technique used by the horse was analysed from the video recordings.

Contacts with the experimenters were counted when a horse turned away from the test apparatus at least 70%, walked 1 or two steps to experimenter 2 (the handling person) or walked 4 m to experimenter 1 (the demonstrator) at her starting position, and stayed in close proximity of 2 m or less for at least 3 s.

Data analysis

We used the R-Project statistical environment (R Development Core Team 2019), Libre Office 4.3.3.2 and Photo shop CC2019 for statistical analysis and the depiction of the data. As most of the data were not normally distributed (*K–S* test) we applied non-parametric tests. Chi square tests and Binomial tests were used for likelihood evaluations. Sequential Bonferroni corrections, after Holms, were used to adapt the significance level for multiple testing. Multivariate Factor analyses were conducted by applying Generalized Linear Models (GLMs). Whether horses reached the learning criterion and the numbers of action types they applied were used as dependent variables, while the demo group, the age, the sex, the type of management, and the contact to experimenters were considered fixed factors. None of the factors were considered to be random, as all were affected by the controlled experimental set up. The full, initial model was reduced to the model with the lowest Akaike information criterion (AIC), and the remaining significant factors from the reduced model were used in a follow-up model. All tests were two-tailed and the significance level was set at 0.05.

Results

More horses learned to open the feed box after receiving a demonstration (40 horses out of 53 = 75%, Hand Demo (N = 12), Head Demo (N = 9), Mixed Demo (N = 10), Foot Demo (N = 9)) than horses which did not receive a demonstration (four horses out of 13 = 31%, No Demo group; GLM: N = 63, SE = 1.48, z = − 2.05, p = 0.04; Figs. 1 and 2; Table ESM_1).

Action types used by the horses

The 63 test animals manipulated the button of the experimental apparatus using six different action types: four with their heads and two with their hoofs. The head action types were (Fig. ESM_3; Tables ESM_4 and ESM_5): "pushing" with the upper lip, "nuzzling" with the upper lip, "licking", and "biting". The hoof action types were "tapping" with the front hoof and "tilting" the button with the front hoof". From the 50 test horses that received a demonstration 17 horses each used between two and five different action types, and

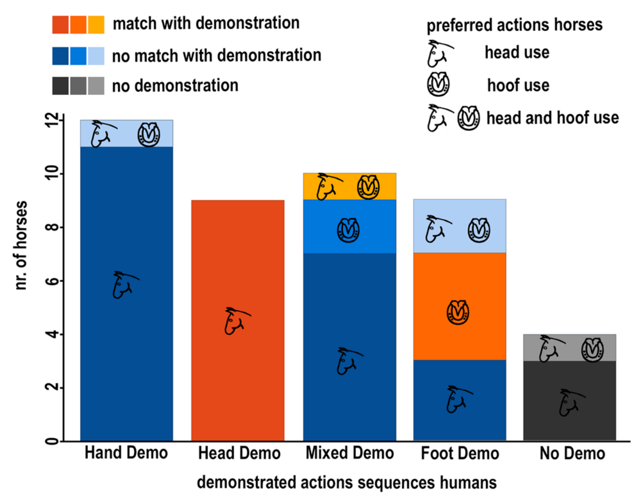

Fig. 2 Action demonstrated by humans and the learner horses' actions for opening a feed box. Most of the 44 horses that reached the learning criterion preferred to use their head (Chi Square Test: N=44, χ^2_2=31.4, p<0.001). Most actions which were applied by the animals did not match the demonstrated actions (GLMM: N=40, z=−0.144, p=0.89). However, the foot demo group had the highest percentage of hoof use (44% of the learners in the foot demo group, Chi Square test: N=5, χ^2_4=118.5, p<0.001) and the lowest percentage of head use (33% of the learners in the foot demo group, Chi Square test: N=5, χ^2_4=36.46, p<0.001)

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33 horses used only one action type, of which 16 "pressed" with their nose. From the test horses that did not receive a demonstration, nine used two or three action types and four used only one action type.

Fulfilling the learning criterion and number of applied action types

Our statistical analysis does not reveal effects of age, sex or type of management on the performance of the horses (GLM: $N=63$, all $p>0.05$). The 44 horses that fulfilled the learning criterion applied more action types when manipulating the apparatus (median three, min. = 1, max. = 4; Fig. ESM_3; Tables ESM_1, ESM_4 and ESM_5) than the 19 horses which did not reach it (median 2, min. = 1, max. = 4; GLM: $N=63$, SE = 0.52, $z=2.94$, $p=0.003$). The horses in the demonstration groups did not differ significantly in the number of action types they applied to opening the box (Mixed Demo: median = 3, min. = 2, max. = 4, Hand Demo: median = 2.5, min. = 1, max. = 3, Head Demo: median = 2, min. = 1, max. = 4; Foot Demo: median = 2, min. = 1, max. = 3, No Demo: median = 2, min. = 1, max. = 3; GLM: $N=63$, all > 0.05; Fig. ESM_3; Tables ESM_1, ESM_4 and ESM_5).

Head and hoof actions and demonstrated action sequences

Of the 44 horses that reached the learning criterion, 33 preferred head actions, six horses preferred hoof actions, and five used both hoof and head actions (Fig. 2; Fig. ESM_3; Tables ESM_4–6). Comparing the demonstrated action sequences with the horses' opening actions we suggest that the horses' hoof actions matched the experimenters' extremity (hand and foot) use, the horses' head actions the experimenters' head use, and no preference in the horses for hoof or head actions was revealed after the combined action of the persons in the Mixed Demo or with no demonstration in the No Demo group.

The Head Demo group was the only one in which all the nine horses reaching the learning criterion preferred the same action as the demonstrator (Binomial test: $N=9$, $p=0.004$; Fig. 2; Fig. ESM_3; Tables ESM_4 and ESM_5). In the three remaining demo groups most of the horses' actions did not significantly match the demonstrated action sequences. They did not match in the Hand Demo (Binomial test: $N=12$, $p=1$; Fig. 2; Fig. ESM_3; Tables ESM_4 and ESM_5), in which 11 animals preferred the head (Binomial test: all $p<0.05$) and one used head and hoof equally (Binomial test: $N=22$, $p=0.29$). In the Foot Demo (Binomial test: $N=9$, $p=0.42$; Fig. 2; Fig. ESM_3; Tables ESM_4 and ESM_5), three animals preferred the head and four the hoof (Binomial test: all $p<0.05$), while two horses showed no clear preference and used both head and hoof (Binomial test: both $p>0.05$). Finally, the animals' actions did not match the unclear "Mixed Demo" (Binomial test: $N=10$, $p=1$; Fig. 2; Fig. ESM_3; Tables ESM_4 and ESM_5), where 7 horses showed a clear preference for the head and two for the hoof (Binomial test: all $p<0.05$), while only 1 horse did not have a clear preference for either the head or the hoof (Binomial test: $N=24$, $p=0.15$). In the No Demo group all four horses that learned the manipulation of the box individually used the head (Binomial test: all $p>0.05$; Table ESM_6).

The highest percentage of hoof use (44% of the learners in the foot demo group compared to learners in other demo groups, Chi Square test: $N=5, \chi^2_4=118.5$, $p<0.001$) and the lowest percentage of head use (33% of the learners in the foot demo group compared to learners in other demo groups, Chi Square test: $N=5$, $\chi^2_4=36{,}46$, $p<0.001$) was in the Foot Demo group. While the lowest percentage of mixed head and hoof use (0%) was in the Head Demo group (Chi Square test: $N=5$, $\chi^2_4=32.92$, $p<0.001$; Fig. 2).

The horses' preference for using the hoof in the four demonstration groups increased from the first to the last successful opening, but not significantly (Chi Square test: $N=8$, $\chi^2_2=4$, $p=0.13$). One horse in the Hand Demo, one in the Head Demo, two in the Foot Demo, and one in the Mixed Demo used the hoof for the first opening. The rate of using the hoof changed from the first opening to the last opening with no horse using the hoof in the Hand and Head Demos, but 6 horses using the hoof in the Foot Demo and 3 in the Mixed Demo (Fig. ESM_3).

Animals contacting the experimenters

Horses that did not reach the learning criterion contacted the experimenters more often than horses that were successful in reaching the learning criterion (GLM: $N=63$, SE = 0.04, $z=-2.87$, $p=0.004$).

Discussion

Most horses' actions during the 20 trials to reach learning criterion did not match the demonstrated human actions. Most of the horses used their head, irrespective of the demonstrated action. Therefore, we suggest, that a few horses may have learned socially through 'Social facilitation' (Zajonc 1965) or 'Response facilitation' (Byrne 1994). As with the detour behaviour shown in a social learning experiment in dogs (Pongrácz et al. 2001) it cannot be excluded that some horses already had the pushing of buttons in their behaviour repertoire. Most automatic drinkers designed for horses require a button or lever to be pressed with the nose, so the presence of a demonstrator close to the button or taking action at the button may have

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caused them to use this behaviour in learning to open the test box. Most horses probably learned through enhancement, as discussed to be the primary social learning mechanisms for apes (Byrne and Whiten 1988; Whiten et al. 2004) dogs (Pongrácz et al. 2001; Mersmann et al. 2011) rats (Thorpe 1963), and social insects (Leadbeater and Dawson 2017). The human demonstrator may have served as an unconditioned, local stimulus indicating where to manipulate the feeding apparatus, i.e. they learned through 'Local enhancement' (Thorpe 1963), or the sight of the demonstrator eating may have stimulated the horse to learn to open the feeder at the location where the demonstrator found food ('Stimulus enhancement', Heyes 1994). In the present study it is impossible to clearly distinguish between local or stimulus enhancement, as the learning stimulus was given at the location of learning (Zentall 2006). Horses that initially learned through enhancement eventually learned to operate the button of the feeding apparatus by individual trial and error learning. This is supported by the observation that horses switched between manipulation techniques throughout the learning process. Combining simple social learning mechanisms with individual learning has been shown to generate fast learning of complex action sequences in mountain gorillas (Whalen et al. 2015) and has been discussed as common in dogs (Mersmann et al. 2011), in social insects (Leadbeater and Dawson 2017) and in many other species (Whalen et al. 2015). Future studies should also monitor potential changes in resolution time, for example latencies to approach the feed box or latencies to open the feed box, in order to provide more insight into the horses' learning process.

At the end of the 20 trials of the learning criterion six of nine learners in the Foot Demo group used the hoof, all learners in the Head and the Hand Demo group used the head and in the Mixed Demo group three used the hoof and seven the head. The increasing conformity with the demonstrator's action sequence could have been the result of observational conditioning. Observing that pushing the button with a particular action is followed by a food reward from the feed box may have served as a conditioned stimulus and established an operant response of using a matching action as in apes (Cook et al. 1985; Whiten et al. 2004) and elephants (Greco et al. 2013).

It is interesting that in the Foot Demo group significantly more horses than in the other demo groups matched the demonstrator's actions and used a hoof and significantly fewer used the head, despite the head being generally preferred in the other groups. This suggests that at least some horses endeavoured to follow the demonstrator's technique and may have copied the human demonstration, as has been mostly discussed in apes (Byrne and Whiten 1988; Whiten et al. 2004; Byrne 2009). This topic needs to be given further attention in a follow-up study.

In total, 80% of the test horses reached the learning criterion of opening the feeding apparatus twenty times in succession after observing a human demonstrator, slightly more than in the study of Schuetz et al. (2017). The large proportion of successful horses in the demonstration groups may have been the result of the studies' age selection, as young horses have been shown to learn better and faster (Nicol 2002; Krueger et al. 2014). Age differences within this preselected group did not have any effect on whether horses reached the learning criterion, as in dogs, where familiarity with the demonstrator appeared to overcome the effects of the dog's age or breed (Pongrácz et al. 2005).

Learning was not primarily due to matching the shape of the mark on the button to the mark on the food box, i.e. by relational discrimination learning (Flannery 1997; Blackmore et al. 2008). The marks on the button and the box increase the visibility of the experimental apparatus but not the learning success, as horses without demonstrations were not as successful in reaching the learning criterion as horses with demonstrations. Both were supplied with the same marks, but additional social information was needed to initiate a learning process.

Finally, it needs to be questioned whether horses actually perceive the demonstrator's hand as an extremity. The lack of matching, particularly in the Hand and Mixed demos, could have been caused by assuming a correspondence between the human hand and the horse's hoof that may not be the case from the horse's point of view. Humans use their hands for carrying and manipulating objects, and for grooming horses (Feh and de Mazières 1993); tasks that horses usually undertake with their head (Nicol 2002; McDonnell and Haviland 1995). Similarly, the head use of the human demonstrator may not have matched the horses' mouth use. If the horses were, in fact, trying to copy the action of the demonstrator, they may simply have used their heads as being what they considered to be the corresponding body part to the persons' hand or head.

Human interference with horse performance

The animals that reached the learning criterion in the present study applied more action types, and approached the human experimenters less often, than horses that did not reach it, as in Schuetz et al. (2017).

Some horses may have been motivated to try more action types and to be more persistent in solving the task, while others may have expected their caretakers to help solve the task and therefore gave up trying for themselves (horses: Sankey et al. 2011; Lesimple et al. 2012; Malavasi and Huber 2016; Ringhofer and Yamamoto 2017; dogs: Topál et al. 1997). In addition, even though the experimental set

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up of the present study tried to prevent unintentional interference by the demonstrating persons, some horses may have been affected by inadvertent cues given by caretakers when their horses were not successful for several trials. As horses react to emotional expressions displayed in pictures of humans (Smith et al. 2016) and in human voices (d'Ingeo et al. 2019), and read unintended human cues precisely (Pfungst 1907), sensitive horses may have been affected by their caretakers' expectations.

Both the mismatch between human and animal extremity use, and the possible inadvertent cues used by some human demonstrators, call for a follow up study with conspecific demonstrators performing several opening techniques for further conclusions on the horses preferred social learning mechanism. Krueger et al. (2014), found that when horse demonstrators opened a feeding apparatus only with their head, most observers used the same actions, but it is not possible to conclude from this whether the observers imitated the demonstration or simply applied a preferred head technique.

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Compliance with ethical standards

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed and approved by the animal welfare board of Nürtingen-Geislingen University. All procedures performed in the study involving human participants were in accordance with the ethical standards of the ethics committee of Nürtingen-Geislingen University and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Informed consent Informed consent was obtained from all individual participants included in the study.

References

Blackmore TL, Foster TM, Sumpter CE, Temple W (2008) An investigation of colour discrimination with horses (*Equus caballus*). Behav Process 78:387–396. https://doi.org/10.1016/j.beproc.2008.02.003

Brubaker L, Udell MAR (2016) Cognition and learning in horses (*Equus caballus*): what we know and why we should ask more. Behav Process 126:121–131. https://doi.org/10.1016/j.beproc.2016.03.017

Byrne RW (1994) The evolution of intelligence. In: Slater PJB, Halliday TR (eds) Behaviour and evolution. Cambridge University Press, Cambridge, pp 223–265

Byrne RW (2002) Imitation of novel complex actions: what does the evidence from animals mean? In: Snowdon CT, Roper TJ (eds) Advances in the study of behavior. Academic Press, San Diego, pp 77–105

Byrne RW (2009) Animal imitation. Curr Biol 19:R111–R114. https://doi.org/10.1016/j.cub.2008.11.027

Byrne R, Whiten A (1988) Machiavellian intelligence. Oxford Univ Press, Oxford

Carroll J, Murphy CJ, Neitz M, Hoeve JN, Neitz J (2001) Photopigment basis for dichromatic color vision in the horse. J Vis 1:80–87. https://doi.org/10.1167/1.2.2

Cook M, Mineka S, Wolkenstein B, Laitsch K (1985) Observational conditioning of snake fear in unrelated rhesus monkeys. J Abnorm Psychol 94:591–610

Custance D, Whiten A, Fredman T (1999) Social learning of an artificial fruit task in capuchin monkeys (*Cebus apella*). J Comp Psychol 113:13–23. https://doi.org/10.1037/0735-7036.113.1.13

Deutsche Reiterliche Vereinigung e.V (2014) Pferde verstehen—Umgang und Bodenarbeit. FN Verlag der deutschen Reiterlichen Vereinigung GmbH, Warendorforey

d'Ingeo S, Quaranta A, Siniscalchi M, Stomp M, Coste C, Bagnard C et al (2019) Horses associate individual human voices with the valence of past interactions: a behavioural and electrophysiological study. Sci Rep 9:11568. https://doi.org/10.1038/s41598-019-47960-5

Dorey NR, Conover AM, Udell MAR (2014) Interspecific communication from people to horses (*Equus ferus caballus*) is influenced by different horsemanship training styles. J Comp Psychol 128(4):337–342. https://doi.org/10.1037/a0037255

Feh C, de Mazières J (1993) Grooming at a preferred site reduces heart rate in horses. Anim Behav 46:1191–1194. https://doi.org/10.1006/anbe.1993.1309

Flannery B (1997) Relational discrimination learning in horses. Appl Anim Behav Sci 54:267–280. https://doi.org/10.1016/S0168-1591(97)00006-3

Galef BG (1989) Enduring social enhancement of rats' preferences for the palatable and the piquant. Appetite 13:81–92. https://doi.org/10.1016/0195-6663(89)90106-2

Greco BJ, Brown TK, Andrews JRM, Swaisgood RR, Caine NG (2013) Social learning in captive African elephants (*Loxodonta africana africana*). Anim Cogn 16:459–469. https://doi.org/10.1007/s10071-012-0586-7

Hall CA, Cassaday HJ, Derrington AM (2003) The effect of stimulus height on visual discrimination in horses. J Anim Sci 81(7):1715–1720

Healy SD, Jones CM (2002) Animal learning and memory: an integration of cognition and ecology. Zoology 105:321–327. https://doi.org/10.1078/0944-2006-00071

Heyes CM (1994) Social learning in animals: categories and mechanisms. Biol Rev 69:207–231. https://doi.org/10.1111/j.1469-185X.1994.tb01506.x

Hopewell L, Leaver L, Lea S, Wills A (2010) Grey squirrels (*Sciurus carolinensis*) show a feature-negative effect specific to social learning. Anim Cogn 13:219–227. https://doi.org/10.1007/s10071-009-0259-3

Hoppitt W, Laland KN (2008) Social processes influencing learning in animals: a review of the evidence. Adv Study Behav 38:105–165. https://doi.org/10.1016/S0065-3454(08)00003-X

Irving-Pease EK, Ryan H, Jamieson A, Dimopoulos EA, Larson G, Frantz LAF (2019) Paleogenomics of animal domestication. In: Lindqvist C, Rajora OP (eds) Paleogenomics: genome-scale analysis of ancient DNA. Springer International Publishing, Cham, pp 225–272

Krueger K, Heinze J (2008) Horse sense: social status of horses (*Equus caballus*) affects their likelihood of copying other horses` behavior. Anim Cogn 11:431–439. https://doi.org/10.1007/s10071-007-0133-0

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Krueger K, Flauger B, Farmer K, Maros K (2011) Horses (*Equus caballus*) use human local enhancement cues and adjust to human attention. Anim Cogn 14:187–201. https://doi.org/10.1007/s10071-010-0352-7

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

Kubinyi E, Topál J, Miklósi Á, Csányi V (2003) Dogs (*Canis familiaris*) learn their owners via observation in a manipulation task. J Comp Psychol 117:156–165. https://doi.org/10.1037/0735-7036.117.2.156

Lamp 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

Leadbeater E, Dawson EH (2017) A social insect perspective on the evolution of social learning mechanisms. Proc Natl Acad Sci USA 114:7838–7845

Lesimple C, Sankey C, Richard M-A, Hausberger M (2012) Do horses expect humans to solve their problems? Front Psychol 3:306. https://doi.org/10.3389/fpsyg.2012.00306

Lovrovich P, Sighieri C, Baragli P (2015) Following human-given cues or not? Horses (*Equus caballus*) get smarter and change strategy in a delayed three choice task. Appl Anim Behav Sci 166:80–88. https://doi.org/10.1016/j.applanim.2015.02.017

Malavasi R, Huber L (2016) Evidence of heterospecific referential communication from domestic horses (*Equus caballus*) to humans. Anim Cogn 19:899–909. https://doi.org/10.1007/s10071-016-0987-0

Maros K, Gácsi M, Miklósi Á (2008) Comprehension of human pointing gestures in horses (*Equus caballus*). Anim Cogn 11:457–466. https://doi.org/10.1007/s10071-008-0136-5

McDonnell SM, Haviland JCS (1995) Agonistic ethogram of the equid bachelor band. Appl Anim Behav Sci 43:147–188. https://doi.org/10.1016/0168-1591(94)00550-X

Mejdell CM, Buvik T, Jørgensen GHM, Bøe KE (2016) Horses can learn to use symbols to communicate their preferences. Appl Anim Behav Sci 184:66–73. https://doi.org/10.1016/j.applanim.2016.07.014

Mersmann D, Tomasello M, Call J, Kaminski J, Taborsky M (2011) Simple mechanisms can explain social learning in domestic dogs (*Canis familiaris*). Ethology 117:675–690. https://doi.org/10.1111/j.1439-0310.2011.01919.x

Miklósi Á, Soproni K (2006) A comparative analysis of animals' understanding of the human pointing gesture. Anim Cogn 9:81–93. https://doi.org/10.1007/s10071-005-0008-1

Mills DS, McDonnell SM (2005) The domestic horse. Cambridge University Press, Camebridge

Nicol CJ (2002) Equine learning: progress and suggestions for future research. Appl Anim Behav Sci 78:193–208. https://doi.org/10.1016/S0168-1591(02)00093-X

Pfungst O (1907) Der Kluge Hans. Ein Beitrag zur nichtverbalen Kommunikation. Frankfurter Fachbuchhandlung für Psychologie, Frankfurt am Main

Pongrácz P, Miklósi Á, Kubinyi E, Gurobi K, Topál J, Csányi V (2001) Social learning in dogs: the effect of a human demonstrator on the performance of dogs in a detour task. Anim Behav 62:1109–1117. https://doi.org/10.1006/anbe.2001.1866

Pongrácz P, Miklósi Á, Timár-Geng K, Csányi V (2004) Verbal attention getting as a key factor in social learning between dog and human. J Comp Psychol 118:375–383

Pongrácz P, Miklósi Á, Vida V, Csányi V (2005) The pet dogs ability for learning from a human demonstrator in a detour task is independent from the breed and age. Appl Anim Behav Sci 90:309–323. https://doi.org/10.1016/j.applanim.2004.08.004

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 (2012) Cross-modal individual recognition in domestic horses (*Equus caballus*) extends to familiar humans. Proc R Soc B 279:3131–3138. https://doi.org/10.1098/rspb.2012.0626

Proops L, McComb K, Reby D (2009) Cross-modal individual recognition in domestic horses (*Equus caballus*). Proc Natl Acad Sci USA 106:947–951. https://doi.org/10.1073/pnas.0809127105

Proops L, Walton M, McComb K (2010) The use of human-given cues by domestic horses, *Equus caballus*, during an object choice task. Anim Behav 79:1205–1209. https://doi.org/10.1016/j.anbehav.2010.02.015

Proops L, Rayner J, Taylor AM, McComb K (2013) The responses of young domestic horses to human-given cues. PLoS One. https://doi.org/10.1371/journal.pone.0067000

R Development Core Team (2019) R: a language and environment for statistical computing. http://www.R-project.org

Rescorla RA, Holland PC (1982) Behavioral Studies of Associative Learning in Animals. Ann Rev Psychol 33:265–308

Ringhofer M, Yamamoto S (2017) Domestic horses send signals to humans when they face with an unsolvable task. Anim Cogn 20:397–405. https://doi.org/10.1007/s10071-016-1056-4

Rørvang MV, Ahrendt LP, Christensen JW (2015) A trained demonstrator has a calming effect on naïve horses when crossing a novel surface. Appl Anim Behav Sci 171:117–120. https://doi.org/10.1016/j.applanim.2015.08.008

Sankey C, Henry S, André N, Richard-Yris M-A, Hausberger M (2011) Do horses have a concept of person? PLoS One. https://doi.org/10.1371/journal.pone.0018331

Schuetz A, Farmer K, Krueger K (2017) Social learning across species: horses (*Equus caballus*) learn from humans by observation. Anim Cogn 20:567–573. https://doi.org/10.1007/s10071-016-1060-8

Shettleworth SJ (1998) Cognition, evolution and behaviour. Oxford University Press, Oxford

Smith AV, Proops L, Grounds K, Wathan J, McComb K (2016) Functionally relevant responses to human facial expressions of emotion in the domestic horse (*Equus caballus*). Biol Lett. https://doi.org/10.1098/rsbl.2015.0907

Thorpe WH (1963) Learning and instinct in animals. Methuen, London

Tomasello M (1990) Cultural transmission in the tool use and communicatory signalling of chimpanzees? In: Parker ST, Gibson KR (eds) Language and intelligence in monkeys and apes. Cambridge University Press, Cambridge, pp 274–311

Topál J, Miklósi A, Csányi V (1997) Dog-human relationship affects problem solving be-havior in the dog. Anthrozoos 10:214–224

Whalen A, Cownden D, Laland K (2015) The learning of action sequences through social transmission. Anim Cogn 18:1093–1103. https://doi.org/10.1007/s10071-015-0877-x

Whiten A, Ham R (1992) On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. Adv Study Behav 21:239–283

Whiten A, Horner V, Litchfield CA, Marshall-Pescini S (2004) How do apes ape? Learn Behav 32:36–52. https://doi.org/10.3758/BF03196005

Zajonc RB (1965) Social facilitation. Science 149:269–274. https://doi.org/10.1126/science.149.3681.269

Zentall TR (2006) Imitation: definitions, evidence, and mechanisms. Anim Cogn 9:335–353. https://doi.org/10.1007/s10071-006-0039-2

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