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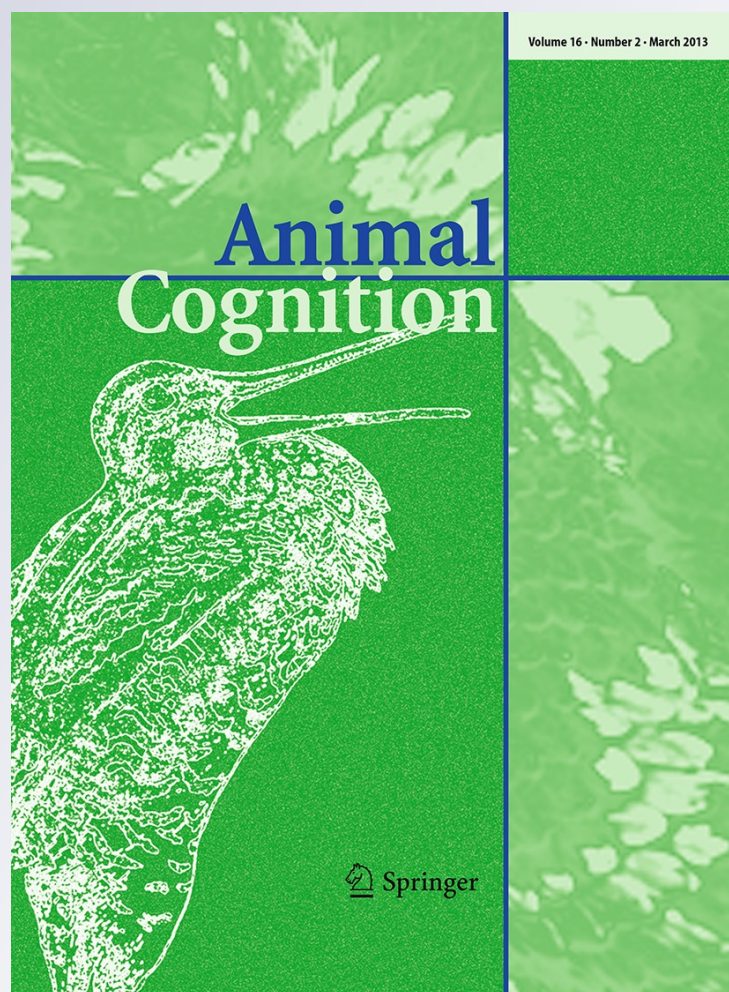
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Spatial cognition and perseveration by horses, donkeys and mules in a simple A-not-B detour task

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Abstract We investigated perseveration and detour behaviour in 36 equids (*Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*) and compared these data to those of a previous study on domestic dogs (*Canis familiaris*). The animals were required to make a detour through a gap at one end of a straight barrier in order to reach a visible target. After one, two, three or four repeats (A trials), the gap was moved to the opposite end of the barrier (B trials). We recorded initial deviations from the correct solution path and the latency to crossing the barrier. In the A trials, mules crossed the barrier significantly faster than their parental species, the horses and donkeys. In the B trials, following the change of gap location, all species showed a reduction in performance. Both dogs and horses exhibited significant spatial perseveration, going initially to the previous gap location. Donkeys and mules, however, performed at chance level. Our results suggest that hybrid vigour in mules extends to spatial abilities.

Keywords Equids · Donkeys · Horses · Mules · Dogs · Detour · Spatial reasoning · A-not-B · Perseveration

Introduction

The aim of this study was to compare the spatial abilities of mules, horses, donkeys and dogs in an initial detour task

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and then to assess their perseverative behaviour when the direction of the detour is changed. In a detour task, the subject must reach its goal by avoiding an intervening object, which means a straight-line solution is not possible. So far, only one study has looked into the performance of horses in a detour task (Baragli et al. 2011). Here, symmetrical and asymmetrical U-shaped barriers were used. Horses showed a persistent side bias and did not preferentially use the shorter detour in the asymmetrical barrier task. There was no change in the detour time between the first and the last trial. Overall, their results indicate that horses can find their way around a U-shaped barrier, but they tend to persevere with their first route even when a shorter route becomes available. Previous research on visual reversal learning in horses has also shown that they have difficulties inhibiting a learned response (Sappington et al. 1997). Donkeys are also able to navigate a barrier (Baragli and Regolin 2008). To our knowledge, mules have not yet been tested on a detour task.

The tendency to maintain a previous route despite the availability of a better one has also been found in dogs (Osthaus et al. 2010). In this study, dogs were able to solve simple detour tasks but persevered with a previously learned route even if this was visibly blocked and even after they had navigated through the new gap several times. This tendency to approach a previously successful location despite obvious visual signs that the location has now been changed is also seen in dogs when locating hidden rewards (Gácsi et al. 2009) and is called the A-not-B error, a phenomenon first described in human infants (Piaget 1954, p. 44).

In this study, we assess for the first time the spatial abilities and perseveration behaviour of horses, donkeys and mules in an A-not-B detour task and compare their responses to those of domestic dogs. The mule, the hybrid

of a male donkey and a female horse, has been bred for centuries because many of its traits display hybrid vigour (superiority to the traits of the parent species) (Travis 1990). Our previous research demonstrated that hybrid vigour in mules may extend to their cognitive abilities, as shown by superior performance in a visual discrimination task (Proops et al. 2009). However, anecdotally, mules and donkeys are known for their stubbornness and inflexibility in learning. We therefore tested horses, donkeys and mules to see whether there would be differences in spatial cognition and perseveration behaviour between these three equids as well as any further evidence of hybrid vigour in the cognitive abilities of mules.

Methods

Study animals

We tested 12 mules (mean age in years = 26, range 20–32, SD = 3), 12 horses (mean age = 18, range 10–31, SD = 7) and 12 donkeys (mean age = 17, range 2–29, SD = 11) and incorporated the data from 12 dogs (mean age = 2, range 1–6, SD = 1.7) randomly selected from our previous experiment (see Osthau et al. 2010 for details). The horses were tested in two different outdoor locations in Kent and the donkeys and mules at Axnoller Farm in Dorset.

Method

We applied the same methodology as in our 2010 study with dogs (Osthau et al. 2010) but with a larger apparatus constructed in outdoor ménages with show jumping poles and mobile fences (see Fig. 1). The animals had to walk unaccompanied from the starting point to the target (a person with a feed bucket) through a gap in the barrier (A trial). The initial position of the gap was counterbalanced with half of the subjects beginning with the gap on the left and half on the right. After either one, two, three or four A trials, the location of the gap was moved to the other end of the barrier (B trials), yet still positioned at the same distance and angle from the starting point. There were three individuals of each species in each experimental group (where A1 means the subject experienced one A trial, A2 two A trials, etc.). Each animal completed four B trials. The reinforcers used were pieces of carrot, apple and horse pellets in a bucket. The animals were allowed to feed for approximately 5 s from the bucket at the end of each trial before they were led back to the starting point around the outside of the enclosure (alternating between left and right routes where possible).

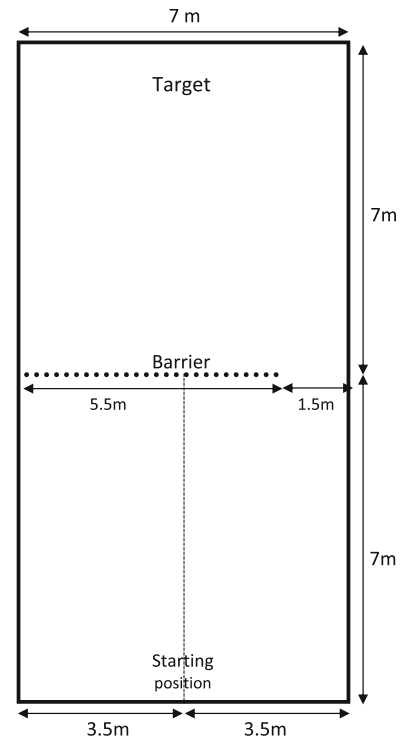


Fig. 1 Diagram of the experimental set-up

Statistical and behavioural analysis

Two measures of performance were recorded, accuracy rates and solution times. A trial was scored as incorrect if the animal crossed an invisible line between the starting point and the target (the dashed vertical line in the lower half of Fig. 1), which represented entering the blocked-off half of the starting area. Solution time was defined as the time taken to move from the starting point to the gap, ending when the shoulders of the animal passed through. Accuracy rates for the equids and dogs were comparable, and so statistical analyses were performed on the four species; due to differences in arena and body size, dogs were not included in the analyses of solution times. The accuracy rates of the equids and the dogs for each A and B trial were compared to chance levels using two-tailed binomial tests, and the differences between the species/conditions in accuracy rates were analysed using 2×4 Fisher's exact tests. Solution times were not normally distributed and could not be corrected by transformations so species differences in solution times were assessed using Kruskal–Wallis tests corrected for ties. To determine where any differences in solution times lay, two orthogonal contrasts per trial were performed, comparing mules to their parental species and horses to donkeys. McNemar tests (calculating exact binomial probabilities) for each species were used to compare changes in accuracy rates from the last A trial to the first B trial. Differences between

the number of subjects improving and regressing from the last A trial to the first B trial across species were analysed using a Fisher's exact test. The effect of the number of repetitions of the A trial on the solution times in the B1 trial was determined using a Jonckheere–Terpstra test and a Spearman's Rho correlation.

Results

Performance in A trials

Accuracy rate

In the first trial, the mules and dogs performed significantly above chance but the donkeys and horses did not (see Table 1). However, comparison of species' performance rates revealed no significant differences in the number of subjects correct in the first trial (Fisher's exact test: $N = 48$, $P > 0.99$). All subjects achieved 100 % correct response rates from the second A trial.

Solution times

There were significant differences between the equid species' solution times in trials A1 and A2, and the differences in solution times for subjects participating in trials A3 and A4 bordered on significance (Kruskal–Wallis tests: A1 trial: $\chi^2_2 = 8.47$, $P = 0.014$, $N = 36$; A2 trial: $\chi^2_2 = 8.92$, $P = 0.012$, $N = 27$; A3 trial: $\chi^2_2 = 5.47$, $P = 0.065$, $N = 18$; A4 trial: $\chi^2_2 = 5.60$, $P = 0.061$, $N = 9$; see Fig. 2). Mules were significantly faster than their parent species, the horses and donkeys, in the first three A trials; in the final A trial, the horses and donkeys were as fast as the mules (Kruskal–Wallis tests: A1 trial: $\chi^2_1 = 6.73$,

$P < 0.025$; A2 trial: $\chi^2_1 = 8.45$, $P < 0.01$; A3 trial: $\chi^2_1 = 5.31$, $P < 0.05$; A4 trial: $\chi^2_1 = 3.20$, $P > 0.05$). There were no differences in solution times between the horses and donkeys in any of the A trials (Kruskal–Wallis tests: A1 trial: $\chi^2_1 = 1.74$, $P > 0.05$; A2 trial: $\chi^2_1 = 0.47$, $P > 0.05$; A3 trial: $\chi^2_1 = 0.15$, $P > 0.05$; A4 trial: $\chi^2_1 = 2.40$, $P > 0.05$).

Performance in B trials

Accuracy rate

After the gap location was moved, both horses and dogs committed the A-not-B error, performing significantly below chance, whereas the mules and donkeys were at chance level. In the second B trial, the donkey group successfully chose the correct direction at above chance levels, whereas the other species groups were at chance. By the third B trial, all equids were performing above chance level, and by the fourth B trial, all four groups were taking the direct route (see Table 1). Comparison of species' performance rates revealed no significant differences in the number of correct responses in any of the B trials (Fisher's exact test: $N = 48$; trial B1: $P > 0.99$; trial B2: $P = 0.44$; trial B3: $P = 0.17$; trial B4: $P > 0.99$).

Solution times

There were significant differences between the equid species' solution times for trials B2, B3 and B4, but the difference in solution times for the first B trials was not significant, probably due to the large variation in solution times (Kruskal–Wallis tests: B1 trial: $\chi^2_2 = 3.89$, $P = 0.14$; B2 trial: $\chi^2_2 = 10.13$; $P = 0.006$; B3 trial: $\chi^2_2 = 9.17$, $P < 0.01$; B4 trial: $\chi^2_2 = 12.34$, $P < 0.002$; see Fig. 2).

Table 1 Accuracy rates for each species group as determined by the number of subjects that initially moved towards the correct side of the barrier without deviation

Trial	Mules		Donkeys		Horses		Dogs	
	Score	<i>P</i>	Score	<i>P</i>	Score	<i>P</i>	Score	<i>P</i>
A1	10/12*	0.039	9/12	0.15	9/12	0.15	10/12*	0.039
A2	9/9*	0.004	9/9*	0.004	9/9*	0.004	9/9*	0.004
A3	6/6*	0.031	6/6*	0.031	6/6*	0.031	6/6*	0.031
A4	3/3*	–	3/3*	–	3/3*	–	3/3*	–
B1	3/12	0.15	3/12	0.15	2/12†	0.039	2/12†	0.039
B2	8/12	0.39	10/12*	0.039	7/12	0.77	6/12	>0.99
B3	11/12*	0.006	10/12*	0.039	12/12*	0.0005	8/12	0.39
B4	12/12*	0.0005	12/12*	0.0005	12/12*	0.0005	11/12*	0.006

P values for binomial probabilities (two-tailed) are given

* Group performing significantly above chance level

† Group performing significantly below chance level

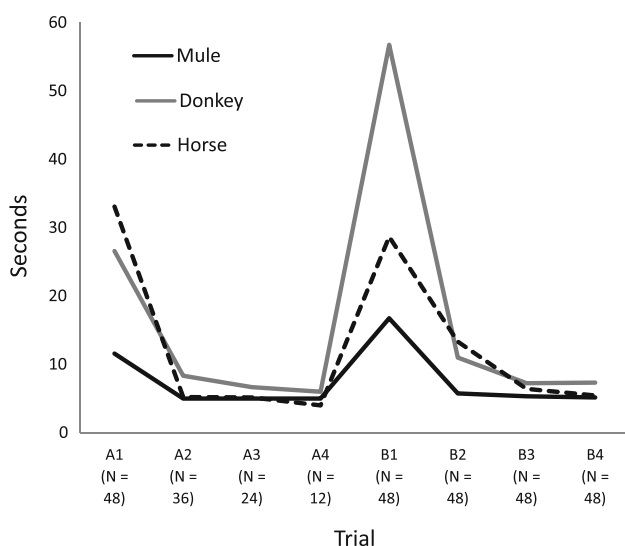


Fig. 2 Mean time to pass barrier in seconds, per equid species across all test trials

Although the mules completed trial B1 in a mean of 16.75 s (SEM \pm 3.3), the horses completed the trial in 44.67 s (\pm 13.2) and the donkeys in 56.75 s (\pm 24.0), this difference was not statistically significant, again probably due to the large variation in solution times (Kruskal–Wallis test: trial B1: $\chi_1^2 = 3.86$, $P > 0.05$); however, the mules were faster than their parent species in all subsequent B trials (Kruskal–Wallis tests: B2 trial: $\chi_1^2 = 9.74$, $P < 0.005$; B3 trial: $\chi_1^2 = 7.31$, $P < 0.025$; B4 trial: $\chi_1^2 = 8.14$, $P < 0.005$). There were no differences in the solution speeds of the donkeys and horses in any of the B trials (Kruskal–Wallis tests: B1 trial: $\chi_1^2 = 0.023$, $P > 0.05$; B2 trial: $\chi_1^2 = 0.40$, $P > 0.05$; B3 trial: $\chi_1^2 = 1.85$, $P > 0.05$; B4 trial: $\chi_1^2 = 4.20$, $P > 0.05$).

Effect of gap position change

Accuracy rate

All four species showed a significant reduction in initial accuracy rates from a subject's last A trial to trial B1 (horses: $P = 0.002$; donkeys: $P = 0.02$; mules: $P = 0.004$; dogs: $P = 0.02$). There were no significant differences between the species in the number of subjects that improved or regressed from their last A trial to trial B1 ($N = 48$, $P > 0.99$).

Solution times

There was no significant difference in the effect of the change in gap location on solution times among species (Kruskal–Wallis test: $\chi_2^2 = 0.73$, $P = 0.70$). The mean

increase in solution time between a subject's last A trial and B1 was 11.42 s (\pm 3.41) for mules, 28.83 s (\pm 12.51) for horses and 39.42 s (\pm 27.45) for donkeys. The solution times for the horse and donkey groups were not significantly longer after the change in gap location compared to the mule group (Kruskal–Wallis test: $\chi_1^2 = 0.62$, $P > 0.05$). The location change in the first B trial did not affect the donkey and horse solution times differently (Kruskal–Wallis test: $\chi_1^2 = 0.10$, $P > 0.05$).

Effect of number of A trials on responses to the first B trial

Accuracy rate

Across all four species, those subjects receiving only one A trial were at chance level in trial B1 ($N = 12$, $K = 6$, $P > 0.99$), whereas the groups receiving two, three or four A trials were all more likely to commit the A-not-B error (2 A trials: $N = 12$, $K = 1$, $P = 0.006$; 3 A trials: $N = 12$, $K = 2$, $P = 0.039$; 4 A trials: $N = 12$, $K = 1$, $P = 0.006$). This difference in perseveration rates according to the number of A trial repetitions bordered on significance (Fisher's exact test: $N = 48$, $P = 0.055$).

Solution times

There were no significant differences in solution times depending on the number of A trial repetitions (Jonckheere–Terpstra test: $J = 484.5$, $Z = 0.967$, $P = 0.333$), nor did the time needed to pass the barrier after the change correlate with the number of A trial repetitions ($r_{34} = 0.044$, $P = 0.80$).

Discussion

All species groups were able to navigate a simple detour, with all subjects travelling directly to the gap from the second A trial. However, the mules were significantly faster than the horses and donkeys when solving this novel detour task, suggesting that the hybrid vigour seen in mules may extend to spatial cognition. In the subsequent B1 trial, in which the location of the gap was moved to the other side of the testing area, all groups showed a significant decrease in performance. In their first trial after the location change, the accuracy of mules and donkeys reduced to chance level, whereas horses and dogs showed significant spatial perseveration, approaching the location of the previous gap more often than the correct one and thus making the A-not-B error. The 'stubborn' donkeys as a group were the first to perform above chance level after the change (in

trial B2), despite their highly impaired solution times in trial B1. Despite similar perseveration rates, there continued to be differences in solution times across species. The mules were faster than the donkeys and horses in subsequent B trials, suggesting that they may also be more flexible in spatial learning tasks.

We believe that the differences in solution times within the equid group reflect genuine cognitive differences rather than the physical or possibly motivational differences of the species. The donkeys generally worked at a slow walking speed, mules at a faster walk and horses sometimes even at a trot, yet the mules had the fastest solution times, while the solution times of the horses and donkeys were similar. By the fourth A trial, the difference between the solution times of the equids disappeared, also suggesting that the observed differences were not due to any physical or motivational limits but rather to different spatial problem solving abilities. The general spatial problem solving abilities and the effects of the gap location change were surprisingly similar in dogs (predators) and in equids (a prey species). Despite their very different evolutionary and domestication history, these animals produce the same spatial A-not-B error, which can also be found in human infants (McKenzie and Bigelow 1986).

As expected, repetition of the A trials appeared to hinder processing of a novel route in subsequent B trials. Subjects receiving more than one repetition of the A trial tended to commit the A-not-B error, whereas subjects receiving only one A trial were at chance level on the first B trial. The mule group that received one A trial was the only group to solve the subsequent B trial faster than the A trial, indicating task flexibility and a potential to 'learn to learn'. This supports previous findings that mules are quicker than horses and donkeys, not only to learn an initial discrimination task, but also to learn subsequent discriminations (Proops et al. 2009).

Horses, mules and donkeys are used in recreation and sport, and knowing more about their cognitive abilities, especially their spatial learning and their flexibility, will improve their welfare through adapted expectations by their trainers. Reluctance to change and perseveration in

spatial behaviour might also influence the outcome of preference tests and, therefore, needs to be taken into account when designing behavioural studies. All equid groups were able to rapidly learn a detour task but were strongly influenced by a prior detour location when the detour location changed, showing significantly reduced performance even if they had only completed the initial detour twice. The dogs and equids displayed similar perseveration rates. But mules were faster than subjects from their parental species in both the initial detour task and the subsequent trials when the gap location had changed, suggesting that their hybrid vigour may well extend to spatial abilities and indicating that, far from being stubborn, they may be more flexible learners than horses and donkeys.

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