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SHORT COMMUNICATION

Spatial perseveration error by alpacas (*Vicugna pacos*) in an A-not-B detour task

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Abstract

Spatial perseveration has been documented for domestic animals such as mules, donkeys, horses and dogs. However, evidence for this spatial cognition behavior among other domestic species is scarce. Alpacas have been domesticated for at least 7000 years yet their cognitive ability has not been officially reported. The present article used an A-not-B detour task to study the spatial problem-solving abilities of alpacas (*Vicugna pacos*) and to identify the perseveration errors, which refers to a tendency to maintain a learned route, despite having another available path. The study tested 51 alpacas, which had to pass through a gap at one end of a barrier in order to reach a reward. After one, two, three or four repeats (A trials), the gap was moved to the opposite end of the barrier (B trials). In contrast to what has been found in other domestic animals tested with the same task, the present study did not find clear evidence of spatial perseveration. Individuals' performance in the subsequent B trials, following the change of gap location, suggests no error persistence in alpacas. Results suggest that alpacas are more flexible than other domestic animals tested with this same task, which has important implications in planning proper training for experimental designs or productive purposes. These results could contribute toward enhancing alpacas' welfare and our understanding of their cognitive abilities.

Keywords Camelids · Spatial cognition · Response inhibition · Inhibitory control

Introduction

Spatial perseveration has been evaluated using an A-not-B detour test in dogs, horses, mules and donkeys, assessing their spatial abilities in an initial detour task and then their tendency to maintain a learned route, in spite of other available alternatives (e.g., a clearly visible change in the location of a gap) being available (Osthaus et al. 2010, 2013). Results from these studies have shown that both dogs and horses exhibited significant spatial perseveration; however, donkeys and mules performed at chance level suggesting that hybrid vigor in mules extends to spatial abilities (Osthaus et al. 2010, 2013). This perseverative behavior, called "perseveration error," implies a lack of inhibition of a previously learned response (Osthaus 2017, Osthaus et al. 2010, 2013). Response inhibition has the advantage of dealing with a relatively simple and straightforward process, the overriding of a learned or already initiated action. Deficient inhibitory processes profoundly affect everyday life, causing impulsive behaviors, which are generally detrimental for the individual (Bari and Robbins 2013). Therefore, the A-not-B detour task can assess the behavioral flexibility of an animal

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in response to a change in their environment (Morand-Ferron et al. 2015).

The alpacas (*Vicugna pacos*) are South American camelids domesticated from vicuñas (*Vicugna vicugna*) (Marin et al. 2007) Throughout their process of domestication that started between 6000 and 7000 years ago (Wheeler 1995), alpacas have had to adapt to several environments (e.g., desert, altiplano and steppe), where the quantities and qualities of the resources can vary and animals must take advantage of the different vegetation forms (Benitez et al. 2006). Their ancestry (traits of the parent species) and their domestication process could have further developed their spatial cognitive abilities allowing them to adapt to unstable environments (Marshall-Pescini et al. 2015; MacLean et al. 2014). Due to these adaptive pressures, alpacas, similarly to goats (Nawroth et al. 2014), could present more flexible foraging behavior than some of the other domesticated animals tested in previous studies (e.g., horses, mules and donkeys) (Osthaus et al. 2013). In addition, these three species and specially also dogs, during their domestication process, have fulfilled a wide variety of roles for humans, receiving a strong selection for docility, fearlessness and non-aggressive behavior toward humans (Hare et al. 2002). This motivational and attentional bias toward humans could partially explain their perseveration behavior in a similar detour task (see Hare and Woods 2013 and Polgár et al. 2015 for a review). On the other hand, alpacas have been mainly selected only for fine fiber production (Wheeler 1995), which involves less human handling and, accordingly, more attentional bias toward the environmental cues than that exhibited by other species tested in this task. Therefore, due to these two differences (flexible foraging behavior and less attentional bias toward humans), alpacas are expected to show good performance in spatial cognitive tests that are similar to those that have been carried out on these other four domestic animals. However, to our knowledge, no studies on this topic have been carried out on alpacas so far.

The present study aims to explore whether they show a flexible learning behavior, through the application of an A-not-B detour test. To our knowledge, this is the first study in which the spatial cognitive abilities and the presence of the perseveration error behavior will be evaluated in this species. The ability that alpacas have to move in a direction, overcoming an obstacle in order to reach a target, such as food, will be determined. In addition, the relation of the number of repetitions of A trials (that is, the number of times a problem is solved in a certain way) with the appearance of the spatial perseveration error behaviors when a change occurs and the problem cannot be solved in the previous way anymore is also studied. Research carried out on horses, mules, donkeys and dogs has shown that the animals which repeated the trial more than once tended to present a perseveration error (Osthaus et al. 2010, 2013). Furthermore, the present study is not only the first to apply this spatial cognition test in alpacas specifically, but also, to our knowledge, it constitutes the first official cognitive study carried out on this species and on a camelid.

Methods

Study subjects

A total amount of 51 alpacas were used (Huacaya and Suri breeds), 22 females and 29 males, each of them belonging to the *Gulmué* Breeding Center in Chile, which is dedicated exclusively to the fiber production. The alpacas were always tested in the same outdoor area of the center.

Method

The experiment was conducted between June 2016 and July 2017. Our test procedure was based on the one used by Osthaus et al. (2010, 2013). For the present study, a rectangular wooden structure was built, using wooden posts and plastic mesh, with the following measurements: 6.40 m (width) × 9 m (length), divided in the middle by a plastic mesh barrier, which had a 1.16-m-wide gap at one end (Fig. 1). This gap was moved from one end of the barrier to the other as required in the experiment in order to determine the ability of alpacas to move through the gap to cross the barrier. A movable chute of plastic mesh was used to drive the animals from the exit of the circuit to the starting point again, in order to reduce, as much as possible, physical restraint and the direct handling of the animal.

Two measures of performance were recorded: the accuracy rates and the solution times. In relation to the accuracy rates, a trial was scored as incorrect when the animal crossed with one foot an invisible line toward the closed gap, in the second blocked-off half of the starting area (the darker gray quadrants to the left of the dashed vertical line in the second half of Fig. 1). This criterion was slightly different from the one used by Osthaus et al. (2010, 2013), who considered a trial was incorrect as soon as the animal crossed with one foot an invisible line toward the closed gap, between the starting point and the target, in the first blocked-off half of the starting area (the light gray quadrants to the right of the dashed vertical line of Fig. 1). Contrary to the animals tested in Osthaus et al.'s (2010, 2013) study, where animals would usually explore the blocked off area only in the first A trial, alpacas in the present study kept exploring the experimental structure in all of the A and B trials, regardless of the number of repetitions, and rarely aimed straight for the gap (see Electronic Supplementary Material ESM videos). For

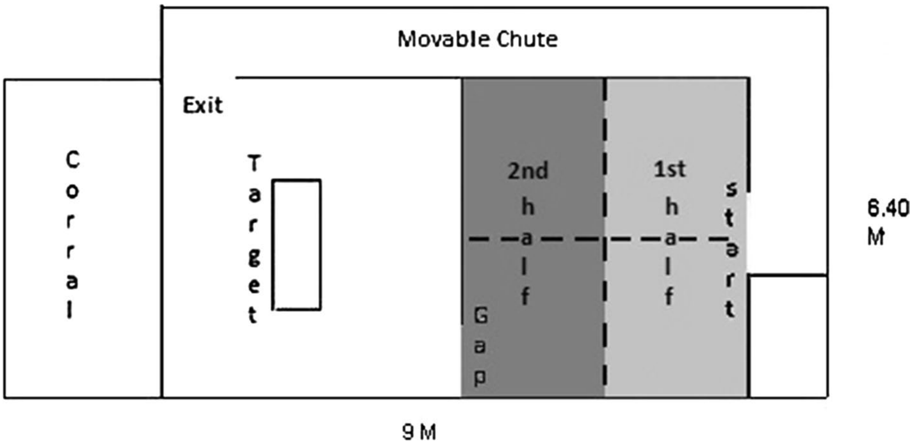

Fig. 1 Diagram of the experimental set up (based on Osthaus et al. 2013)

comparative purposes, data were also coded and analyzed using Osthaus et al.'s (2010, 2013) criterion (see ESM). In addition, a potential side bias was analyzed using a Chi-square test of independence, to control for the fact that the animals were driven by the experimenters from the right of the outside of the enclosure to the starting point located at the middle of the testing area. Accordingly, using Osthaus et al. (2010, 2013) criterion, a bias to the left was found for all trials (potentially explained by the fact that the animals were continuing their previous trajectory). Side bias was only found in 3 of 8 trials using the present study's criterion, which could be explained by chance (see details in ESM). This supports the idea that in this specific test, the present study's criterion is a better measure to study error perseverance in this species.

The solution time was defined as the time used by the animal to move from the starting point to the gap, ending when the shoulders of the animal passed through it. Time was measured using video recordings of each trial.

To study the influence of the number of A trials in subsequent B trials performance, the alpacas were randomly assigned to four groups which differed in the number of A trials they received before the position of the gap was change (after one (G1), two (G2), three (G3) and four (G4) A trials). Group G1, group G2 and group G3 consisted of 10 individuals each. Twenty-one individuals were assigned to G4, the group with four A trials, which was the group expected to be more influenced by previous A trials. Due to the sample size's influences on power, a bigger sample size was necessary for the analyses needed in this last group as more information from the group would be required in the case of persistence of the error. In G4, after four A trials, the gap was moved to the opposite side (trial B). In G3, G2 and G1, A trials were carried out three, two and one times, respectively, and then, the gap was changed to the opposite side, carrying out four B trials four times. To identify each animal, the earmark number, sex and the assigned experimental group assigned were recorded.

Animals walked from the starting point to the target (consisting of a feeder with alfalfa as a positive reinforcement), going through a gap in the barrier (trial A). After alpacas completed one, two, three or four A trials, the gap was moved to the opposite side of the barrier (trial B).

The presentation of the gap was counterbalanced across subjects for A and B trials; thus, half of the animals in each group began the test with the gap located on the left side and the other half with the gap located on the right side. At the end of each test, the animals were fed for a couple of seconds at the feeders, and then, they were returned driven by the experimenter to the starting point through a movable chute made of plastic mesh outside of the structure.

On thirteen occasions, the trials were suspended when within a period time of 3 min, the animals did not cross the barrier to get to the target and when the animals showed stress-related behavior, such as holding its tail above its back, emitting loud screaming vocalizations, or kicking and trying to escape (Lund et al. 2012).

Data coding and analysis

Coding was performed by one experimenter. All trials were videotaped. To obtain the accuracy rate, an experimenter watched the videos for each test trial and recorded whether the subject's action was correct or incorrect (see "Method" section). All sessions were videotaped and coded by the same experimenter. To perform the reliability analysis, a second experimenter watched 50% of a randomly chosen set of trials, after the study had been completed, and recorded whether the subject's action was correct or incorrect. Inter-observer reliability was calculated (Cohen's kappa = .849, % of agreement = 95, $p < .001$).

The accuracy rates for each A and B trials were compared to chance levels ($p = .5$) using two-tailed binomial tests. For G4 (the group which experienced 4 A trials), McNemar tests (calculating exact binomial probabilities) were used to compare changes in accuracy rates from the last A trial to the first B trial and for the last A trial to the last B trial. Solution time for each trail was also coded. Differences in solution times between A trials and their corresponding B trials were analyzed using Wilcoxon signed-rank tests.

The effect of the number of repetitions of the A trial (one, two, three or four) on the solution times in the B1 trial was tested using: (1) a Kruskal–Wallis *H* test to determine whether there were differences in solution time between four groups with different number of A trials and (2) a Spearman's Rho correlation between the number of repetitions and the solution time. All statistical analyses were performed in SPSS 24.

Results

Accuracy rate

Performance in A trials

None of the groups (G1, G2, G3 and G4) differed statistically from chance levels in their first A trial (G1: 80%, $p = .109$; G2: 70%, $p = .34$; G3: 50%, $p < .999$; G4: 67%, $p = .181$) but were above chance level in subsequent A trials, in A2 (G2 and G3: 90%, $p = .021$; G4: 86%, $p = .001$), A3 (G3: 90%, $p = .021$ and G4: 86%, $p = .001$) and in A4 (G4: 81%, $p = .007$) (see Fig. 2).

Performance in B trials

None of the groups (G1, G2, G3 and G4) differed significantly from chance levels neither in their first B trial after the swap of the gap location (G1: 70%, $p = .344$; G2: 60%. $p = .754$; G3: 50%, $p > .999$; and G4: 67%, $p = .189$) nor in the second B trial (G1 and G2: 70%, *p*s = .344; G3: 60%, $p = .754$; and G4: 67%, $p = .189$). All groups performed significantly above chance level in B3 trials (G1, G2 and G3: 90%, $ps = .021$ and G4: 90%. $p < .001$) and in B4, all but G2 performed significantly above chance (G1: 90%, $p = .021$; G2: 70%. $p = .344$; G3: 90%, $p = .021$; and G4: 76%, $p = .027$) (see Fig. 2).

Changes in accuracy rates from the last A trial to the first B trial

The McNemar test for G4 showed no statistically significant differences between accuracy rates from the last A trial to the first B trial (80 vs. 70%, $p = .219$) or between those from the last A trial to the last B trial (80 vs. 75%, $p > .999$) as well.

The same was found for the other groups: G1 (A1 vs. B1: 80 vs. 70%, $p > .999$; A1 vs. B4: 80 vs. 90%, $p > .999$); G2 (A1 vs. B1: 90 vs. 60%, $p = .375$; A1 vs. B4: 90 vs. 70%, $p = .625$); G3 (A1 vs. B1: 90 vs. 50%, $p = .219$; A1 vs. B4: 90 vs. 90%, $p > .999$).

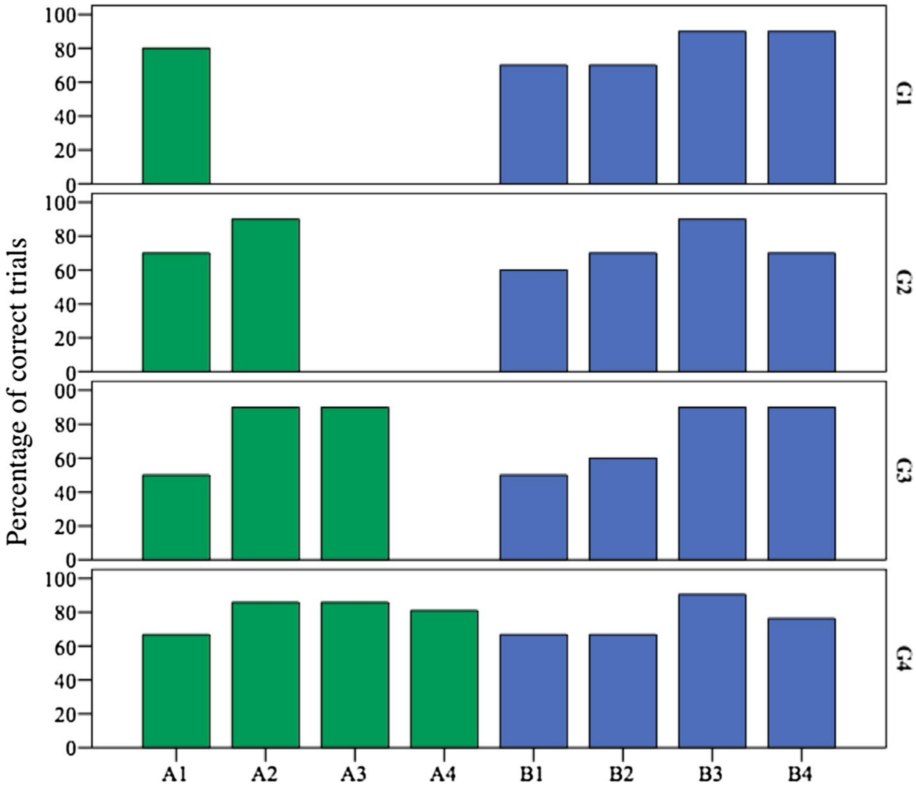

Fig. 2 Accuracy rates (i.e., percentage of subjects that after crossing with the fronts legs—shoulders—the second blocked-off half of the starting area moved toward the correct side of the barrier without deviation) for each group across all trials (A and B)

Comparison of solutions times from A to B trials

Wilcoxon signed-rank test showed that there was a statistically significant median increase in solution times in B2 and B3 trials, compared to their corresponding A trials (A2 and A3) only for G4 ($z = -2.31$, $p = .021$ and $z = -2.29$, $p = .022$, respectively). In G4, no statistically significant increase was found between A1 and B1 ($z = -.17$, $p = .986$) or A4 and B4 ($z = -1.77$, $p = .076$). In the rest of the group, the crossing time in B trials did not differ significantly from the corresponding A trials (G1: A1/B1, $z = -1.01$, $p = .314$; G2: A1/B1, $z = -.051$, $p = .959$; A2/B2, $z = -.356$, $p = .722$; G3: A1/B1, $z = -1.88$, $p = .059$; A2/B2, $z = -.76$, $p = .443$; and A3/B3, $z = -1.58$, $p = .114$) (see Fig. 3).

The effect of the number of repetitions of the A trial on the solution times in B1

No statistically significant differences were found for solution time as a function of the number of A trials ($\chi2(3) = .21$, $p = .97$).

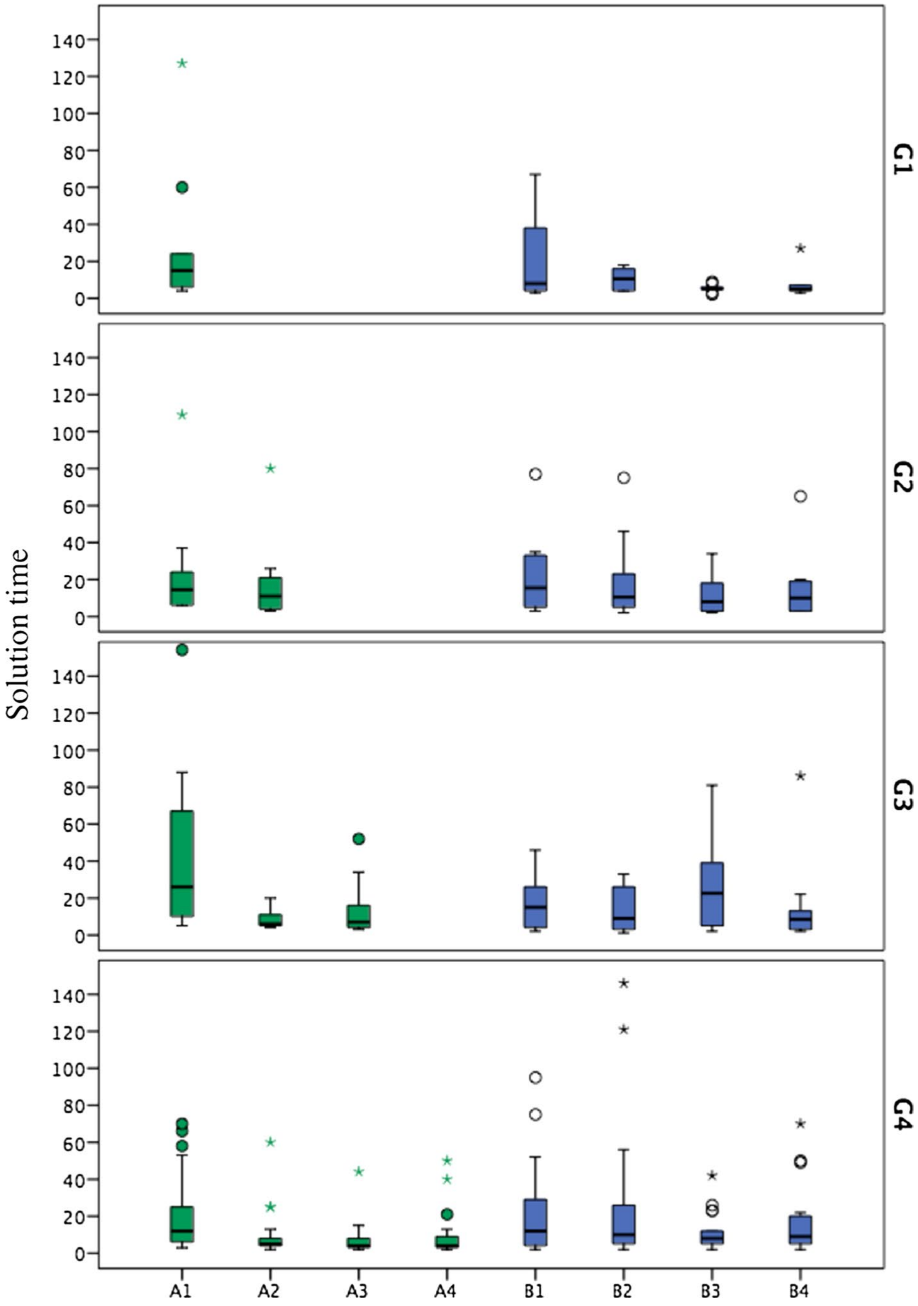

Fig. 3 Box plots of the solution time responses (time to cross the gap) with the fronts legs (shoulders) in seconds, for each group (G1, G2, G3 and G4) across all A and B trials

No statistically significant correlation was found between the time needed to pass the barrier after the change and the number of A trial repetitions ($r_s = .004$, $p = .977$, $n = 51$).

Discussion

The alpacas learned to solve an A-not-B detour task, with all groups performing significantly above chance level from the second A trial (similarly, from the third A trial, using Osthaus et al. 2010, 2013 criterion). In the subsequent B trials, in which the location of the gap was moved to the other side of the barrier at the testing area, all groups performed significantly above chance level in the third one. The groups did not show performance significantly below chance level in their first B trial, which would be expected if they had error persistence. Furthermore, no statistically significant decrease in accuracy rate from the last A trial to the first B trial was found in G4. This was the group with more A trials, and thus, the one which was expected to be more affected by persistence error, similarly, using Osthaus et al. 2010, 2013 criterion, none of the groups differed significantly from chance levels in any of the B trials (see ESM). In sum, following Osthaus et al. (2010, 2013) criterion, although the performance was worse, the results did not change substantially from the ones obtained with the criterion used in the present study, that is, performance in B trials was not significantly below chance level. Nevertheless, it is possible that Osthaus et al. (2010, 2013) criterion (given the exploratory behavior of alpacas previously mentioned) introduces experimental noise that could be responsible for this lower performance.

Although no significant differences in solution times as a function of number of A trials repetitions were found, for G4, there was a statistically significant median increase in solution times in B2 and B3 trials compared to their corresponding A trials but not in B1 and B4. In the rest of the groups, including G3 that received three A trials, their crossing time in B trials did not differ significantly from the corresponding A trials. Thus, contrary to what has been found in other domestic animals which showed perseveration after the gap location was moved (Osthaus et al. 2010, 2013), the present study did not find evidence of spatial perseveration, and conversely, the present results suggest no error persistence in alpacas (see Fig. 2).

To our knowledge, alpacas are the first animals to be tested in an A-not-B task, for which no clear evidence of spatial perseveration in this task has been found (Osthaus et al. 2010, 2013). One of the reasons that might explain this result is that alpacas, similarly to goats, present more flexible foraging behavior than most of the other domesticated animals tested in previous studies (dogs, horses, mules and donkeys) (Nawroth et al. 2014). Throughout their years of domestication, alpacas have had to adapt to several places with variable quantity and quality of resources (Benitez et al. 2006) which could have further developed their spatial cognitive abilities allowing them to adapt to unstable environments (Marshall-Pescini et al. 2015; MacLean et al. 2014). However, this suggestion must be taken with caution as recent reports suggest that results in inhibitory control testing in dogs and crows depend on the task that has been carried out (Bray et al. 2013; Jelbert et al. 2016; Brucks et al. 2017).

In addition, the results of the present study could be related, partly, to their visual perception, since alpacas have a horizontal streak across the retinal meridian, which, apart from providing a panoramic visual field, also has an important function in predator surveillance, acquiring food and guarding herds (Wang et al. 2013). In fact, alpacas have recently begun to be used to guard sheep from fox attacks (Mahoney and Charry 2005). This feature could be associated with the behavior observed during the present study, as alpacas, unlike the other species on which this test has been performed, not only explored in the first A trial (Osthaus et al. 2010, 2013), but also they continued to explore the experimental structure in subsequent tests before heading toward the gap in the barrier. In any case, we must be cautious, since we cannot rule out that the worse performance of the alpacas in A trials (they never reached 100%) compared to other species could be due in part to a motivational issue (e.g., reward did not attract the attention sufficiently).

Another plausible explanation that deserves special attention is that the other four species previously tested in this task during their domestication process fulfilled a wide variety of roles for humans, receiving a strong selection for docility, fearlessness and non-aggressive behavior toward humans (Hare et al. 2002). This motivational and attentional bias toward humans could explain the poor performance of dogs in some spatial cognitive tasks, and their perseveration behavior in a similar detour tasks (see Hare and Woods 2013 and Polgár et al. 2015 for a review). Accordingly, a comparative study between identically raised packs of dogs and wolves found that, in a detour task, wolves outperformed dogs showing a shorter latency to success and less perseverative behavior than dogs (Marshall-Pescini et al. 2015). On the other hand, alpacas have been mainly selected only for fiber production (Wheeler 1995), which means lower and infrequent human handling. Accordingly, alpacas may have paid more attention to the environmental cues than the other species tested in this task.

In conclusion, the results of the present study showed no clear evidence for spatial perseveration behavior in alpacas, and therefore, alpacas have outperformed other domestic species previously tested in the A-not-B detour task. Hence, it is suggested that alpacas are more flexible than other domestic animals tested in this same task. However, this suggestion must be taken with caution, as studies carried out with dogs have shown that this ability could be context specific. Finally, this absence of clear evidence for perseverance behavior in alpacas may have important implications to the planning of proper training for scientific (Lund et al. 2012) and productive purposes or for animal-assisted therapy training (Grassberger et al. 2013), which, in general, could contribute toward enhancing their welfare during routine handlings. Some alpaca farmers may refuse to move their animals in order to avoid the stress caused by novelty and thus miss out on opportunities such as exchanging breeders between farms or transporting them to participate in animal-assisted therapies. However, our results suggest that alpacas could be easily trained to take different switching gaps as needed during these procedures, thus enhancing their welfare, as animals' lack of control to adapt to and learn from a changing environment is associated with poor welfare (Brando 2012).

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Compliance with ethical standards

Conflict of interest The authors declared that they have no conflicts of interest with respect to their authorship and/or the publication of this article.

Ethical standards This research adhered to the legal requirements of the country (Chile) in which the work was carried out and all institutional guidelines.

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