7-2012

Does terrain slope really dominate goal searching?

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Abstract

If you can locate a target by using one reliable source of information, why would you use an unreliable one? A similar question has been faced in a recent study on homing pigeons, in which, despite the presence of better predictors of the goal location, the slope of the floor in an arena dominated the searching process. This piece of evidence seems to contradict straightforward accounts of associative learning, according to which behavior should be controlled by the stimulus that best predicts the reward, and has fueled interest toward one question that, to date, has received scarce attention in the field of spatial cognition: how are vertical spaces represented? The purpose of this communication is to briefly review the studies on this issue, trying to determine whether slope is a special cue—driving behavior irrespective of other cues—or simply a very salient one.

Keywords Goal location Reorientation Slope or slant Vertical dimension Cue salience

Introduction

The bulk of the literature on spatial cognition has analyzed flat, horizontal environments. However, the dry surface of the earth is remarkably bumpy. Even though most times we neglect the vertical component of a path, in most regions of the world—with hills, valleys, dunes, mountains and, in general, any uneven ground—traveling entails a substantial displacement also in the vertical dimension. On a relatively uniform, extended slant, the slope gradient can be used as a compass, in the sense that the slope can specify stable, reference directions (like uphill and downhill; Miniaci et al. 1999; Restat et al. 2004). However, what is the specific role of terrain slope compared to other spatial cues?

Research on homing pigeons

In 2009, Nardi and Bingman trained pigeons to locate food hidden in an isosceles trapezoid arena (see Fig. 1; Nardi and Bingman 2009). Like most of the literature on reorientation,1 subjects had to use the geometry of the environment to determine the rewarded corner; however, this experiment was distinct because the arena was placed on a 20° slant rather than on a flat floor. As a consequence, the goal could be identified with respect to two cues: the geometry of the arena (e.g., the goal is in the acute corner with a long wall on the right and a short wall on the left) or the slope (e.g., the goal is in the downhill corner on the right). Pigeons learned the task, and a subsequent conflict test was carried out to assess which cue was relied upon (the arena was placed on the slope with an opposite orientation from training, such that now the geometry and slope strategy dictated two different goal locations; see Fig. 1). According to the (then) prevailing views that reorientation is specifically attuned to the shape of the environment, above and beyond other features (Cheng 1986), it was expected that searches would be directed to the geometric-correct corner. Instead, pigeons chose the slope-correct corner overwhelmingly (see Fig. 1), suggesting that slope—and not geometry—was controlling their behavior. This result was very surprising because in similar settings, when geometry and another cue (e.g., visual landmarks) predict the goal location, behavior is typically controlled by geometry (e.g., Nardi and Bingman 2007).

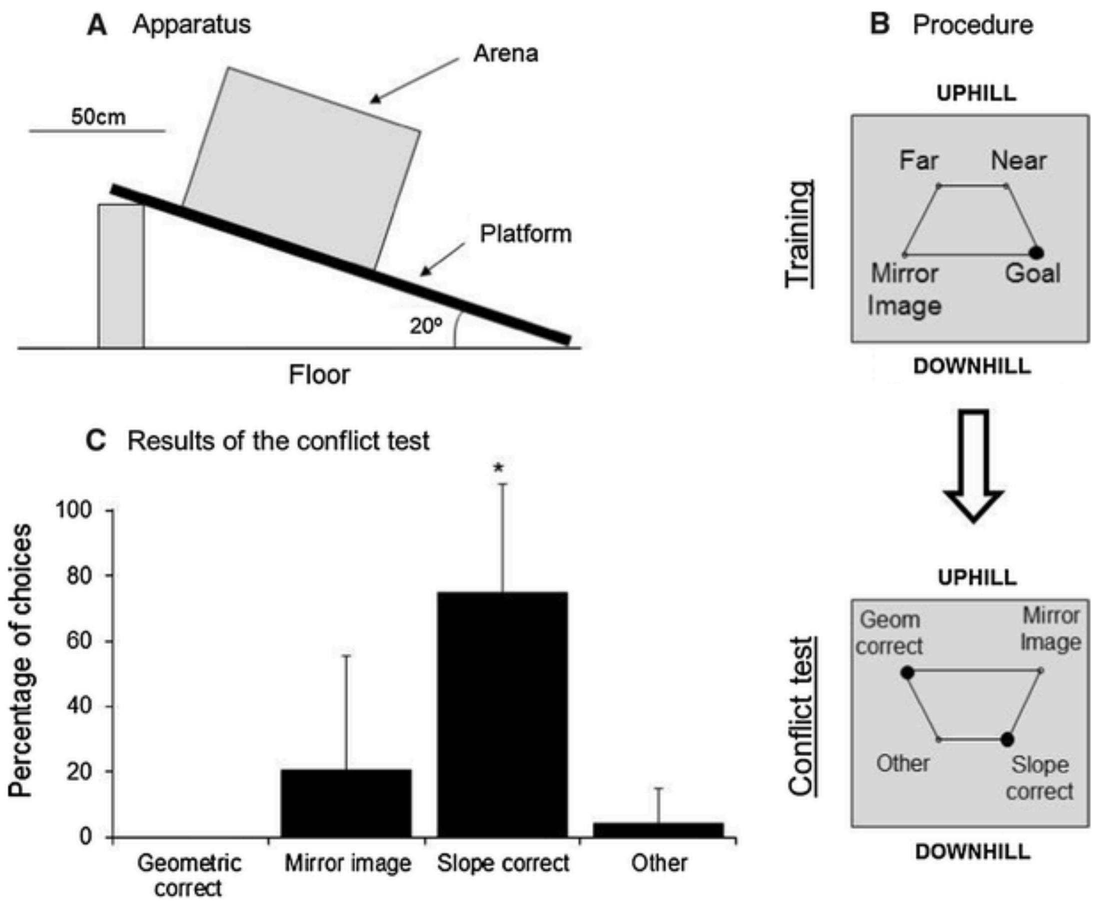

Fig. 1
a Schematic representation of the apparatus used in the studies on pigeons. b Procedure used in Nardi and Bingman (2009). It is important to note that, during training, for half of the sample, the goal was downhill (as represented in this figure), and for the other half, the goal was uphill. This counterbalancing procedure was carried out in every study. c Mean percentage of choices (± 95 % confidence intervals) in the conflict test in Nardi and Bingman (2009); the slope-correct corner was chosen significantly more than any other corner (*p < .01)

To further investigate the salience of slope, we carried out a follow-up experiment (Nardi et al. 2010). Using the same set-up as in Nardi and Bingman (2009), again, we trained pigeons to locate food hidden in a corner of a trapezoid arena presented on a 20° slope. However, this time, instead of having a fixed orientation relative to the slope, the arena was presented with 2 or 3 different orientations. As a consequence, the goal could be identified with certainty only relying on the geometry of the arena (the goal was always in the same corner); conversely, slope only predicted the goal 1/2 or 1/3 of the times (the goal was uphill in some training trials and downhill in other). According to associative models of spatial learning (e.g., Miller and Shettleworth 2007), searching behavior should be controlled by the stimulus that best predicts the reward, that is, geometry. However, subsequent test trials revealed, again, that pigeons were searching the goal by virtue of its position relative to the slope—even though this was not a reliable predictor and led to a systematic error (searching at a geometrically incorrect corner). In sum, slope was being relied upon when it had equal (Nardi and Bingman 2009) and even less predictive validity (Nardi et al. 2010) compared to other available cues. Such a strong dependence on a spatial cue is striking, and a similar effect in reorientation found by Cheng in 1986 led to the claim of modularity (in that case, geometry was dominating searching behavior, so it was referred to as "geometric module"). Why was the slope of the environment dominating searching behavior?

The salience of slope

There are many plausible reasons why slope resulted in such a strong cue for reorientation. From an ecological point of view, during navigation, it is adaptive to weight the topography of the land (slopes, hills, mountains, etc.)—a relatively stable environmental property—more than other features that may change during the course of a day (e.g., celestial cues) or of a season (e.g., foliage of trees, the river flow). Furthermore, from a perceptual point of view, traveling on a tilted surface provides a multimodal sensory experience (including visual, vestibular, and kinesthetic cues); this sensory redundancy makes slope unique compared to other spatial cues, most of which are perceived through uni-modal input. But perhaps more importantly, slope may be salient because it is a vertical property of the environment. The vertical dimension of space is qualitatively different from the horizontal dimensions because it is parallel to the force of gravity. In fact, when moving on a vertically extended surface, greater energetic expenditure and a motoric/behavioral adjustment are required in order to contrast gravity. Comparative evidence indicates that, both in aquatic and terrestrial environments, vertical information is very salient (fish: Holbrook and Burt de Perera 2011) and behavior is different when navigating in vertical compared to horizontal spaces (Jovalekic et al. 2011). Finally, a qualitative difference between the encoding of the horizontal and vertical axes of space has also been suggested by neurological evidence: compared to horizontal distances, vertical distances seem to be represented more coarsely by grid cells and place cells (Hayman et al. 2011). All these suggest a theoretical distinction of slope—and vertical information in general—from horizontal cues.

Studies on humans

Does slope dominate also in human reorientation? Two main lines of research have tested slope use in human adults. Nardi et al. (2011) have shown that human adults can use the slant of a floor to locate a goal in a real-world, square enclosure; however, large individual differences were present and some participants—mainly women—exhibited a difficulty. Follow-up studies providing slope plus landmark information indicated that, differently from pigeon studies, slope did not overwhelmingly control behavior; rather, people were using the two cues approximately equally (Nardi et al. under review). However, the inclination used in these studies was substantially less than the one used in the research on pigeons (only 5° as opposed to 20°). It is possible that slope dominates goal searching behavior only at steeper inclinations; in order to ascertain whether this is the case or whether the difference lies in the ecological distinction between humans and pigeons, future research will have to investigate slope use in humans at steeper inclinations.

Another line of research on humans tested the use of directional cues (including, but not limited to, slope) and positional cues (e.g., landmarks) in virtual environments (Chai and Jacobs 2009). Results have shown sex-specific strategy preferences, but have failed to show a strong superiority of directional cues in cue weighting. Notwithstanding the fact that slope was provided together with other types of directional cues (e.g., distant landmarks), there is a more important methodological issue that hampers comparison with the results obtained from homing pigeons. In Chai and Jacobs' study (2009), the environment was presented on a desktop computer, so slope could be perceived only through vision. This is a very different experience from perceiving slope also with the vestibular and kinesthetic information normally available when walking in natural environments; it is plausible that using only a subset of the sensory information normally associated with slope decreased its salience.
In sum, even though the present (scarce) research on humans does not corroborate any privileged status of slope, crucial experimental differences preclude drawing a confident conclusion on the matter.

A recent experiment

A more systematic continuation of the research on slope salience was addressed by a recent experiment. So far, the line of work on pigeons had examined reliance on slope by comparing it to geometric cues only. However, in order to ascertain whether slope is really a privileged cue, exerting strong dependence for goal searching, this has to generalize also when tested with other cues. Nardi et al. (2012) trained pigeons to locate a goal in a square, tilted arena (20°) with colored cards placed in each corner; the baited corner was associated with a card of different color from the other 3 corners (see Fig. 2). Therefore, the task could be solved using the slope strategy (e.g., the goal is in the upper-right corner), but also using the feature cue strategy (e.g., the goal is at the corner with the blue cards). It is important to note that when a distinct feature cue marks the goal, it is referred to as a beacon, it supports a very simple search strategy (find the beacon to locate the goal), and it is a highly salient cue (Chamizo et al. 2006). Following a procedure analogous to previous experiments, after training, the typical conflict manipulation changed the arrangements of the cards, such that now the slope and the cards dictated 2 different correct corners. A preference for the slope-correct corner as opposed to the feature-correct one would significantly reinforce the hypothesis of slope dominating searching behavior. However, for the first time in this series of experiments, slope failed to capture most of the associative strength, and pigeons chose almost equally the two correct corners (see Fig. 2; Nardi et al. 2012).

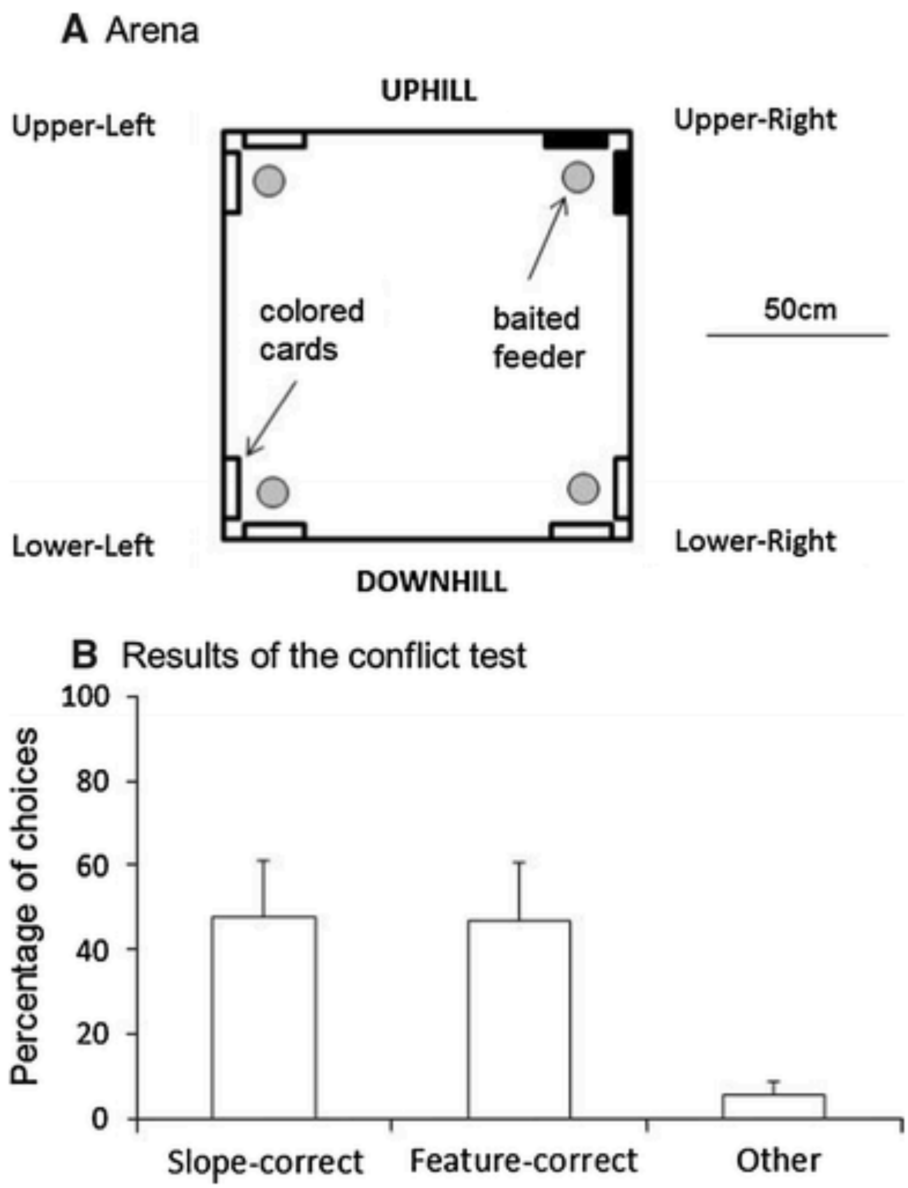

Fig. 2
a Arena used in Nardi et al. (2012). b Mean percentage of choices (± SEM) to each corner in the conflict test in Nardi et al. (2012); overall, the two correct corners were chosen approximately equally

Conclusions

The finding from Nardi et al. (2012) substantially weakens the claim of slope having a special status—driving searching behavior irrespective of other task-relevant cues. Instead, considering this whole line of research on pigeons, slope seems to obey the principles of associative learning, because the associative strength it gained depended on the salience of the competing stimulus: when paired with a less salient cue (the geometry of the environment), slope guided behavior, but when paired with a more salient cue (a beacon), slope gained a comparable amount of associative strength as the other cue. Put in other words, rather than being qualitatively superior to other spatial reference frames, it is more plausible that—as an associative model of spatial learning would predict (e.g., Miller and Shettleworth 2007)—the reliance on slope is determined by cue competition. Slope is a very salient stimulus, and it can override another, less salient competing stimulus (such as geometry), even if this has a greater predictive value. However, when the salience of the competing stimulus is higher, the associative strength gained by slope decreases, so that it is less relied upon.

Future research will have to confirm this. In particular, effort should be focused on systematically examining how slope salience varies by changing the floor inclination and whether the salience of slope can be reduced to the point that cue competition occurs also with geometry. As of now, however, it is safer to assume that slope, rather than being a special cue, is simply an especially salient one.

Conflict of interest

This supplement was not sponsored by outside commercial interests. It was funded entirely by ECONA, Via dei Marsi, 78, 00185 Roma, Italy.

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Footnotes

1 For the purpose of this brief review, we use the term "reorientation" and "goal searching" interchangeably. For a more precise definition of reorientation, see Nardi et al. (2011).