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Rats average entire vectors when navigating toward a hidden goal: A test of the vector sum model in rodents

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ABSTRACT

Cheng and colleagues (Cheng, 1988, 1989, 1990; Cheng and Sherry, 1992; Spetch et al., 1992) have shown that birds use vector information from landmarks to return to hidden goal locations. Cheng (1994) subsequently showed that pigeons average the distance and directional components of landmark-to-goal vectors separately, rather than as a single entity (distance-averaging model). Cheng reasoned that other animals might also average the distance and directional components of landmark-to-goal vectors separately, in part, given commonalities in the neural architecture of visual systems. We used procedures developed by Cheng (1994) to examine how rats utilize landmark-to-goal vectors. In contrast to the results with pigeons, we found evidence indicating that rats average whole vectors rather than their separate scalars (vector-averaging). The ways that pigeons and rats use vectors may be related to evolved differences in the visual systems between these two species.

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Many animals navigate from one place to the next in their environment to obtain resources for survival. Animals need a system of navigation that will allow them to accurately and efficiently travel in their environment. One such system that has been well studied is landmark navigation. Landmarks are objects or surfaces of the environment that are tied to the earth. Animals can use landmarks as a reference to determine their current location or the position of important locations in their environment (see Healy, 1998; Shettleworth, 2010; Gallistel, 1990 for reviews). Animals may encode distance and angle information between the object serving as a landmark and a goal or destination (landmark-to-goal vector). This directional vector can later be used to help an animal determine its current position or that of a goal.

Ken Cheng and colleagues have studied landmark navigation in the pigeon and other birds (Cheng, 1988, 1989, 1990; Cheng and Sherry, 1992; Spetch et al., 1992; Cheng et al., 2006; Kelly et al., 2010). Cheng and Sherry (1992) had pigeons and chickadees search for food that was hidden in substrate on a tray. A tall object near the hidden goal served as a landmark (see Fig. 1 as an example). The researchers then moved the landmark on the tray during transformational tests to determine the nature of the information used to encode the location of the hidden goal. Over the course of several papers Cheng and colleagues (Cheng, 1988,1989, 1990, 1994; Cheng and Sherry, 1992; Kelly et al., 2010) outlined evidence for the vector sum model of navigation. The model proposes that birds (and presumably other animals) encode the distance and direction from one or more landmarks to the goal (landmark-to-goal vectors, such as b_1 in Fig. 1). When later returning to the goal the animal calculates a self-to-goal vector consistent with its current view of the environment. Specifically, the bird adds the vector from its current location to the familiar landmark (self-to-landmark vector) to the previously recalled landmark-to-goal vector. Vector addition generates the self-to-goal vector that can be used by the bird to locate hidden food. During transformational tests in which the landmark is shifted, the location that the landmark-to-goal vector points to (g_2) would be shifted by the same amount (Fig. 1, b_1 and b_2). The revised self-to-goal vector, and the subsequent location that an animal searches should be based on a weighted average of the landmark-to-goal vectors (for displaced and non-displaced landmarks).

Cheng and colleagues found that the predictions of the vector sum model held when a landmark was shifted parallel or perpendicular to the edge of the testing arena. That is, the animals searched primarily in a location that was consistent with the degree and direction of the landmark displacement. However when the researchers displaced a landmark diagonal to the edge (such as in Fig. 1) both pigeons and chickadees shifted their peak place of search more in the direction parallel than perpendicular to the edge. The results conflicted with the vector sum model that predicted following a diagonal displacement of the landmark of the peak place of search should be displaced equally in both planes. Cheng

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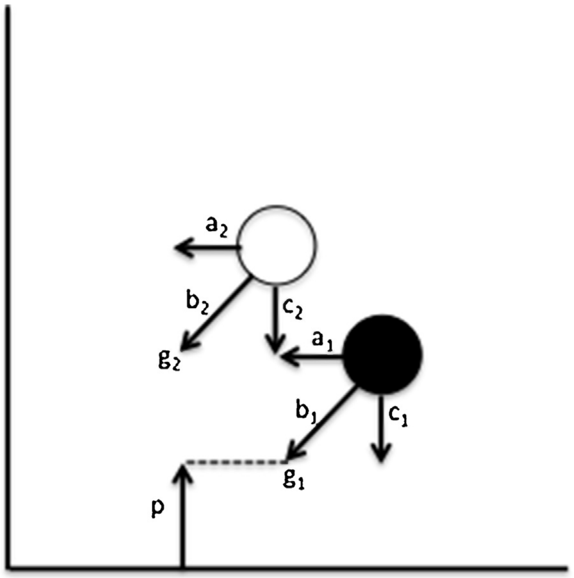

Fig. 1. A top down view of a landmark prior to (filled circle) and after (unfilled circle) displacement along a diagonal path away from an edge shown at the bottom. The perpendicular distance of the goal (g_1) from the edge is indicated by p. The landmark-to-goal vector prior to displacement that indicates both distance and direction is b_1 and the individual scalars for b_1 are indicated by a_1 and c_1. If an observer is behaving consistent with the vector averaging model, then they would average the perpendicular distance of the goal from the edge (p) with b_1 to determine the location of the goal (g_1) to located the hidden food. If an observer is averaging distances and directions separately, then they would average p with both scalars a and c independently (redrawn from Cheng, 1994). Following displacement of the object in a diagonal plane the location of search should reflect a weighted average of the landmark-to-goal vectors (for displaced and non-displaced objects).

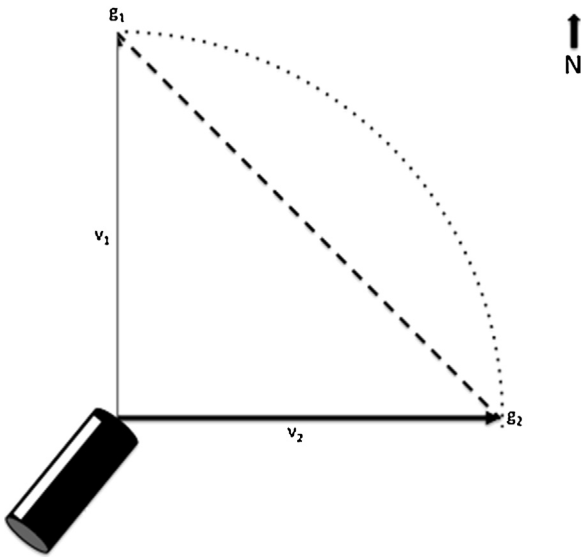

Fig. 2. The conflict test and theoretical locations of search based on vector- and distance- averaging models (see text). The black cylindrical landmark with the vertical white stripe points to the location of the hidden goal (g_1) during training in Experiment 1. Vector v_1 indicates this landmark-to-goal vector. Following a 90° clockwise rotation (during testing in Experiment 1) vector v_2 points to a new location of the goal (g_2) making the location of the goal ambiguous. Search is predicted to occur between the two potential goal sites g_1 and g_2. An observer averaging the distance and direction components of vectors v_1 and v_2 separately (distance averaging model) would tend to search at points along the arc connecting g_1 and g_2, whereas, an observer averaging entire vectors would search at points along the dashed line connecting the two goal locations. The figure was reconstructed from Cheng (1994).

suggested that the birds had incorporated vector information from the edge during the averaging process and some evidence supported this position. However, the specific nature of vector information that was added to the edge-to-goal vector remained unclear (Cheng et al., 2006).

One possibility was that prior to displacement the birds were averaging the landmark-to-goal vector (b_1 in Fig. 1) with the edge-to-goal vector (p) as initially proposed by the vector sum model. Cheng (1994) labeled this revision to the vector sum model, the vector-averaging model. However, another possibility was that the birds were averaging the distance and directional components (a_1 and c_1 in Fig. 2) of the landmark-to-goal vector separately with the edge-to-goal vector. To test between these two possibilities Cheng (1994) presented pigeons with a series of conflict tests in which the two models made separate predictions about where the birds should search. During training Cheng had pigeons search for a hidden goal (g_1 in Fig. 2) that was always the same direction and distance from a vertical stripe on a cylindrical landmark. The landmark to goal vector v_1 pointed to the location of food during training. During testing, Cheng rotated the landmark with the stripe 90° to create a potential compromise in search behavior. On the one hand, the birds might ignore the rotation of the object and search at the location of the goal during training (g_1). On the other hand, the stripe on the cylinder now pointed to a position 90° clockwise from the training location. If the birds were followed the stripe, the birds might be expected to search at g_2 using vector v_2 (Fig. 2). Cheng anticipated that given the conflict the birds might search at locations intermediate to these two extremes (between g_1 and g_2). These compromise positions are informative since they indicate how the birds are using vector information from the landmark. If the pigeons were using a weighted average of the two complete landmark-to-goal vectors (v_1) and (v_2) then they would be expected to search at points along the line segment connecting the endpoints of the two vectors during the conflict test (vector-averaging). However, if the pigeons were averaging the distance and direction components of these two vectors separately then they should search on the arc connecting the end points of the two vectors (Cheng called this distance-averaging). The results of a number of related conflict tests supported the distance-, rather than the vector-averaging model for pigeons.

To our knowledge, tests of these two models of vector averaging have yet to be conducted on other species. How different species utilize vector information may be an important function of the evolution of their visual system. One the one hand, the visual system of vertebrates has likely evolved once (Husband and Shimizu, 2001; Shimizu and Karten, 1993) and there may be a high level of similarity across vertebrates in how visual information may be used during navigation. Cheng (1994) speculated that the use of vectors by many animals might conform to the distance-averaging model, since the neural architecture of many sensory systems processes information somewhat independently as it proceeds upstream. Likewise, Kamil and Cheng (2001) reviewed behavioral data (e.g., Kamil and Jones, 2000) with the Clark's nutcracker that also supports the separate processing of distance and direction information (but see Kelly et al., 2010). On the other hand, the visual ecology of vertebrates is rich and the visual system of different species has become adapted to very different environments. Correspondingly, this adaptation may have influenced how different vertebrates utilize vector information from objects when navigating and returning to familiar locations. In the current study we used procedures similar to those by Cheng (1994) to examine the use of vectors by Long-Evans rats when returning to a hidden goal. As we discuss below, although rats and pigeons are vertebrates, rats have a very different visual ecology than the avian species utilized by Cheng and colleagues. Therefore, rats serve as a good comparison species for examining the use of vector averaging models among vertebrates.