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Review

The influence of locomotory style on three-dimensional spatial learning

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The degree of three-dimensional movement exhibited by animals depends, in part, on their style of locomotion. For example, surface-bound animals such as humans are always in contact with the ground and, consequently, their travel in the vertical dimension is largely dictated by the topography of the terrain. In contrast, nonsurface-bound (flying and swimming) animals can move equally in all three dimensions. Research from the last 20 years has indicated that many animals learn and remember information about the vertical and horizontal dimensions with different degrees of accuracy, and that this may be influenced by their style of locomotion; however, there has been no overview to determine whether these differences follow general patterns and there have been few attempts to explain the reasons behind them. The aims of this article are twofold. First, we review the literature on vertical and horizontal navigation, comparing the relative accuracy of these processes in surface-bound and nonsurface-bound animals, and critically appraising the key contributing factors. Second, we hope to establish a framework to help direct researchers interested in the effects of locomotory style on navigation to areas of the field where data are lacking or where there have been contradictory findings that need to be resolved. We suggest that as there are currently few studies investigating three-dimensional navigation, the field would benefit from more studies in a larger variety of species, in particular flying and swimming species that nest and forage on the ground or in the benthic zone and arboreal surface-bound animals that must regularly move in three dimensions through the canopy. This will enable us to determine whether real differences in spatial learning exist between animals exhibiting different styles of locomotion and, if differences do exist, allow us to establish general principles that can explain these differences in spatial learning between species.

Resources such as food, mates and nesting sites are distributed unevenly in the wild, and animals must visit different parts of the environment if they are to exploit these resources to survive and reproduce. As they travel between regions, animals are vulnerable to predation, conflict with conspecifics and energy depletion. As a result, natural selection favours individuals that remember the spatial locations of frequently visited places, as this allows them to minimize the time and energy that they spend travelling.

The neurophysiological and behavioural mechanisms that underlie spatial navigation have been studied in a wide variety of vertebrates and invertebrates (Collett, 2009; Healy, 1998). In the past, most of this research has been limited to exploring navigation in the horizontal dimensions alone; however, the world is three-dimensional and, consequently, for most mobile animals there is an element of both vertical and horizontal travel in their natural movement. Not all animals move in the vertical dimension to the same extent; their degree of vertical travel depends, in part, on whether their movements are surface-bound or nonsurface-bound (Davis, Holbrook, Schumacher, Guilford, & Burt de Perera, 2014). Surface-bound animals are in continual contact with a substrate as they move, be it the ground, the seabed or the branches of a tree. Among these surface-bound species are humans, lobsters and lizards, and all such species move with three degrees of freedom (Fig. 1a): two translational (forwards/backwards and left/right) and one rotational (yaw) (Holbrook & Burt de Perera, 2013), meaning the extent to which they move vertically is dictated by the topography of the surface that they move over. In contrast, nonsurface-bound animals such as those that can swim or fly are able to disengage from the substrate for extended periods (beyond leaps

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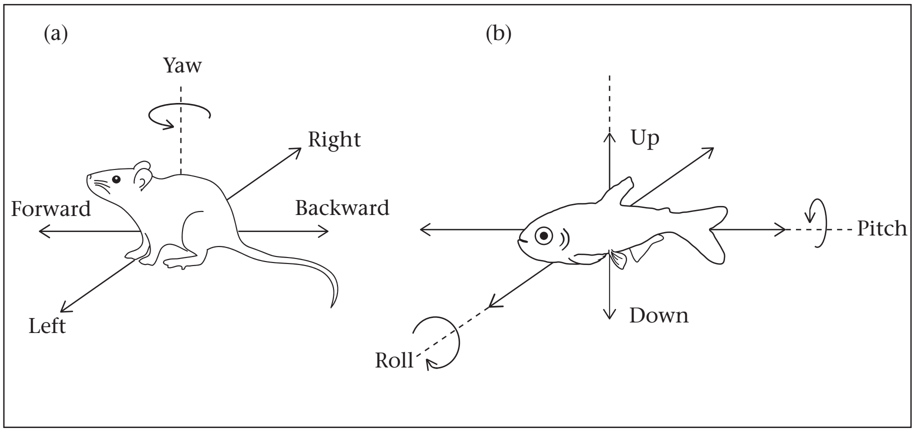

Figure 1. A schematic diagram of the hypothetical translational (solid lines) and rotational (dotted lines and circular arrows) degrees of freedom that (a) rats (surface-bound) can move through and (b) the additional degrees of freedom that freely swimming fish (nonsurface-bound) can move through. For many animals up/down and left/right movements cannot be performed independently of pitch and yaw rotations, respectively.

and jumps), and can thereby move with six degrees of freedom (Fig. 1b): three translational (forwards/backwards, left/right and up/down) and three rotational (yaw, pitch and roll) (Holbrook & Burt de Perera, 2013). As a result, the vertical movement of nonsurface-bound animals is not controlled by the topography of the land but by the animals themselves. In most cases the vertical movements of all animals, regardless of their style of locomotion, are constrained by the energetic costs associated with moving against gravity (Grobéty & Schenk, 1992; Jovalekic et al., 2011).

Recently there has been an increase in the number of studies investigating spatial cognition in three-dimensional environments. Some of these studies have indicated that animals may learn, encode and remember vertical and horizontal information to different levels of accuracy, and that the degree to which they do this may depend on their style of locomotion (Flores-Abreu, Hurly, Ainge, & Healy, 2014; Holbrook & Burt de Perera, 2013; Jovalekic et al., 2011; Yartsev & Ulanovsky, 2013). These comparisons have so far been made on a case-by-case basis; thus, it has remained unclear whether the accuracy with which animals learn vertical and horizontal information differs consistently between (1) surface-bound and nonsurface-bound animals and (2) surface-bound animals that regularly travel vertically, such as arboreal species, compared to those that do not. Moreover, the reasons that animals learn and remember vertical and horizontal information with different accuracies are largely unknown.

Over the last two decades, three-dimensional spatial cognition has been studied using two main approaches: first, from the perspective of the neurophysiological processes happening during navigation, and second, investigating the behavioural responses of animals faced with navigational decisions. Here, we review and synthesize literature from these two approaches to investigate, first, whether there are differences in three-dimensional spatial learning between species that exhibit different styles of locomotion and, second, the factors that might explain these differences. By collating this information, we hope to establish a useful framework to direct researchers interested in the effects of locomotory style on navigation to the most profitable areas of the field where data are lacking or where there have been contradictory findings that need to be resolved.

REVIEW OF VERTICAL AND HORIZONTAL SPATIAL LEARNING

Here, we consider three-dimensional spatial learning from the point of view of species' abilities to accurately remember vertical versus horizontal information. Considering spatial cognition in this context is a useful approach for several reasons. First, the vertical and horizontal dimensions can be separated according to the cues available during travel, for example, gravitational forces inform movement in the vertical dimension only, whereas celestial cues are informative in the horizontal dimensions (Jeffery, Jovalekic, Verriotis, & Hayman, 2013); therefore, whether an animal is travelling vertically or horizontally dictates the environmental cues available to them as well as the sensory systems they might evolve. Second, because animals travel in the vertical dimension to different extents depending on their style of locomotion, their learning of information in the vertical dimension may differ in accuracy from their learning of information in the horizontal dimensions. If we can determine whether this is the case, we may be able to elucidate the way three-dimensional spatial information is learned and stored by animals.

The research exploring three-dimensional navigation, where the accuracy of vertical versus horizontal learning was explicitly tested, has been carried out in rodent (mainly rat, *Rattus norvegicus*), dog, *Canis lupus familiaris*, ant and human models as examples of surface-bound behaviour, and in fish, bats, bees and hummingbirds representing nonsurface-bound behaviour. The studies that we review in this paper have taken two approaches to exploring animals' three-dimensional spatial cognition: (1) investigating how animals solve three-dimensional spatial tasks based on observations of their behaviour, either in the laboratory or in the wild, and (2) direct neurophysiological recordings of individual neurons involved in spatial cognition. We therefore divide our review accordingly, discussing behavioural and neurophysiological studies separately. For a summary of the findings from the current literature see Table 1.

Findings from Behavioural Studies

Surface-bound animals

Of the three behavioural studies investigating three-dimensional spatial cognition in rats, two found that rats remembered the horizontal component of a three-dimensional location more accurately than the vertical component (Flores-Abreu et al., 2014; Jovalekic et al., 2011). Notably, the rat's lower accuracy in the vertical dimension was not because they spent less time exploring vertically, as this same result was found irrespective of whether rats spent more time travelling horizontally (Jovalekic et al., 2011) or vertically (Flores-Abreu et al., 2014) over the