Learning to navigate in a three-dimensional world: From bees to primates

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Abstract: We discuss the idea that environmental factors influence the neural mechanisms that evolved to enable navigation, and propose that a capacity to learn different spatial relationship rules through experience may contribute to bicoded processing. Recent experiments show that free-flying bees can learn abstract spatial relationships, and we propose that this could be combined with optic flow processing to enable three-dimensional navigation.

Experiments that have investigated navigation in insects add considerably to the generality of the arguments presented by Jeffery et al., in revealing additional evidence for potential bicoded processing in animal brains. A contemporary point of interest in neuroscience is whether solving complex cognitive problems actually requires large mammalian brains (Chittka & Niven 2009). In this regard, free-flying bees are an interesting model for understanding how visual systems deal with navigation in a three-dimensional world.

It is known that the mechanism by which both stingless bees (*Melipona panamica*) and honeybees (*Apis mellifera*) judge distance in the horizontal plane is visually driven by optical flow, where the velocity of angular image motion is integrated over time to enable a bee to estimate the flown distance with accuracy (Dacke & Srinivasan 2007; Eckles et al. 2012). Interestingly, when honeybees are presented with the equivalent type of visual problem requiring judgment of distance using optic flow in the vertical plane, they solve this task with a much lower level of precision (Dacke & Srinivasan 2007). We argue that the relative accuracy of navigation in the horizontal and vertical dimensions makes sense in terms of normal ecological imperatives, and that brain plasticity can be recruited to facilitate robust bicoded processing if required.

Studies on honeybees suggest that visual processing of optic flow is dominated by information impinging on the ventral visual field (Dacke & Srinivasan 2007), which makes ecological sense for an animal that predominantly flies in the horizontal plane when foraging for nutrition. In contrast, the stingless bee operates in dense tropical environments where flower resources are typically scattered horizontally and throughout a range of vertical heights of up to 40 metres in the forest canopy. These stingless bees have been shown to be equally proficient at gauging distance in both the horizontal and vertical planes, potentially using optic flow mechanisms in both ventral and lateral visual fields (Eckles et al. 2012). Nonetheless, honeybees do sometimes also have to operate in complex three-dimensional environments such as tropical forests. How might they deal with the complexity of reliable orientation in the vertical plane? We suggest below that honeybees are able to use information other than optic flow, and that their brains can learn to combine different visual perceptions to solve novel problems, in a manner consistent with the bicoded hypothesis.

Whilst honeybees do communicate horizontal direction and distance to hive mates through a symbolic dance communication language, this does not reliably communicate elevation (Dacke & Srinivasan 2007). It is therefore likely that individual foragers must learn through their own experience to determine vertical components of their three-dimensional world. One possible solution to this problem is relationship learning – estimating vertical position by understanding the relative relationships, such as above/below, between different elemental features in the environment. The capacity to process such relationship rules is not innate for a brain. Three-months-old human babies do not show evidence of relationship processing, although by 6 months of age this capacity has developed (Quinn et al. 2002). Other adult primates, such as capuchin monkeys (*Cebus apella*), also show a capacity for solving problems requiring the learning of above/below rules (Spinozzi et al. 2004). Recent work in honeybees shows that while their brains do not innately code spatial relationship rules, individual free-flying bees can learn such relationships through visual experience, including the reliable processing of above/below (Avarguès-Weber et al. 2012).

The relationship rule processing mechanism observed in honeybees would thus give the potential for experienced individuals to forage in complex environments with acquired knowledge about relative vertical positions between biologically plausible objects, such as flowers and tree limbs (Chittka & Jensen 2011; Dyer et al. 2008). Could "vertical knowledge" then be combined with the perception of optic flow in the horizontal plane, to give a true bicoded perception of three-dimensional space? We believe so. The work on how honeybees process complex visual relationship rules, including above/below and same/different, suggests that there is also a capacity to learn simultaneously two separate rules or types of visual information, and then combine this acquired knowledge to solve novel problems (Avarguès-Weber et al. 2012). Thus, although the honeybee appears to process horizontal and vertical optic flows as separate signals (Dacke & Srinivasan 2007), it does appear that their brains have the capacity to combine multiple sources of sensory perception and other spatial cues to make novel decisions in complex environments.

In summary, learning to build concepts to process multiple dimensions of three-dimensional navigation using a bicoded system as hypothesised by Jeffery et al. may represent a more general biological capacity, which likely extends to relatively simple brains such as those of insects. Further, we suggest that the opportunity for a brain of an individual to learn complex tasks through experience is critical to revealing the true behavioural capabilities in animals, irrespective of the relative number of neurons and synapses involved.

Spatial language as a window on representations of three-dimensional space

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Abstract: Recent research investigating the language–thought interface in the spatial domain points to representations of the horizontal and vertical dimensions that closely resemble those posited by Jeffery et al. However, the findings suggest that such representations, rather than being tied to navigation, may instead reflect more general properties of the perception of space.

Jeffery et al. propose that bicoded representations may support the encoding of three-dimensional space in a wide range of species, including non–surface-travelling animals. Only humans, however, have the ability to draw on their representations of space to talk about their spatial experience. Here we highlight the potential of spatial language – not traditionally considered in the study of navigation through space – to provide insight into the nature of nonlinguistic spatial representation. In particular, we suggest that recent research on spatial language, spatial

cognition, and the relationship between the two offers an unexpected source of evidence, albeit indirect, for the kinds of representations posited by Jeffery et al. Such evidence raises the possibility that bicoded representations may support spatial cognition even beyond navigational contexts.

There are several striking parallels between Jeffery et al.'s account of spatial representation and the semantics of spatial language. Jeffery et al. argue that animals represent the vertical dimension in a qualitatively different manner than they do the two horizontal dimensions, in large part due to differences in locomotive experience. This distinction between vertical and horizontal is also evident in spatial language. Clark (1973) noted that English spatial terms rely on three primary planes of reference, one defined by ground level (dividing above from below) and the other two defined by canonical body orientation (dividing front from back and left from right). In a similar vein, Landau and Jackendoff (1993) pointed to axial structure (e.g., the vertical and horizontal axes) as a key property encoded by spatial prepositions, which otherwise tend to omit much perceptual detail (see also Holmes & Wolff 2013a). More recently, Holmes (2012; Holmes & Wolff 2013b) examined the semantic organization of the spatial domain by asking native English speakers to sort a comprehensive inventory of spatial prepositions into groups based on the similarity of their meanings. Using several dimensionality reduction methods to analyze the sorting data, including multidimensional scaling and hierarchical clustering, Holmes found that the first major cut of the domain was between vertical terms (e.g., *above*, *below*, *on top of*, *under*) and all other prepositions; terms referring to the left-right and front-back axes (e.g., *to the left of*, *to the right of*, *in front of*, *behind*) tended to cluster together. These findings suggest that the vertical-horizontal distinction may be semantically, and perhaps conceptually, privileged.

Holmes's (2012) findings are also consistent with Jeffery et al.'s claims about the properties that distinguish horizontal from vertical representations. Jeffery et al. propose that horizontal representations are relatively fine-grained, whereas vertical representations are coarser and nonmetric in nature. In Holmes's study, prepositions encoding distance information (e.g., *near*, *far from*) clustered exclusively with horizontal terms, implying that metric properties are more associated with the horizontal dimensions than the vertical. Further, vertical terms divided into discrete subcategories of "above" and "below" relations, but horizontal terms did not; English speakers regarded *to the left of* and *to the right of* as essentially equivalent in meaning. Perhaps most intriguingly, Holmes found that the semantic differences among the dimensions were mirrored by corresponding differences in how spatial relations are processed in nonlinguistic contexts (see also Franklin & Tversky 1990). When presented with visual stimuli depicting spatial relations between objects (e.g., a bird above, below, to the left of, or to the right of an airplane), participants were faster to discriminate an "above" relation from a "below" relation than two different exemplars of an "above" relation – but only in the right visual field, consistent with the view that the left hemisphere is specialized for categorical processing (Kosslyn et al. 1989). Though observed for vertical relations, this effect of lateralized categorical perception, demonstrated previously for color (Gilbert et al. 2006) and objects (Holmes & Wolff 2012), was entirely absent in the case of horizontal relations: Participants were just as fast to discriminate two different exemplars of "left" as they were to discriminate "left" from "right." That the vertical dimension was perceived categorically but the horizontal dimension was not suggests differences in how the mind carves up spatial information along different axes. In characterizing the nature of the bicoded cognitive map, Jeffery et al. use color merely as a way of illustrating the nonmetric property of vertical representations, but such an analogy seems particularly fitting: Whereas the vertical axis may be represented in the same way that we see a rainbow as forming discrete units, the horizontal axis may be represented more like color actually presents itself, namely as a continuous gradient.

Together, the findings reviewed above tell a story about spatial representation that is, in many respects, similar to that proposed by Jeffery et al. in the target article. However, such findings suggest an alternative explanation for the many differences observed between the horizontal and vertical dimensions. Early in the target article, Jeffery et al. briefly distinguish between spatial navigation and spatial perception more generally, implying that the representations supporting navigation may not extend to other spatial contexts. But given the parallels between spatial language and the representations implicated by Jeffery et al.'s account, and the fact that spatial terms often refer to static spatial configurations rather than motion through space, bicoded representations may constitute a more general property of spatial perception, rather than being specifically tied to navigation. This possibility could be examined in future research on the representation of three-dimensional space. More broadly, our observations suggest a role for research on the language–thought interface in informing accounts of cognitive abilities ostensibly unrelated to language, lending support to the enduring maxim that language is a window into the mind (Pinker 2007).

Multi-floor buildings and human wayfinding cognition

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Abstract: Multilevel wayfinding research in environmental psychology and architecture exhibits a strong compatibility with Jeffery et al.'s "bicoded" representation of space. We identify a need for capturing verticality in spatial analysis techniques such as space syntax and argue for investigating inter-individual differences in the ability to mentally integrate the cognitive maps of separate floors in buildings.

Our commentary focuses on navigating multilayer environments and extends Jeffery et al.'s view to an architectural and environmental psychology perspective.

The functions of buildings are generally organized horizontally, probably reflecting the constraints that humans encounter: A horizontal plane is neutral to the axis of gravity and allows for stable walking, sitting, and storing of objects. Humans and buildings "inhabit" the same "two-dimensional" ecological niche, and buildings stack floors on top of one another. As a consequence, the structure of typical buildings is highly compatible with the "bicoded" representation: Whereas the horizontal plane is continuous (albeit subdivided by corridors and partitions) and in line with the floors, the vertical axis is discontinuous and discretized; that is, floors are on top of one another, with only local connections via stairs or elevators. Unless one has a view along a multi-storey atrium, the vertical dimension is visually limited to the current or directly adjacent floor. Verticality is presented as "contextual," at ordinal rather than metric scale, and perceived indirectly or derived by inference processes.

Tlauka et al. (2007) describe a systematic bias in vertical pointing between floors. Across several studies in our group we have observed a pattern in the process of pointing that links to the bicoded representation: Pointing appears to be based on categorical and discretized rather than continuous information, visible in smooth horizontal pointing and stepwise vertical pointing. Participants report counting floors, rather than making spontaneous