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Comment

## Of global space or perceived place? Comment on Kelly *et al*.

biology

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Animal behaviour

Recently, Kelly et al. presented results of an orientation experiment with chicks and pigeons that involved training in a rectangular-shaped environment followed by testing in an L-shaped environment [1]. They interpreted the distribution of searches in the L-shaped environment as supporting a primarily local geometry strategy followed by a medial axis strategy for chicks and a primarily medial axis strategy for pigeons. Contrary to recent research [2] and theory [3-5], search behaviour was not supportive of a principal axis strategy. Here, we offer a potential alternative interpretation of its results based upon something analogous to a principal axis-based strategy. We suggest that this strategy may explain the results obtained for both chicks and pigeons without reference to a local geometry or medial axis strategy.

In considering the L-shaped environment presented during the test phase, we acknowledge that the principal axis as computed by the authors for this objective global shape is indeed not able to explain the search behaviour for either chicks or pigeons. One potential issue with this interpretation of the use of the principal and/or medial axis surrounds the mechanism(s) by which subjects determine a global shape from subjectively experienced views. Specifically, the subjective experience of any environment must necessarily be piecemeal. In order to perceive any global shape, subjects would be required to continually update a representation based upon the integration of successively experienced views of an environment [6].

This commentary is intended to broach this issue by asking the question: Is it possible that subjects extract a summary parameter derived from the limited part of the environment they are able to perceive rather than an objective summary parameter from the global shape of the environment? Such a summary parameter derived from the perceived part of the environment may be analogous to the principal axis in that it would pass through what could be considered the centroid of the perceivable space. For example, both legs of the L-shaped environment may not have been experienced simultaneously. Instead, the enclosure may have been perceived as successive presentations of rectangular-shaped environments. Similarly, as we sit in an office typing this commentary, the environment in which we currently find ourselves has a shape-a somewhat rectangular shape. If we must

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orient within this office we may be able to use a summary parameter of this environment. However, this office is attached to a hallway. If we were to walk out of this office and look down the hallway, we would find ourselves located within a different part of the environment—one that is narrower and longer. Again, we may be able to orient via a summary parameter of this perceivable part of the environment. Importantly, these two summary parameters would be independent of each other.

In short, if we sit in this office or stand in the hallway, there seems to be no functional need to continually integrate both environments in order to determine a useful summary parameter for the part of the environment we are currently able to perceive. This is not to say that we (or other organisms) are incapable of doing so, just that on a moment-to-moment basis, such integration seems unnecessary to orient within either environment. The issue is complicated by the fact that integration of additionally experienced views must necessarily continue nearly *ad infinitem*. For example, the hallway is connected to other offices, these offices to other hallways, these hallways to other hallways, stairwells, bathrooms, classrooms and so on ... leading to a problem of combinatorial explosion.

Within this framework, the principal axis as calculated by the authors for the global L-shaped environment may not have been the summary parameter extracted from the testing environment because the parts may have been experienced successively. We suggest that if something like the principal axes were calculated for these two separate rectangular-shaped environments, then these summary parameters derived from the perceivable environment appear to account for the search behaviour for both the chicks and pigeons in the L-shaped environment presented during testing (figure 1). A benefit of such an interpretation is that only a single environmental parameter is required for each successive experience without whatever costly and cumbersome processes may be involved in continually updating a global representation of a successively experienced environment.

If the L-shaped environment was partitioned into two separate rectangular-shaped environments, then a summary parameter derived from each partition was identical to that experienced during training within the rectangular-shaped environment. As a result, application of a strategy learned during the training was possible. Specifically, for the groups trained to the AC corners, a strategy of searching at the left-hand side of the summary parameter derived from each partition appears to explain the obtained distribution of searches during the L-shaped environment. Conversely, for the groups trained to the BD corners, a strategy of searching at the right-hand side of the summary parameter derived from each partition appears to explain the distribution of searches during the L-shaped environment. Importantly, such a strategy appears to explain the search behaviour for both the chicks and pigeons.

Of additional importance is that the starting position within the L-shaped environment is unclear [1]. Because proximity to a location has been shown to influence search behaviour [7], it remains unknown to what extent proximity to a location influenced search within the L-shaped environment (especially



Figure 1. Results reproduced (fig. 2) from Kelly *et al.* [1]. Means and standard errors of the means for searches during testing in an L-shaped environment following training in a rectangular-shaped environment. We have overlayed (dashed lines) something analogous to the principal axes, assuming that subjects partitioned the L-shaped environment into two separate rectangular-shaped environments. Numbers represent hypothetical start positions. Circles indicate response locations specified by the application of a strategy learned during training (i.e. search on the same side of the summary parameter derived from each partition as was rewarded in the rectangular-shaped environment).

with respect to hypothetical start position 2). However, to whatever extent proximity to a location is unable to explain searches to corner K by pigeons, this location is to some extent specified by the left-hand side of a derived summary parameter for the AC group (at least from hypothetical start position 1) and the right-hand side of a derived summary parameter for the BD group (at least from hypothetical start position 3).

The strength of this potential alternative explanation lies not only in its parsimony but also in its economy. Whereas continually updating a global representation through integration of successively experienced views faces a problem of combinatorial explosion (something that medial axes would also face in the presence of environments of increasing complexity [4]), extraction of a summary parameter derived from the perceived space allows for a reliable orientation cue that is minimal with respect to effort of computation and execution [4,5]. As an environment becomes more complex, this summary parameter derived from the perceived part of the environment avoids the problem of combinatorial explosion and results in a relatively simple and efficient strategy by which to orient with respect to the environment.

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