

The authors [8] suggest that postinsemination associations in other species could evolve either via the previously described more conventional pathway of sexual conflict and coercion, or through cooperation and mutual benefit, such as in crickets. An important component to their study is the natural setting in which it was conducted; most studies of mate guarding in crickets and other insects have taken place in small laboratory cages that do not allow the participants much mobility. Females thus confined might have been unable to evade the efforts of males to prevent them leaving or removing a spermatophore, making it difficult to evaluate the effectiveness of mate guarding under natural circumstances.

Variation in features such as the availability of suitable burrow habitat, the sex ratio, or the population density will influence the probability of finding a new mate and hence the costs and benefits of mate guarding for both sexes [10]. For example, if females are relatively scarce, males would benefit by remaining with mates longer than if females were common. In

species that form pair bonds but also engage in extra-pair copulations, such as many songbirds, males must balance the gains of prolonged mate guarding against the costs of losing opportunities to find extra-pair mates, while females might be less able to exercise mate choice when being guarded [10].

The generality of the findings by Rodríguez-Muñoz and colleagues [8] also remains to be seen. In many animals, including many species of crickets and other insects, males do not have a resource such as the refuge of a burrow to offer to females, and remaining with a mate after copulation could simply prolong a period of vulnerability to predators [11]. Regardless, 'mate guarding' may be too narrow a term, as the behaviors exhibited may include activity, as well as benefits, to both sexes [12].

References

1. Alcock, J. (1994). Postinsemination associations between males and females in insects – the mate-guarding hypothesis. *Annu. Rev. Entomol.* 39, 1–21.
2. Buss, D.M. (2002). Human mate guarding. *Neuroendocrinol. Lett.* 23 (Suppl. 4), 23–29.

3. Parker, G.A. (1974). Courtship persistence and female-guarding as male time investment strategies. *Behavior* 48, 157–184.
4. Birkhead, T.R. (1988). Behavioral aspects of sperm competition in birds. *Adv. Study Behav.* 18, 35–72.
5. Simmons, L.W. (2001). *Sperm Competition and its Evolutionary Consequences in the Insects* (Princeton: Princeton University Press).
6. Simmons, L.W. (1991). On the post-copulatory guarding behaviour of male field crickets. *Anim. Behav.* 42, 504–505.
7. Arnqvist, G., and Rowe, L. (2005). *Sexual Conflict* (Princeton: Princeton University Press).
8. Rodríguez-Muñoz, R., Bretman, A., and Tregenza, T. (2011). Guarding males protect females from predation in a wild insect. *Curr. Biol.* 21, 1716–1719.
9. Rodríguez-Muñoz, R., Bretman, A., Slate, J., Walling, C.A., and Tregenza, T. (2010). Natural and sexual selection in a wild insect population. *Science* 328, 1269–1272.
10. Kokko, H., and Morrell, L.J. (2005). Mate guarding, male attractiveness, and paternity under social monogamy. *Behav. Ecol.* 16, 724–731.
11. Gwynne, D.T. (1989). Does copulation increase the rate of predation? *Trends Ecol. Evol.* 4, 52–56.
12. Zaldivar-Rae, J., and Drummond, H. (2007). Female accompaniment by male whiptail lizards: is it mate guarding? *Behavior* 144, 1383–1402.

Department of Biology, University of California, Riverside, California 92521, USA.
E-mail: marlene.zuk@ucr.edu

DOI: 10.1016/j.cub.2011.09.043

Neuroscience: How Is Three-Dimensional Space Encoded in the Brain?

A recent study in the rat has shown that hippocampal place cells and entorhinal grid cells exhibit vertically-elongated firing fields, indicating that the rat's brain may encode the animal's elevation less accurately than its horizontal position.

Nachum Ulanovsky

We live in a three-dimensional world. Questions about how we perceive and represent the three-dimensional world that surrounds us have occupied humankind for centuries. In art, the perception of three-dimensional space has been a central theme, from the gradual development of geometrical perspective methods, in antiquity and the Middle Ages, to modern three-dimensional films. In philosophy, many thinkers have debated the nature of three-dimensional space:

While Newton argued that space is an objective, absolute entity, Kant argued that space is an *a priori* mental

framework that our mind uses to coordinate external sensations [1]. In science, the physicists of the 20th century, from Einstein onward, have made great progress in understanding the nature of three-dimensional space and its distortions. Very little progress, however, has been made in understanding the mental representation of three-dimensional space in the brain. A recent study by Hayman *et al.* [2] starts to close this gap between the physics and neuroscience of three-dimensional space.

While few previous studies have examined the neural representation of three-dimensional space, the

representation of two-dimensional planes in the brain has been studied extensively for the past 40 years [3,4]. The neural machinery that represents two-dimensional spatial planes includes 'place cells' in the hippocampus — neurons that become active when the animal traverses a particular location in space, termed the 'place field' [3–5] — and 'grid cells' in the entorhinal cortex and adjacent regions — neurons that are activated when the animal passes through the vertices of a hexagonal two-dimensional lattice that spans the environment [4,6]. Together with neurons that encode the animal's head-direction [7], and neurons which encode the positions of the geometric borders of the environment [8], these types of space-coding cells form the essential components of the brain's 'navigation circuit' for two-dimensional environments. But what about the third dimension?

Previous experiments in three-dimensional environments included a study of hippocampal place cells in rats walking on a surface titled

by 30 degrees [9], two studies of bats walking on a nearly-vertical surface [10,11], and another study in rats that was conducted in microgravity conditions aboard a space shuttle, where rats walked on horizontal and vertical tracks [12]. All of these studies [9–12], on both tilted and vertical surfaces, showed place fields that seemed quite circular and isotropic, with field shapes being very similar to the circular place fields that are typically found in horizontal two-dimensional arenas. However, because all these three-dimensional studies used movement surfaces that were essentially two-dimensional planes embedded in three-dimensional space, and because the dataset in the space-shuttle experiment [12] was rather limited, it became apparent that a more extensive experiment would be needed to better elucidate the representation of three-dimensional space in the mammalian brain.

In their new work, Hayman *et al.* [2] have taken an important step in this direction. The authors trained rats to walk in two setups, a vertical climbing wall (‘pegboard’) and a helical track (Figure 1A). Both of these setups allowed measuring the animal’s vertical position. Rats zigzagged horizontally or diagonally on the pegboard, or they shuttled up and down the helical track, while the experimenters recorded the neural activity of hippocampal place cells or of entorhinal grid cells. Hayman *et al.* [2] found that, in the pegboard apparatus, the firing fields of hippocampal place cells were elongated in the vertical dimension (z) more than in the horizontal dimensions (x and y) (Figure 1A). A similar result was found on the helical track, where place cells fired at the same horizontal position on several consecutive laps (coils) of the helix, with firing positions located one above the other, resulting in an overall vertical orientation of the place field (though the vertical elongation on the helix was weaker than on the pegboard). Grid-cell firing patterns were even more vertically elongated than those of place cells, both on the pegboard and on the helix. The elongated shapes of the firing fields of place cells and grid cells, in both types of apparatus, implied that the neuronal activity conveyed less information about the rat’s vertical position than about its horizontal position. The authors concluded that

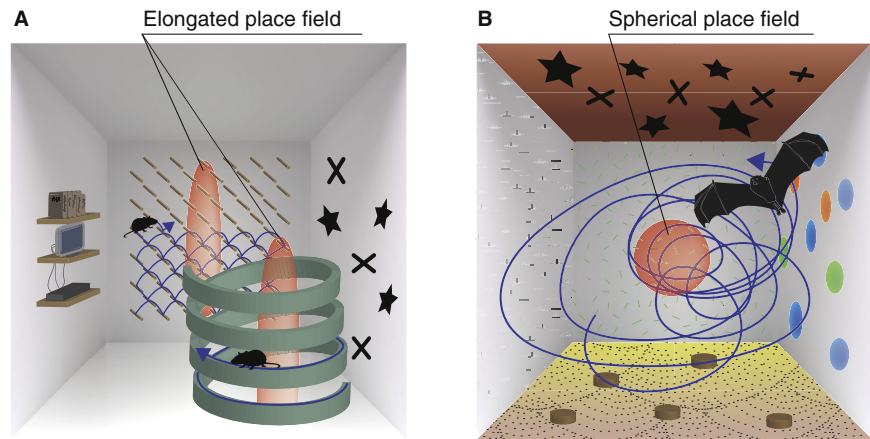


Figure 1. Representation of three-dimensional space in the brain under different conditions: Experiments and predictions.

(A) In the study of Hayman *et al.* [2], rats were trained to walk on a climbing ‘pegboard’ apparatus (far wall), or on a helical track, while neural activity was recorded in the hippocampus or entorhinal cortex. The authors found that place fields and grid fields were vertically elongated. Notably, the trajectories of rats on the helical track and on the pegboard contained mostly horizontal movement components (blue lines), with very little vertical velocity. Additionally, the floor had uniform gray color, contrasted with many visual landmarks on the walls. Thus, both the movement patterns and visual inputs were highly anisotropic — which may have led to the anisotropic, vertically elongated place fields and grid fields. (B) Prediction for how three-dimensional space may be represented in the brain of freely flying bats, mammals that move much more isotropically in three-dimensions, and which exhibit a substantial vertical movement component (blue line). An experimental room could be constructed where sensory landmarks (visual or echolocation-based landmarks) are positioned roughly isotropically on the walls, floor and ceiling (in contrast to the lack of landmarks on the floor and ceiling in panel A). Under these circumstances of isotropic movements and isotropic sensory landmarks (echoic/visual), the prediction is for isotropic, spherically shaped three-dimensional place fields in the hippocampus of freely flying bats.

the representation of three-dimensional space in the mammalian brain may be less precise in the vertical dimension than in the horizontal dimensions.

What is the source of the differences between the findings of Hayman *et al.* [2] — of vertically elongated place fields and grid fields — and previous findings that demonstrated roughly circular place fields in the hippocampus of rats and bats running on tilted or vertical surfaces [9–12]? There are several possibilities. Firstly, the structure of the helix apparatus was highly elongated in the vertical dimension [2]. A previous study [13] on a two-dimensional plane found that place fields in an elongated horizontal box tend to be stretched in the direction of the box’s long axis. The strong vertical elongation of the helical track used by Hayman *et al.* [2] may have contributed to the vertical elongation of the place fields and grid fields recorded on the helix. This explanation, however, does not account for the results of the pegboard experiment, because the pegboard had square proportions.

Secondly, the elongation of place fields and grid fields observed by Hayman *et al.* [2] is reminiscent of recent results from rats running in repetitive two-dimensional horizontal environments — one study in a repetitive ‘hairpin maze’ [14], and another study in a repetitive ‘W-maze’ [15] — where the firing of place cells and grid cells formed elongated stripes, which were related to the repetitive structures of these experimental environments [14,15]. This suggests that the neuronal firing fields in the study by Hayman *et al.* [2] were not necessarily elongated in the vertical dimension *per se*, but rather reflected the repetitive structure of the environment along the vertical dimension, in both the pegboard, and even more so in the helical track.

Thirdly, in the study by Hayman *et al.* [2], the rat’s body was positioned mostly horizontally, unlike the fully vertical body orientation that was exhibited in previous studies by climbing rats [12] and bats [10,11] — a difference which may have affected the shape of the firing field.

Finally, the most likely explanation for the difference between the studies is that in the previous experiments [10–12], the movement patterns of the animals were quite isotropic — leading to isotropic, circular place fields — whereas in the experiments of Hayman *et al.* [2], the movement patterns were highly anisotropic, with mostly horizontal movement components (Figure 1A, blue lines). Similarly, the visual inputs in previous studies seemed quite isotropic [10–12], while the visual inputs in the study by Hayman *et al.* [2] were quite anisotropic, with gray-colored uniform floors that provided little visual information in the vertical dimension, in contrast to the walls that were covered with many objects and provided a rich set of cues in the horizontal dimension [2]. This asymmetry in sensory inputs and in behavior may have led to the anisotropic, vertically elongated firing fields of place cells and grid cells in the study by Hayman *et al.* [2] (Figure 1A). In other words, the hypothesis is that isotropic movement patterns and isotropic sensory inputs lead to isotropic spatial representation [10,12], while anisotropic movement patterns and anisotropic sensory inputs lead to anisotropic spatial firing patterns [2].

How could one test this hypothesis? One possibility would be to perform recordings from place cells and grid cells in a mammal that can move freely and isotropically through real three-dimensional space: Namely, record from the brains of flying bats. On two-dimensional planes, place cells in bat hippocampus and grid cells

in bat entorhinal cortex exhibit remarkably similar spatial activity patterns to those of two-dimensional place cells and grid cells in rats [10,16]. In flight, bats exhibit highly complex three-dimensional flight maneuvers [17,18]. Therefore, the prediction is that in bats flying freely in three-dimensional space (Figure 1B, blue line), the three-dimensional place fields of hippocampal neurons should be isotropic, with roughly spherical shape (Figure 1B). Such experiments require the development of either wired or wireless telemetric recording techniques in freely flying bats — methods which we recently developed in our laboratory [19]. It remains to be seen whether this prediction for isotropic firing fields indeed holds true in the case of three-dimensional spatial representation in the brain of freely flying bats.

References

1. Kant, I. (1787). Critique of Pure Reason, 2nd Edition.
2. Hayman, R., Verriotes, M.A., Jovalekic, A., Fenton, A.A., and Jeffery, K.J. (2011). Anisotropic encoding of three-dimensional space by place cells and grid cells. *Nat. Neurosci.* 14, 1182–1188.
3. O'Keefe, J., and Nadel, L. (1978). *The Hippocampus as a Cognitive Map* (Oxford: Oxford University Press).
4. Moser, E.I., Kropff, E., and Moser, M.-B. (2008). Place cells, grid cells, and the brain's spatial representation system. *Annu. Rev. Neurosci.* 31, 69–89.
5. Wilson, M.A., and McNaughton, B.L. (1993). Dynamics of the hippocampal ensemble code for space. *Science* 261, 1055–1058.
6. Hafting, T., Fyhn, M., Molden, S., Moser, M.-B., and Moser, E.I. (2005). Microstructure of a spatial map in the entorhinal cortex. *Nature* 436, 801–806.
7. Taube, J.S., Muller, R.U., and Ranck, J.B., Jr. (1990). Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. *J. Neurosci.* 10, 420–435.

8. Solstad, T., Boccara, C.N., Kropff, E., Moser, M.-B., and Moser, E.I. (2008). Representation of geometric borders in the entorhinal cortex. *Science* 322, 1865–1868.
9. Jeffery, K.J., Anand, R.L., and Anderson, M.I. (2006). A role for terrain slope in orienting hippocampal place fields. *Exp. Brain Res.* 169, 218–225.
10. Ulanovsky, N., and Moss, C.F. (2007). Hippocampal cellular and network activity in freely moving echolocating bats. *Nat. Neurosci.* 10, 224–233.
11. Ulanovsky, N., and Moss, C.F. (2011). Dynamics of hippocampal spatial representation in echolocating bats. *Hippocampus* 21, 150–161.
12. Knierim, J.J., McNaughton, B.L., and Poe, G.R. (2000). Three-dimensional spatial selectivity of hippocampal neurons during space flight. *Nat. Neurosci.* 3, 209–210.
13. O'Keefe, J., and Burgess, N. (1996). Geometric determinants of the place fields of hippocampal neurons. *Nature* 381, 425–428.
14. Derdikman, D., Whitlock, J.R., Tsao, A., Fyhn, M., Hafting, T., Moser, M.-B., and Moser, E.I. (2009). Fragmentation of grid cell maps in a multicompartiment environment. *Nat. Neurosci.* 12, 1325–1332.
15. Singer, A.C., Karlsson, M.P., Nathe, A.R., Carr, M.F., and Frank, L.M. (2010). Experience-dependent development of coordinated hippocampal spatial activity representing the similarity of related locations. *J. Neurosci.* 30, 11586–11604.
16. Yartsev, M.M., Witter, M.P., and Ulanovsky, N. (2010). Spatial maps in the medial entorhinal cortex of the Egyptian fruit bat. *Soc. Neurosci. Abstr.* 203.15.
17. Ulanovsky, N., and Moss, C.F. (2008). What the bat's voice tells the bat's brain. *Proc. Natl. Acad. Sci. USA* 105, 8491–8498.
18. Yovel, Y., Falk, B., Moss, C.F., and Ulanovsky, N. (2010). Optimal localization by pointing off axis. *Science* 327, 701–704.
19. Yartsev, M.M., and Ulanovsky, N. (2011). Three-dimensional spatial representation in the hippocampus of flying bats. *Soc. Neurosci. Abstr.* 937.25.

Department of Neurobiology, Weizmann Institute of Science, Rehovot 76100, Israel.
E-mail: nachum.ulanovsky@weizmann.ac.il

DOI: 10.1016/j.cub.2011.09.031

Face Recognition: Vision and Emotions beyond the Bubble

A new study of how neurons in the human amygdala represent faces and their component features argues for a holistic representation.

Hanlin Tang¹ and Gabriel Kreiman^{1,2,3}

Visual input from the retina travels through a cascade of processes in the neocortex to the highest echelons of the brain, eventually feeding into areas that govern memory, emotion, cognition and action. An important

step to explaining these higher brain functions is to first understand and quantitatively characterize the neuronal circuits behind the transformation of the pixel-like visual input to the complex behaviorally relevant format in higher brain centers.

As reported recently in *Current Biology*, Rutishauser *et al.* [1] courageously attacked this question by recording the activity of individual neurons in the human brain while subjects view and act upon images of faces. The researchers focussed their study on the amygdala, a region of the brain that receives direct visual input from the inferior temporal cortex and plays a central role in processing emotions [2]. Higher brain centers that govern complex behavior are typically difficult to study, and the amygdala is no exception. Studies in rodents and non-human