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A role for terrain slope in orienting hippocampal place fields

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Abstract The three-dimensional topography of the environment is a potentially important source of orienting information for animals, but little is known about how such features affect either navigational behaviour or the neural representation of place. One component of the neural place representation comprises the hippocampal place cells, which show location-specific firing that can be oriented by directional cues in the environment. The present study investigated whether a simple topographical feature, terrain slope, could provide such orienting information to place cells. Place cells were recorded as rats explored a tilted (30°) square box located in the centre of a dark, curtained and visually symmetrical circular enclosure. The orientation of the tilted surface was varied, first in conjunction with that of a visible cue card (to stabilise the system) and then in the absence of the cue card, when the slope of the box was the only remaining stable polarising cue in the environment. In the latter condition, place fields continued to be reliably oriented by the slope. Thus, terrain slope provides sufficient orienting information to set and probably maintain the orientation of the hippocampal place system. This may explain previous behavioural observations that spatial orientation is improved when slope information is available.

Keywords Hippocampus · Place cells · Direction · Topography · Idiothetic cues · Visual cues · Terrain gradient

Introduction

The neural mechanisms of spatial orientation in mammals have been well-studied in two dimensions, (i.e., in

the horizontal plane), but relatively little is known about the contribution of the third, vertical dimension. Three-dimensional information includes surface features that vary in the vertical dimension, such as surface topography (bumps and hollows) and terrain slope, and volumetric features such as the continuous three-dimensional space comprising a volume of air or water (for flying and swimming animals, respectively) or the three-dimensional connectedness of a burrow or tree system or, in the case of humans, a multi-storey building. Volumetric features are difficult to study at the neural level because of the practical difficulties of using cable-based recording in a three-dimensional space, particularly one with obstructions such as branches or tunnel walls. Surface features are, however, much more accessible with current methodologies, and physiologists have recently begun to explore the neural correlates of topographical features in three dimensions (e.g., Knierim and McNaughton 2001; Stackman et al. 2000). The focus of the present study was on the simplest three-dimensional surface characteristic—terrain slope. The question we addressed was: does terrain slope provide an input into the neural place representation?

The neural place representation, or at least a major component of it, was discovered in the 1960s in the hippocampus of rodents (O'Keefe and Dostrovsky 1971), and the discovery provided great impetus to the study of how the brain encodes the spatial layout of the environment. This hippocampal representation is instantiated by the place cells, pyramidal cells in the CA3 and CA1 hippocampal subfields whose activity correlates highly with the spatial location of the animal regardless of which way it is oriented. Closely related to the place cells are the head direction cells (Taube et al. 1990), found in a number of limbic structures (Sharp et al. 2001), that signal the orientation of the animal's head, regardless of actual location in the environment. The place and head direction cells together have the capacity to represent both position and orientation of the animal at any given moment. Observing how these cells react in the face of environmental

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manipulations provides useful insights into the structure of the spatial representation, and may also provide insights as to how the animals as a whole process such changes cognitively.

One such set of insights concerns the kinds of cues that signal direction. A number of studies of place and head direction cells have pointed to the importance of environmental landmarks in setting the orientation of the place representation: that is, in allowing orientation to be retrieved when the animal enters the environment, even if it was incorrectly oriented upon entry, and in resetting it if the animal subsequently became disoriented (Etienne et al. 2000; Taube and Burton 1995; Etienne and Jeffery 2004). In addition, a number of so-called “internal” cues, such as vestibular and proprioceptive signals, serve to update the representation of orientation as the animal moves around, even if it loses sight of the setting/resetting cues (Knierim et al. 1998). Identifying the kinds of cue that can set and reset the orientation of the place representation is critical in achieving a full understand of how animals orient themselves. The present study undertook an examination of how one particular kind of three-dimensional information—terrain slope—might help to set the directional representation.

Emerging evidence from behavioural studies indicates that animals and humans can use terrain slope as an orienting cue (Restat et al. 2004; Miniaci et al. 1999; Moghaddam et al. 1996). This makes adaptive sense, since slope can be determined using either visual or kinaesthetic cues, and thus is almost always available, whatever the lighting conditions. This would be particularly useful for burrow-dwelling animals like rats, which may be trying to navigate in complete darkness. It thus follows that the place cells might also be sensitive to slope, and so the present study observed place cells in order to find out whether they can use slope in perhaps its simplest role: as an orienting cue in an environment that is otherwise perceptually symmetrical.

Methods

Subjects

Subjects were three male Lister hooded rats, 350–450 g, housed singly in Perspex cages. Each rat was maintained at approximately 90% of its free-feeding weight. All procedures in this study were licensed by the UK Home Office and adhered to the restrictions and provisions contained in the Animals (Scientific Procedures) Act 1986.

Electrode assembly and implantation

Implantation of chronic indwelling recording electrodes into the hippocampus took place using methods that

have been described in detail elsewhere (Jeffery et al. 2003). For each rat, four tetrodes were constructed from four interwound 25- μ m diameter platinum–iridium wires (California Fine Wire, USA), attached to a microdrive assembly and implanted under isoflurane anaesthesia into the neocortex overlying the right hippocampus (3.8 mm posterior and 2.2 mm lateral to bregma, 1 mm below brain surface). The microdrive, which was protected with paper tape between recording sessions, allowed the tetrodes to be moved through the brain in steps of as little as 25 μ m at a time. To provide post-operative analgesia, at the completion of implantation surgery, the animals were given an intramuscular injection of buprenorphine (0.1 ml) and for the following three days were given buprenorphine jelly (Flecknell et al. 1999). The animals were allowed at least 2 weeks to recover from surgery before electrophysiological recording began.

Apparatus

The recording room was a standard laboratory room containing a central curtained-off circular arena, 2 m in diameter, in the centre of which was the place cell recording apparatus. To minimise extraneous and potentially orienting auditory cues, the preamplifier of the recording system was located within the recording room but the data acquisition system itself, including the computer, were in the adjacent room, connected via long cables passing under the door. During recording the room lights were turned off to minimise visibility of the extra-box environment.

The recording environment consisted of a low-walled box with a fibreboard floor, 60 cm², overlaid with four interlocking rubber tiles, embossed with a square pattern that provided grip for the rats' paws when the box was tilted. The box walls were made from white foamboard pieces, 10 cm high. To provide a dim, even level of illumination, these were painted on the inwards-facing side with Ultra Blue photoluminescent paint (Glow Inc., MD, USA) mixed with polyurethane matt finish paint. After charging under electric lights, this paint emits light in the blue-green range—the region of maximum sensitivity of the rat retina (Jacobs et al. 2001)—for several hours. The glowing walls enabled the rat to dimly see the local environment, thus helping its spatial localisation, while preventing the uneven casting of shadows that would occur under external lighting and that could provide an unintended visual polarising cue. The walls of the box and the four square floor tiles could be shuffled to disrupt configurations of olfactory cues.

Having tried to eliminate uncontrolled polarising cues with the above manipulations, two kinds of controlled polarising cue were introduced. First, the box was tilted by propping it up under one edge so that the floor was inclined at an angle of 30° from the horizontal. The tilted box rested on a 70 cm high swivel chair, enabling ease of rotation. Between trials, the box was

usually rotated 90° or 180° in the plane of its floor, so that the different sides of the box took turns at being uppermost. This was done to discourage orientation by the use of local cues, such as odours on the floor or visual irregularities in the painted walls. The box ensemble was also rotated on its swivel so that the orientation of the tilt varied with respect to the outside room. This was to discourage orientation by use of remote cues such as sounds and focal odours emanating from outside the arena.

The second controlled polarising cue was a cue card, present for some trials only. This was introduced because pilot data had suggested that when deprived of too many orienting cues simultaneously, place fields often seemed to “break down” (i.e., become scattered and unstable). Although this was hard to quantify (since place fields not infrequently break down anyway, in a long series of recording trials), to be on the safe side we attempted to “stabilize” the system first. Previous observations had shown that with appropriate experience, the place system can acquire information about the stability of orienting cues (Jeffery 1998), and so in the present experiment we gave each rat prior information about the apparent stability of slope as an orienting cue, before probing the effects of slope alone. Thus, for some so-called “training trials”, in addition to the slope of the box, supportive orienting information was supplied with a large photoluminescent cue card hung on the curtains located nearest to the lowermost edge of the box where it was maximally visible from the box. Previous experiments had shown that a salient visual cue like this exerts strong control over the orientation of the place system (Muller and Kubie 1987; Jeffery and O’Keefe 1999) and is easily able to override fainter, extraneous cues from outside the environment. When the box was rotated on the swivel stand, the cue card was rotated too so that the tilted box always faced it. The card’s function was to gain control over the orientation of the place cell representation, and to allow the rat to experience that the slope bore a stable relationship to this strong cue and was thus also, itself, a reliable directional indicator. This procedure also helped disconnect the directional system from uncontrolled distant cues, since these would seem to rotate randomly with respect to the strong, local polarising cues. In the probe trials, the cue card was removed so that terrain slope provided the only remaining salient polarising cue in the environment.

Between trials the rat rested in a bucket that was suspended from a string in the centre of the arena, above the recording box. At the start of recording the bucket was unclipped from the string and removed so as not to obscure the camera view. The reason for this inter-trial procedure was that the hanging bucket would, it was hoped, be unstable enough to slightly disorient the rat, encouraging it to reorient in the recording box using the re-perceived orienting cues (the terrain slope and/or the cue card), and yet not so unstable as to introduce a large sensory conflict and cause the rat to disregard the sensory cues altogether and rely instead on its internal

direction sense [see Knierim et al. (1995) and Rotenberg and Muller (1997) for a more complete explanation of this potential conflict].

Recording procedure

When the rats had recovered from the implantation, screening for place cells began. Screening took place in a room separate from the actual experimental room, to minimize the learning of extraneous cues in the recording environment by the rats. During screening the tetrodes were advanced, by turning the microdrive screw, in small increments (25–200 μm) daily until complex spikes appeared. Once place cells were isolated in the screening room, the rat was transported to the experimental room in an opaque box. There, the rat was connected to the recording cables and placed in the holding bucket until the commencement of recording trials.

Prior to a recording trial the apparatus was configured appropriately for that trial (see below). To begin a trial the rat was gently lifted out of the bucket and placed in the box by the experimenter, who then removed the bucket and set it on the floor to one side of the box. The rat then foraged for rice grains for the next 4 min while the experimenter threw additional grains into the apparatus to encourage the animal to move around.

Place cell data were collected using a Dacq multi-channel recording system (Axona Ltd., St. Albans, UK). The potentials detected by the electrodes were amplified (20,000–40,000 times) and bandpass filtered (500–7 kHz). Each of the four wires of one tetrode was recorded differentially with respect to one of the wires of another tetrode. During recording, continuous tracking of the rat’s position was achieved via a small infrared LED on the head-stage assembly which was monitored by a monochrome video camera mounted in the ceiling. The video image was passed to a tracking system (Axona Ltd.) which detected the position of the infrared LED and converted this into x – y coordinates, to provide the location of the rat for off-line comparison with unit activity. While recording unit activity from neurons, each channel was monitored every 20 μs , and 50 points per channel were sampled whenever the signal on any of the four channels exceeded a given threshold (a presumptive spike). Each spike event was then stamped with the time elapsed since the beginning of the recording and stored along with the concurrent location of the animal. All data were collected and stored on hard disk for offline analysis at a later time.

At the end of the trial the rat was lifted out of the box and placed into the hanging bucket, where it remained while the experimenter rearranged the apparatus. Rearrangement consisted of some combination of (a) local cue rotation (rotating the box in the plane of its floor), (b) slope rotation (rotating the whole box on its swivel, around a vertical axis passing through the

box-floor centre, so that the slope now faced a different direction) and (c) cue card rotation [aligned with the rotation in (b)] or removal. Figure 1 shows examples of different configurations of the apparatus. At least four trials were run with the cue card and box tilt in alignment. When place cells were identified and determined to be reliably controlled by the cue combination, the cue card was removed and further trials run with slope and local olfactory cues being the only remaining polarising cues.

Data analysis

Data analysis was performed as described in more detail elsewhere (Jeffery et al. 2003). In brief, cells were isolated using a clustering method (Tint, Axona Ltd), and the location of the rat on a moment-by moment basis was determined by smoothing the path that had been recorded by the tracking system. To determine the location of each cell's place field within the experimental environment, the tracking camera's viewing area was divided into a 64x64 grid, each square pixels of side ~1.0 cm, and the location of place cell firing determined by associating each action potential ("spike") with the place where the rat was at the time. The firing rate for a given cell in each pixel was then evaluated by dividing the number of spikes in that pixel by the amount of time spent by the rat there. The firing rate maps were smoothed using an algorithm that replaced the value in each pixel with the average of the value in that pixel plus the adjacent eight pixels.

Further analysis was conducted using custom-written programs in MATLAB (The MathsWorks, Natick, MA, USA). Cells with a peak frequency (taken from the pixel

with the highest rate) of less than 1.0 Hz or with a total number of spikes of below 20 in any trial were eliminated from further analysis. These cells were considered not to have fired in that particular trial, and the map was represented as empty.

Analysis was performed on a given place field to determine how the firing in a given trial compared with the firing of other trials in the same session. We have found in previous experiments (Jeffery and O'Keefe 1999) that when directional stimuli are manipulated, simultaneously recorded cells always orient their place fields together. Inspection of our current data revealed this also to be the case, so for ease of analysis we chose the best isolated and/or most stable cell from each session to act as an index of ensemble orientation (see Chakraborty et al. 2004 for confirmation of the reliability of this index). The firing of this index cell in each trial was compared with its firing in the preceding trial by generating a place field map and comparing the maps from the two trials, on a pixel by pixel basis, using Pearson's correlations (Jeffery et al. 2003). Although the tilt of the box rendered the place cells maps slightly trapezoidal, due to foreshortening, this effect was slight and did not impact on the correlation values so no attempt was made to correct for this distortion.

Three sets of correlations were conducted. In the first, the place field maps were straightforwardly correlated as described above, thus being aligned as they had been oriented with respect to the room. For the remaining two sets the maps were rotated so as to align them according to, respectively, the slope of the box (or slope plus cue card, for the training trials) or local box cues. The correlations produced from each trial pair were statistically compared with repeated-measures ANOVAs to determine which was the principal influence on place

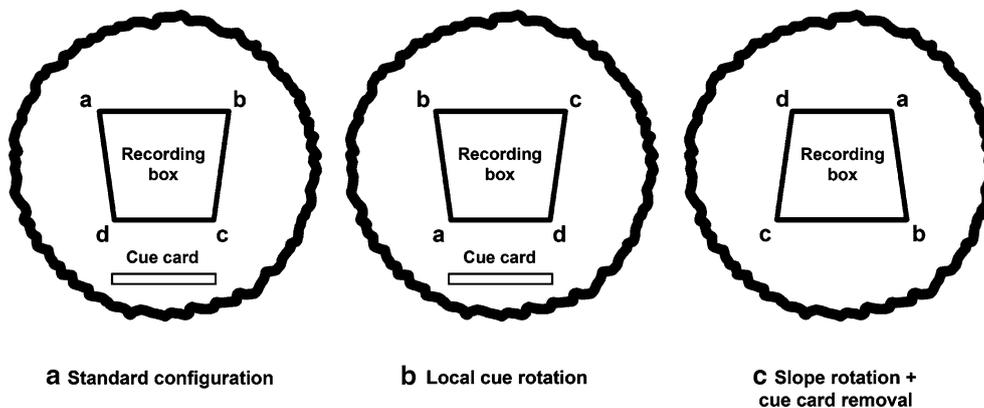


Fig. 1 Different ways in which the apparatus could be configured to test the relative contributions of local cues, a visual landmark and the slope of the environment. The environment is being viewed from the position of the centrally placed overhead camera and the tilt of the box is depicted graphically by exaggerating the foreshortening that results in the square box appearing trapezoidal to the camera. The physical orientation of the box is indicated by labelling the corners *a-d*. **a** In the standard configuration, the square box has been tilted with the high end north, and the cue card

placed to the south so that it was maximally visible to the rat. **b** The box has now been rotated 90° CCW in the plane of its floor, so that the physical corners have rotated but all else remains the same. This procedure tests for the influence of local cues. **c** Now the box has been rotated 180° around a central vertical axis so that the slope faces in the opposite direction (note that this also has the effect of rotating the local cues with respect to the outside world) and the cue card has been removed. The only remaining polarising cues are the local olfactory cues and the slope of the box

cell rotation (room, local cues or slope). Prior to all statistical analysis, correlation coefficients were adjusted using Fisher's *r*-to-*Z* transformation. Where necessary, Griesser-Greenhouse adjustments to the degrees of freedom were made.

Results

In general, there was a relative paucity of place cells in the recording environment, probably because of the impoverished sensory inputs supplied by the darkened environment and scrambled local cues (Save et al. 2000). Nevertheless, it was generally possible to isolate at least one good cell in each set of trials. Fifty-one cells were recorded from the three rats, who received, respectively, 13, 6 and 11 training trials, and 7, 7 and 6 test trials (Table 1).

As expected from previous studies, rotation of the box on its swivel, together with the cue card, reliably caused place fields to rotate too, thus successfully disconnecting the place representation from possible external cues. Conversely, and also as expected, rotation of the box alone, in the plane of its floor, failed to cause a corresponding rotation of place fields, thus indicating that the cells did not use local olfactory or uncontrolled visual cues from the box to establish the orientation of their fields. However, when the cue card was removed, the local box cues rotated *and* the box rotated on its swivel, the place fields aligned themselves with the slope of the box rather than with either the local cues or the distant cues supplied by the laboratory reference frame (Fig. 2). Thus, terrain slope alone enabled place cells to disambiguate the orientation of the box.

This observation was quantified by comparing the place fields in a given trial with the fields recorded in the preceding trial. As described in the Methods, the comparison was made by dividing the environment into pixels and correlating the firing in each pixel of the first trial with the corresponding pixel in the second trial. In a stable situation with no environmental changes, place fields remain in the same location and thus the pixel correlation tends to be high (i.e., if the cell fired at a high rate in a given pixel on the first trial, it would tend to do so on the next trial too). If, on the second trial, place

fields rotated to follow an orienting cue, then a straightforward correlation would be low. However, by introducing a counter-rotation of the pixel array, the correlation could be restored again. By testing various counter-rotations to see which produced the highest correlation, it is possible to deduce by how much the place fields had rotated—and hence, which cue or cues they had followed.

The correlations for counter-rotations testing the influences of slope, room cues and local cues were analysed with a repeated-measures ANOVA (see Table 1). Four trials were removed from the analysis at this stage because, although the cue card had been removed, the local cues were not also rotated (this happened because cues were sometimes removed piecemeal to prevent the cells from getting confused and breaking down by too sudden an environmental change). Tests on the remaining trials revealed significant differences between rotation comparisons [$F_{(1,47)} = 42.235$, $P < 0.001$]. Post hoc one-tailed paired *t*-tests revealed that orientation according to slope yielded significantly greater correlation coefficients than the other two conditions [slope vs. local cues: $t(15) = 2.97$, $P < 0.01$; slope vs. room cues: $t(15) = 3.48$, $P < 0.01$]. These data are depicted graphically in Fig. 3.

In one of the trials, in order to determine how quickly the orientation was established, the rat was placed into the environment in the region of the place field. Figure 4 shows that the cell began firing almost as soon as the rat entered the region of the field. It thus appears, from these preliminary data, that geographical slope is probably ascertained rapidly.

Although every effort was made to eliminate the rats' vision of extramaze cues, while leaving enough of the intramaze environment visible to help support place fields, a small possibility remains that the rats could use residual vision to detect a slight difference in the cardinal directions conferred by the tilt of the box. To rule this unlikely possibility out, a test trial in an additional rat was made in a translucent enclosed box, which permitted tracking of the infrared LED while preventing the rat from seeing any external cues at all. Place fields here also rotated with the slope (data not shown), confirming that the effect was due to slope and not to residual influences from subtle uncontrolled extramaze visual cues.

Table 1 Correlations between place cell maps when the data were compared by aligning the maps according to the local cues, the room cues or the terrain slope

Rat	No. training trials	No. test trials	Correlation with local cues	Correlation with room cues	Correlation with slope
1	13	7	-0.06	-0.27	0.53
2	6	7 (4)	0.42 (0.16)	0.01 (-0.03)	0.68 (0.62)
3	11	6 (5)	0.18 (0.10)	0.05 (0.06)	0.21 (0.13)

In four of the probe trials, the cue card was removed but the local cues were not rotated, and so the influence of local versus slant cues is confounded. The numbers obtained if these trials are removed from the data set are shown in brackets

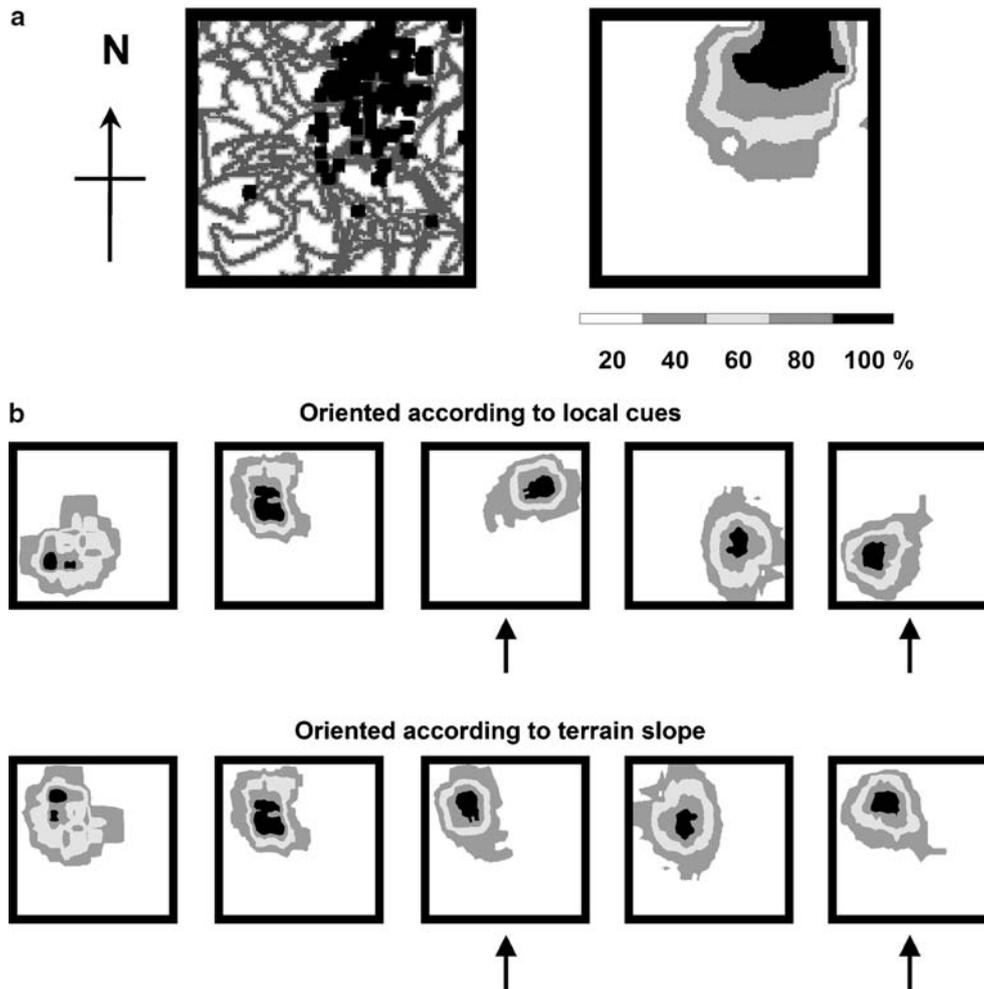


Fig. 2 **a** Example of a place field to show how the data were recorded. The *square* represents the 60 cm² box in which the rat foraged during the 4-min trial. The path of the rat is shown in *grey* and the place where the cell fired action potentials is shown as *black squares*. This cell's place field was located in the north-east corner of the box. The right-hand box shows the same data expressed as a contour plot, generated by normalising to the peak rate and smoothing. Each gradation in the contour map represents a step of 20% of the peak rate. **b** Pattern of place cell activity for a single place cell, recorded during successive 4-min trials, as viewed when the trials are aligned according to the local cues (*top row*) or

according to the terrain slope (*bottom row*). The actual rotations made from trial to trial were as follows: (1) Cue card and slope rotated 90° CW, local cues unchanged; (2) Cue card removed, slope rotated 90° CW, local cues rotated 90° CCW; (3) Slope rotated 90° CW and cue card reinstated, local cues rotated 180°; (4) Cue card removed, slope rotated 90° CW and local cues rotated 180°. The test trials, when the cue card was removed, are shown with *arrows*. Note that the orientation of the fields always conformed to the slope (with or without the cue card), rather than the local cues, showing that slope could override the local cues

Discussion

The present study found that the hippocampal place representation could use the slope of the terrain [sometimes known as geographical slant (Restat et al. 2004)] as an orienting cue in the absence of any other stable polarising cues. The orientation appeared to be established rapidly and was stable throughout the course of a given trial. As well as supporting previous behavioural evidence that animals and humans can use terrain slope to aid navigation, this finding is the first demonstration that gravity can be used to set the orientation of the place system, as discussed below.

How was terrain slope assessed by the place system? The only difference between the various cardinal directions, when the box was tilted in near-darkness, was the differential orientation of the floor with respect to the vertical as defined by gravity, and so detection of gravity—either directly or indirectly—must somehow have been involved. The two possibilities are (1) that the animals used dynamically acquired information, for example by determining the effort involved in moving in the various directions, or (2) that they used static sensory cues such as proprioception and vestibular input. The latter would require some combination of information from different sensory modalities: for example, a combination of proprioception and vestibular informa-

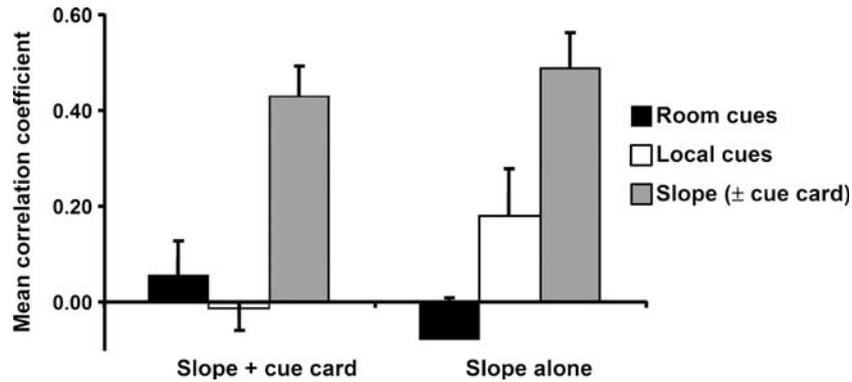


Fig. 3 Histogram showing correlations between place cell maps in training and probe for all three rats combined. The maps were aligned according to either orientation in the room, orientation with respect to the local box cues or orientation according to the terrain slope. The *left-hand bars* show the data for the training trials

(when the box slant was supplemented with a cue card) and the *right-hand bars* show the data for the test trials (when the card was removed). The place field maps correlated most highly when they were aligned according to slope, showing that this was the most powerful orienting cue

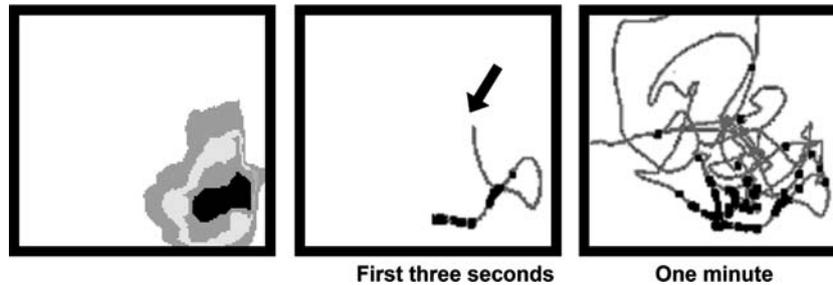


Fig. 4 Rapid orientation of a place field by terrain slope. The *panel on the left* shows the contour plot of the field after the whole trial. The *middle panel* shows the first 3 s of the trial, recorded from the moment the rat was placed into the environment in the vicinity of

the field (*arrow*), with the location of the cell's action potentials shown in blue. The *right panel* shows the first minute of the trial, in which the place field remained robust and well localised

tion from the otoliths that signals a particular relationship between joint angles with respect to the floor versus the vertical as determined with respect to gravity. Evidence from human studies suggests that both proprioception and gravity may be used to determine surface inclination (Kluzik et al. 2005). Another sensory modality of possible significance is vision. Although the extra-box environment was in near-total darkness, the box itself was illuminated by the glowing walls. Although vision alone could not disambiguate the directions based on slope, vision in conjunction with, say, vestibular input could in principle do so. For example, if the rat were to hold its head level with respect to the absolute (gravity-defined) horizontal, it would experience a different visual panorama when facing towards the tilted floor than when facing away from it. Experiments in complete darkness would help determine the contribution of vision. As with most other spatial capabilities, it seems likely that determination of terrain slope is multimodal, with the system making use of whatever information is available.

Terrain slope is a new addition to the collection of sensory cues that are known to orient the place cells. Orientation has two components: the first is a setting (or

re-setting) component, that establishes the orientation at the moment the animal first enters the environment, and allows it to re-orient if necessary at a later stage. The second is an updating component that maintains this orientation stably and continuously so that it is always correct even if the animal is moving (and thus not always perceiving the setting cues). Setting cues that have been identified to date include visual stimuli (Muller and Kubie 1987), olfactory or tactile stimuli (Goodridge et al. 1998) and the point of entry of the animal into the environment (Sharp et al. 1990; Hynes et al. 2000). These cues are often focal, and thus able to provide a clear directional signal at a single moment (e.g., the moment of entry). Updating cues convey information to the place system about the movements the animal made since the orientation was set, and the sensory sources of this information have been less clearly identified. Nevertheless, it is likely that such cues probably include motor efference, signalling the intended movement, and vestibular, proprioceptive, and optic cues (optic flow) signalling actual movement. These cues are sometimes collectively called *idiothetic* (Mittelstaedt and Mittelstaedt 1982). Updating/idiothetic cues are often (though not invariably) dynamic and non-focal since their func-

tion is to indicate not a state per se, but rather a change in state. To the list of cues described above we must now add a new kind of cue: terrain slope. Clearly, terrain slope can act as a setting cue: it remains to be determined whether it is also used during path integration to update the directional system.

The question arises as to what degree the specificity of directional information is conveyed by the slope. The present experiment was deliberately designed so as to ask the simplest question: can slope orient the place representation at all? With this in mind, the environment was constructed with fourfold rotational symmetry so that some orientation information would be provided by the geometry of the enclosure. Thus, slope, if it were to be used at all, would only need to help the cells decide between the four possible orientations. Having established that slope can indeed help orient place cells, the next step is to repeat the experiment in a circular environment so that it can be determined whether slope is sufficient in the absence of any geometric orienting information at all. From there, it is a matter of determining by what route this information is gathered and transformed, and how it interacts with other kinds of orienting information. In this way we will begin to build a picture of the neural mechanisms underlying the use, by animals, of three-dimensional environmental cues in orientation and navigation.

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