Variable place-cell coupling to a continuously viewed stimulus: evidence that the hippocampus acts as a perceptual system

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SUMMARY

A key feature of perception is that the interpretation of a single, continuously available stimulus can change from time to time. This aspect of perception is well illustrated by the use of ambiguous figures that can be seen in two different ways. When people view such a stimulus they almost universally describe what they are seeing as jumping between two states. If it is agreed that this perceptual phenemonon is causally linked to the activity of nerve cells, the state jumps would have to occur in conjunction with changes in neural activity somewhere in the nervous system.

Our experiments suggest that hippocampal place cells are part of a perceptual system. We conducted variations of a 'cue-card rotation' experiment on rats in which the angular position of a prominent visual stimulus on the wall of cylinder is changed in the rat's presence. The three main results are that (i) place-cell firing fields remain stationary if the cue is rotated by 180°, so the relation between the cue and the field is altered; (ii) firing fields rotate by 45° when the cue is rotated by 45°, so the relation between the field and the card is maintained; and (iii) if the cue is first rotated by 180° and then rotated in a series of 45° steps, the field winds up at a different angular position relative to the card when the card is back in its original position. Thus, place cells can fire in two different ways in reponse to a continuously viewed stimulus. We conclude that place cells reveal that the hippocampal mapping system also has properties expected of a perceptual system.

1. INTRODUCTION

Although place-cell discharge is reliably affected in a variety of ways by the configuration of external ('allothetic') and internal ('idiothetic') cues available to a freely moving rat, a great deal of work has consistently shown that place cells do not behave as if they are sensory units. Place cells do not act as if they are triggered by specific stimulus conditions; they are neither pattern-recognition units nor path integrators. Instead, place cells have been interpreted as components of neural representations of space or 'cognitive maps' since their discovery (O'Keefe & Dostrovsky 1971; O'Keefe 1976; O'Keefe & Nadel 1978; Muller *et al.* 1991) what is meant by a 'perceptual' system is stated just below. The suggestion that place-cell activity reflects ongoing perceptual processes is not meant to replace the mapping concept. On the contrary, involvement of perception implies that the map has an integrity of its own and that its coupling to the environment is flexible.

This viewpoint is expressed in a quotation from the Introduction of Hebb's *The organization of behavior* (1949), which is nearing its fiftieth anniversary: 'The central problem with which we must find a way to deal . . . is the problem of thought: some sort of process that is not fully controlled by environmental stimulation and yet cooperates closely with that stimulation'. This provocative idea can be couched in current notions about the nervous system by using an analogy.

Consider a 'Necker cube' (figure 1), which is a well known type of 'ambiguous figure' (Gregory 1970). The Necker cube illustrates the distinction to be made here between sensation and perception. At the sensory level, a Necker cube consists of 12 joined line segments in the plane. The six outer segments form a hexagon, and the six inner segments form two Y-shapes. At this level, a Necker cube is a particular retinal image. In contrast, at the perceptual level, the two-dimensional stimulus pattern is interpreted by most people as a cube, even though it is not remotely cubical. The cube interpretation does not depend on binocular processing; it is just as compelling when the stimulus is viewed monocularly.

It is a deep question to ask how two-dimensional images can be reliably interpreted as three-dimensional

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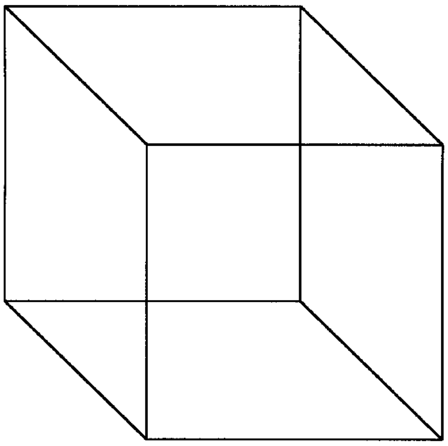

Figure 1. A drawing of a Necker cube. The Necker cube is an example of an ambiguous figure that can be seen to jump between between two different states while continuously viewed.

shapes. The focus of this paper, however, is on the bistability of the Necker cube. At any instant, the viewer sees the cube in one of two configurations. In one, the cube is seen from above, with the accented vertex at the front of the cube; in the other, it is seen from below, and the accented vertex is at the back of the cube. The configuration jumps from one state to the other with time; there is a large literature on the alternation (Gomez *et al.* 1995; Long *et al.* 1992; O'Donnel *et al.* 1988; Peterson & Gibson 1991).

This brings us to a working notion of perception: sensory events shade into the perceptual realm when a single, invariant stimulus is seen in at least two different ways. But how is it possible to know, beyond one's own experience, that a fixed stimulus is indeed able to evoke two or more interpretations? In the context of the connectionist theory of the nervous system, the confirmation must lie in the electrical activity of individual nerve cells; the private experience of seeing the Necker cube jump between configurations must be reflected at the neuronal level.

Consider a thought experiment in which it is possible to non-invasively record from any neuron in a person's nervous system as a Necker cube is viewed. Most likely, retinal neurons would show no correlate of the jumps; variations of cellular activity would not be locked to the instant at which the interpretation shifted. Probably, the same lack of relationship between cell activity and perceptual state would be true of lateral geniculate units, and perhaps of primary visual cortical cells. Nevertheless, on the assumption that perception is causally tied to brain state, it is clear that somewhere in the brain there exists neuronal activity that shifts when the perceived configuration jumps, and that is different depending on which of the cube configurations is current. The signal may be weak, and may be distributed over many cells, but the signal is necessarily there. It is a fundamental assumption of Hebb's resurrection of connectionist theory that 'a particular perception depends on the excitation of particular cells at some point in the central nervous system' (Hebb 1949, p. 17).

The purpose of this paper is to demonstrate that single-cell activity can be coupled to a particular stimulus in a way that strongly resembles expectations from the notions of perception considered above. It is shown that the discharge of individual place cells can be linked in several distinct ways to a single, continuously viewed stimulus. Specifically, the firing field of a place cell can exist stably at more than one angular distance from a white cue card attached to the inside wall of a cylindrical recording chamber. From these findings, the inference is drawn that place cells reflect the operation of a perceptual system. Experimental means of reinforcing the inference are mentioned in § 4.

2. METHODS

The methods are substantially the same as those used by Muller *et al.* (1987). The experimental task is designed to make the rat visit all parts of the environment so that the positional distribution of place-cell firing can be measured. To this end, rats were trained to retrieve 20 mg food pellets randomly scattered into a grey plywood cylinder (76 cm diameter, 51 cm high). Training lasted about two weeks and the rats were thoroughly familiar with the environment and the task before surgery. The floor of the apparatus was a sheet of grey photographic backdrop paper that was replaced each time the rat was removed from the cylinder between sessions. Three nearly identical cylinders in three similar recording rooms were used at different times during the experiment.

Both male and female adult (less than 12 weeks old) Long–Evans hooded rats were used. The animals were initially handled from 30 min to 1 h per day for 1–3 days until they appeared accustomed to the experimenter. During this time, they were fed *ad libitum* standard rat chow mixed with about 5 g of the 20 mg food pellets to motivate the rats to run. After the rats were used to being handled, they were food-deprived to 85% adult body mass and maintained at this level for the duration of the experiment. They received variable amounts of rat chow every evening, depending on the experimenter's estimate of how many 20 mg pellets the animal consumed during the day's experiments.

For training, rats were put into the recording chamber once per day for a session lasting 1–1.5 h. During this session, food pellets were scattered into the cylinder at about six pellets per minute and the rat's behaviour was observed. If a rat did not search for pellets or ran very little after two or three sessions, it was eliminated from the study. Pre-selection of subjects on the basis of their early performance in training is based on experience that poor runners do not alter their behaviour over long times. Some rats were excluded from the study because signs of respiratory illness were detected. Animals with audible wheezing were not used for fear they would not survive surgery.

(*a*) *Surgical procedures*

Surgery was done under sterile conditions and general anaesthesia. After training was complete, rats were anaesthetized with pentobarbital ($40\,\mathrm{mg\,kg^{-1}}$ given intraperitoneally) and placed in a stereotaxic instrument. The skin was cut along the midline of the skull and four small holes were drilled in the skull over the right and left olfactory bulbs, left frontal cortex and left parietal cortex. These holes were used for screws to anchor the recording-electrode array. The electrodes themselves were introduced through a 2 mm hole in the lateral portion of the right parietal bone. The exposed dura was cut and reflected back. An electrode array of 10 or 30 microwire, movable electrodes (Kubie 1984) was stereotaxically implanted about 1 mm above the stratum oriens of CA1 of the dorsal hippocampus. The electrodes were positioned so that their tips would pass through 3.3 mm posterior to bregma and 3.1 mm lateral to the midline and therefore through the CA1 layer of the dorsal hippocampus (Paxinos & Watson 1986). Once the electrodes were placed, sterile petroleum jelly was applied to the surface of the brain and around the guide tube of the electrodes. Next, dental acrylic was put over the jelly and around the guide tube to cover the skull hole. Finally, the exposed skull was covered with Grip cement (Ranson and Randolph Ceramics, Maumee, Ohio) and the bottoms of the three drive-screw assemblies were cemented to the skull via the skull screws. The rat was given 3–5 days to recover after surgery before recordings were made. No recordings were made if the rat struggled or vocalized when the recording cable was attached to the connector of the electrode array.

(*b*) *Place-cell recordings*

For recordings, the cylinder was placed in the centre of a cylindrical curtain, 2 m in diameter. The inner surface of the cylinder was uniformly grey except for a vertical seam where the single sheet of plywood was joined to complete its circumference. The seam was filled with paint to minimize its contrast with the rest of the interior wall. The seam nevertheless provides a potential orienting cue. It is only one of many 'static background cues' (Sharp *et al.* 1991) that the animal might use to orient itself relative to the laboratory frame.

The only intentionally introduced inhomogeneity in the cylinder was a 60 cm × 51 cm rectangular white cue card. The card extended from the floor to the rim of the cylinder and covered 100° of arc. The reference angular position for the card was with its middle at 0° in the angular coordinate system. When the cylinder is seen from overhead, 0° corresponds to 3:00. Angles are measured in degrees moving anticlockwise, so that 90° corresponds to 12:00.

Recordings were made from CA1 and CA3 complex-spike (pyramidal) cells that showed strong location-specific activity and were therefore classified as place cells. In previous work, no differences had been found between place cells in CA1 and CA3 with regard to control by cue cards; none were seen here. Accordingly, the field of Ammon's horn from which the cell is recorded is ignored. A screening procedure was used to obtain discriminable place cells. The recording cable was attached to the connector on the electrode array and the rat was put into the cylinder. All the wires were then scanned for single-unit activity. If none was seen, the cable was detached and the electrodes were advanced about 40 μm by turning the drive screws. The rat was then returned to its home cage for about an hour to allow any distortion of the brain to relax. The screening procedure was then repeated.

Once at least one recurring waveform of usable amplitude (greater than about 150 μV) was seen, the unit was classified as a complex-spike cell or a theta cell. To be called a complex-spike cell the unit had to meet three criteria. (i) It had to generate complex spikes, which are high-frequency bursts of from two to perhaps six spikes whose amplitudes decrease. (ii) It had to commonly show long interspike intervals (>1 s). (iii) The duration of the initial phase of the filtered (100 Hz–10 kHz) waveform had to be at least 200 μs. In contrast, interneurons (theta cells) had to: (i) never generate complex spikes; (ii) never fire at rates lower than about 10 spikes $\mathrm{s^{-1}}$; and (iii) have an initial phase of about 100 μs (Ranck 1973; Fox & Ranck 1975; Muller *et al.* 1987; Kubie *et al.* 1990).

Waveform discrimination was done in two ways. In the earlier work, three Bak time-and-amplitude window discriminators arranged in series had been used to select waveforms. With this method, the time of each action potential was not saved. Instead, the number of action potentials was accumulated for 1/60 s intervals, the reciprocal of the 60 Hz frequency at which position was measured. Thus, the temporal resolution of spike recording was equal to the temporal resolution of tracking.

In the second discrimination method, waveforms were digitized at 40 kHz per wire with a Datawave workstation. A burst of 32 samples (for a duration of 800 μs) was captured each time the electrode voltage exceeded about 100 μV. Sorting of waveforms into single unit time series was done retrospectively after recording. Often, when the initial negative peak of captured waveforms was plotted against the later positive peak a single elliptic region was seen, as if the positive and negative peaks yielded a two-dimensional Gaussian distribution. A rectangle that encompassed most of the elliptic region was drawn. In this case, all waveforms that fell into the circumscribed rectangle were considered to have been generated by a single unit. If it appeared that two similar waveforms were being classified as a single unit, additional criteria (e.g. spike duration) were used in sorting. It is emphasized, however, that little effort was devoted to extracting any but the largest waveforms, so that in practice this method yielded the same results as the use of the window discriminators.

(*c*) *Tracking*

To determine the positional firing distribution for place cells, it is necessary to track the position of the rat's head in parallel with single-cell recordings. To this end, a light-emitting diode (LED) is attached to the electrode carrier and made the brightest source in the view of an overhead television camera. The signal from the camera is sent to a threshold device that detects the LED. At the time of detection, the values in two counters are registered and held until the end of the televisual field. The Y counter holds the number of lines that have been scanned since the beginning of the field; the X counter holds the number of pulses generated by a fast clock that is synchronized with the beginning of each video line. At the end of the field an interrupt causes the X and Y values to be read by a computer. Because the light position is detected once per field, the temporal resolution is 60 Hz. Position was detected in a 64×64 grid of square regions (pixels) 2.4 cm on a side. To calculate firing rate as a function of position, spikes were assigned to the pixel in which the rat's head was detected at the beginning of each 16.7 ms 'sample'. If the LED was not detected for a sample, spikes in the associated 16.7 ms interval were ignored.

(*d*) *Display and analysis*

The positional firing distribution for a cell was calculated by dividing the number of spikes fired in each pixel by the total time for which the light was detected in each pixel. Colour-coded firing-rate maps were used to visualize positional firing-rate distributions. Pixel rates were sorted in ascending order and partitioned into six categories encoded in the sequence yellow, orange, red, green, blue, purple. Yellow encodes pixels in which the firing rate was exactly zero, orange the lowest non-zero pixels, and purple the highest non-zero pixels. The boundaries between non-zero firing-rate categories were picked such that the number of pixels in a given category was 0.8 times the number in the next lower rate category. Pixels in the apparatus that were not visited were coded white, as were inaccessible pixels outside the cylinder. Colour-coded maps were used as the main method of analysis in this paper; visible changes in the positional firing pattern are relied on to demonstrate how experimental manipulations affect place-cell discharge.

(*e*) *Experimental manipulations*

The attempt to show that hippocampal place cells are part of a perceptual system is based on investigating the control that the white cue card exerts over place-cell firing. The basic experiment is to change the angular position of the white card on the cylinder wall; such manipulations are called 'card rotations'. The basic question is whether firing fields rotate in register with the card rotations; it is concluded that the cue card has stimulus control if the fields rotate, and that control is absent if the fields stay in the same place. Note that control is defined strictly in terms of what happens to the field and in no way implies that the animal in some sense ignores or is unaware of the stimulus or its altered position. Indeed, the fact that the card can exert strong stimulus control immediately after it had no stimulus control implies that information about the card is continuously available (see below). Because the present experiments involved only cue card rotations of 180° and 45°, the amount of field rotation was easily detected by inspection of the colour-coded firing-rate maps.

Two types of card rotation were done. The first was done with the rat out of the recording chamber. Because these cue-card movements could not be observed by the animal they are referred to as 'hidden'. For hidden rotations the card was put into its standard position and a session was recorded. The rat was taken out of the cylinder and put into its home cage. The card was then rotated (usually by 180°) and a second recording session was run.

The second type of card rotation was done while the animal was inside the recording cylinder. Such rotations could be observed by the animal and are called 'visible'. To make a visible rotation, recording was stopped after a predetermined time had elapsed. The experimenter then stepped through the cylindrical curtain, detached the card from the wall and re-attached it at a new position that was either 45° or 180° away from the previous card position. The experimenter then left the curtained area and the recording room itself and restarted data acquisition. Again, comparisons were made between the amount of card rotation and the amount by which firing fields rotated.

Floor paper was renewed each time the rat was removed from the cylinder. Thus, floor markings made by the rat in the course of a sequence of hidden rotations could not serve as orienting cues in the next session. In contrast, floor markings made during a sequence of visible rotations could serve as orienting cues when the card was in different positions.

3. RESULTS

The results were obtained from four different variations of the card-rotation experiment.

(*a*) *Variant 1: hidden card rotations of 180°*

In a hidden card rotation, the firing field of a place cell is recorded with the card in its standard position, the rat is put into its home cage, the angular position of the card on the wall is changed, the rat is returned to the cylinder and a second session is done. In previous work, it was shown that hidden card rotations almost always result in equal field rotations, so that the position of the field relative to the card remained constant (see, for example, Muller *et al.* 1987; Bostock *et al.* 1991). Additional 180° hidden card rotations were done for this work and the same effect was found, as illustrated for two cells in figure 2*a*. The field of cell A1 in figure 2*a* was at 7:30 with the card in its standard position (cell A1, session 1). When a hidden 180° rotation was done, the field also rotated by about 180° to 1:30 (cell A1, session 2). The effects of the same manipulations on a second cell (cell A2) are also shown in figure 2*a*. Hidden 180° rotations caused equal field rotations for six out of seven cells in four rats. Thus, as shown in previous work, the white cue card is salient and its angular position exhibits nearly ideal stimulus control over the angular position of firing fields.

(*b*) *Variant 2: visible 180° card rotations*

Does the angular position of the cue card have absolute control over field position? The control demonstrated with hidden rotations could mean that the angular position of the card sets the angular position of firing fields regardless of when or how the card is moved. Alternatively, it could be that the hidden rotations are effective only because they are hidden and that the rat would ignore the card if it could know it had been moved. These possibilities were explored by doing visible card rotations in the rats' presence. It is important that the rats' behaviour indicates that they were aware of the visible card movement. The rat would usually orient toward the card as soon as the experimenter detached it from the wall. The rat would then chase one of the card edges as it was moved along the cylinder wall. When the card rotation was complete, however, the rat always resumed its pellet-chasing activity. Thus, the card-rotation procedure had no long-term effect on behaviour.

It was found that the field stayed at the same angle relative to the laboratory frame in 25 out of 28 cases after visible 180° rotations. (The visible rotations include the first two sessions of the 12 replications of variant 4 described below.) Thus, cue-card control was almost always absent when the card was rotated in the rat's presence. The ineffectiveness of visible 180° rotations is illustrated for two cells in figure 2*b*. For one of the remaining three cells, the field rotated after the visible 180° rotation. For the other two cells, the visible 180° rotation caused an apparent 'remapping': the angular position of the field, the radial position of the field and the field shape all changed (Bostock *et al.* 1991). The main conclusion is that moving the cue card by 180° produces very different effects depending on whether the rat can or cannot see the card movement. The outcome of the visible 180° rotation makes it clear that cue-card control over the angular position of firing fields is not absolute. In addition, the remappings suggest that in some cases the change in the environment is enough for the hippocampus to produce a new representation rather than 'reattach' the original representation to the card.

(*c*) *Variant 3: visible 45° card rotations*

In contrast to visible 180° rotations, visible 45° rotations almost always caused equal firing-field rotations. In addition, firing fields followed sequences of visible 45° rotations so that the field could be caused to rotate by 180° by doing four 45° rotations in a row without removing the rat from the chamber. Thus, there is nothing special about the 180° position itself that precludes fields from following visible rotations. Continuing to do visible 45° rotations after reaching 180° caused fields to continue to rotate, so that after eight such rotations the field was back to its original position.

Two sequences of visible 45° rotations are shown in figure 3*a*, where it is clear that each field accurately followed the card position for the four steps that are shown. The same fields continued to follow the card for an additional four sessions so that in the end the fields returned to the original location. A total of five cells in five animals were tested with sequences of eight visible 45° rotations. The fields followed accurately in all cases. It is worth repeating the observation that rats oriented to the card when it was detached and followed one of its edges during the visible 45° rotations, just as was true for the visible 180° rotations. Thus, even though the rat seemed aware that the card was moving, the firing fields were almost ideally controlled by the card.

(*d*) *Variant 4: combinations of visible 180° and 45° card rotations*

The discovery that the magnitude of visible card rotations determines whether or not the fields follow the card suggests at least two additional lines of investigation. One experiment would be to vary the magnitude of the visible rotation to look for a threshold: a rotation such that slightly smaller rotations yield cue-card control and slightly larger rotations leave the field fixed in the laboratory frame. The decision was made to ask instead what would happen if visible 45° rotations were done after a visible 180° rotation? That is, would the ordinarily effective visible 45° rotations now fail to cause the field to move, or would they continue to be effective?

A total of 12 sequences were carried out in which a visible 180° rotation was followed by a series of eight 45° rotations all in the same direction. Remarkably, even though the field did not move after the 180° rotation, in five of these experiments in three rats the field rotated with every one of the eight 45° rotations. Two examples of the first six sessions of such sequences are shown in figure 3*b*. The key point is that in the sixth session the firing field is 180° away from its angular position in the first, standard session. *Thus, precisely the same configuration of a continuously visible stimulus is associated with two different states of firing of the cell.* In none of these cases was the change in angular relation between the card and the field permanent. On the contrary, in each case when the rat was taken out of the cylinder and replaced, the field resumed its original position relative to the card.

In 7 out of 12 cases, the field failed to follow the cue card perfectly for all eight visible 45° rotations. In every case, however, the field was controlled by the visible 45° rotations several times. Moreover, the control generally occurred for several of the rotations in a row. For many of the card rotations that did not produce equal field rotations, the cell was nearly silent. When firing resumed, the field usually began to rotate again, but in a way as if it had 'slipped' relative to the card. That is, for these cells, the field always rotated by less than 360° during the 45° steps. The remaining cell also showed rotations during the sequence of eight 45° rotations. It was anomalous in that its field rotated after the visible 180° rotation.

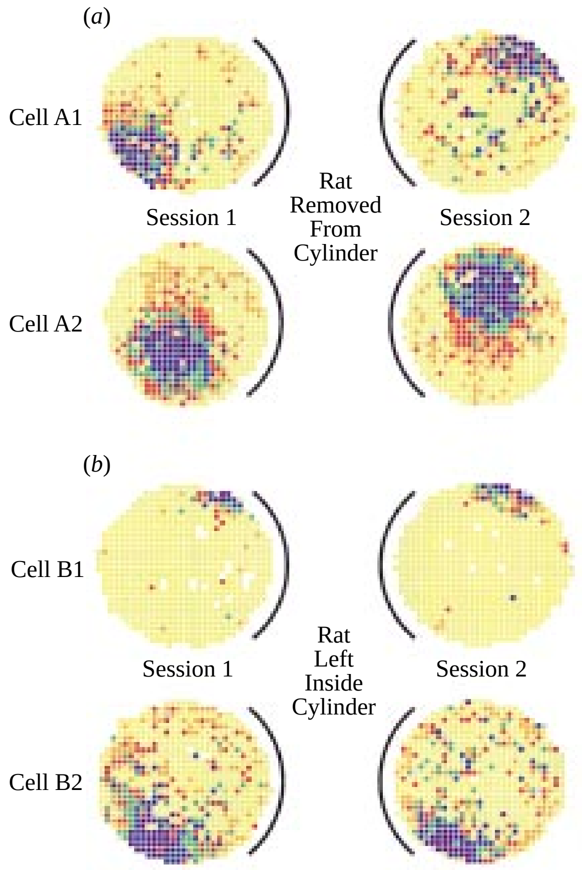

Figure 2. (*a*) Outcome of experimental variant 1: the effects of hidden 180° cue-card rotations on two independently recorded place cells. The baseline position of the firing field for each cell was established during a standard session (session 1). For each cell, the rat was removed from the recording room after session 1 and the cue card was rotated 180°. The rat was then put back in the cylinder for session 2. Under these conditions, the firing fields rotated by 180°, demonstrating that the cue has strong stimulus control over the positional firing pattern. (*b*) Outcome of experimental variant 2: the effects of visible 180° cue-card rotations on two independently recorded place cells. The baseline positions of the firing fields were established during session 1 with the cue card at its standard position. The card was then moved by 180° while the rat was in the cylinder and could view the card. It is evident from the rate maps for session 2 that the firing field of each example cell stayed at its original angular location in the laboratory frame.

In summary, all place cells followed at least some visible 45° rotations. Thus, two different field positions were observed for every place cell with the card in its standard location. The effect is most dramatic when the field follows all eight visible 45° rotations, but it is also clear that the angular position of fields is not controlled in an absolute way by either external (allothetic) or internal (idiothetic) cues.

4. DISCUSSION

(*a*) *Cue-card control over the angular position of firing fields depends on the magnitude of visible rotations*

The work presented bears similarities to several other experiments on place cells and head directional cells in which different sources of sensory information are put into conflict with each other (Sharp *et al.* 1995; Taube & Burton 1995; Blair & Sharp 1995). These studies were designed to test the relative importance of external cues and idiothetic cues. In each case, it was found that visual cues set field position in preference to idiothetic cues, although in each case there were conditions under which idiothetic cues instead controlled firing-field position.

These experiments can be interpreted along similar lines. A single experimental manipulation, namely cue-card rotation in the animal's presence, almost always results in either equal rotation of firing fields or no rotation of firing fields. Specifically, visible rotations of 45° almost always cause 45° rotations of fields, whereas visible 180° rotations almost always leave field position unaffected. Thus, the magnitude of the rotation determines which stimulus class will be prepotent. It could be said that small card rotations cause the place-cell system to 'ignore' static background and idiothetic cues. (Static background cues are potential orienting stimuli that are fixed relative to the laboratory frame. Examples are the eccentric position of the overhead commutator, the seam in the cylinder wall or markings of the floor made by the rat. In this case, the idiothetic cue is that the change in card position was not caused by self-motion.) In contrast, it could be said that large card rotations cause the place-cell system to ignore the cue card and to stay in register with static background cues or idiothetic cues or both. It is interesting that the system does not reach a compromise between the two sets of cues but instead seems to go with one or the other. Bistability is not, however, the only possible outcome. In experiments with two cue cards, one black and one white, changing the angular distance between the cards reveals that they exert about equal control over firing fields (Fenton & Muller 1997).

The dependence of the effects of visible rotations on the amount the card is moved has several interesting implications with regard to the place-cell system. First, in agreement with earlier work, the existence of circumstances (visible 180° rotations) in which the card lacks control shows that place cells are not simply triggered by cell-specific cues (Muller & Kubie 1987; Sharp *et al.* 1990; Quirk *et al.* 1990; Markus *et al.* 1994). As we have argued before, findings of this type belie the notion that place cells are properly described as high-order sensory cells or pattern recognition units. In a similar vein, the existence of circumstances (visible 45° rotations) in which the cue card is fully effective in the face of conflict with idiothetic cues that are supported by static background cues suggests that place cells are not dominated by self-motion information. By inference, the place-cell system should therefore probably not be considered to be fundamentally concerned with path integration (see McNaughton *et al.* (1996) for the opposite view).

The ineffectiveness of idiothetic and static background cues during small visible rotations has a simple interpretation in terms of a path integration scheme: it can be said that the path integrator is reset so that the 'binding of the cue card to the place cells is maintained.

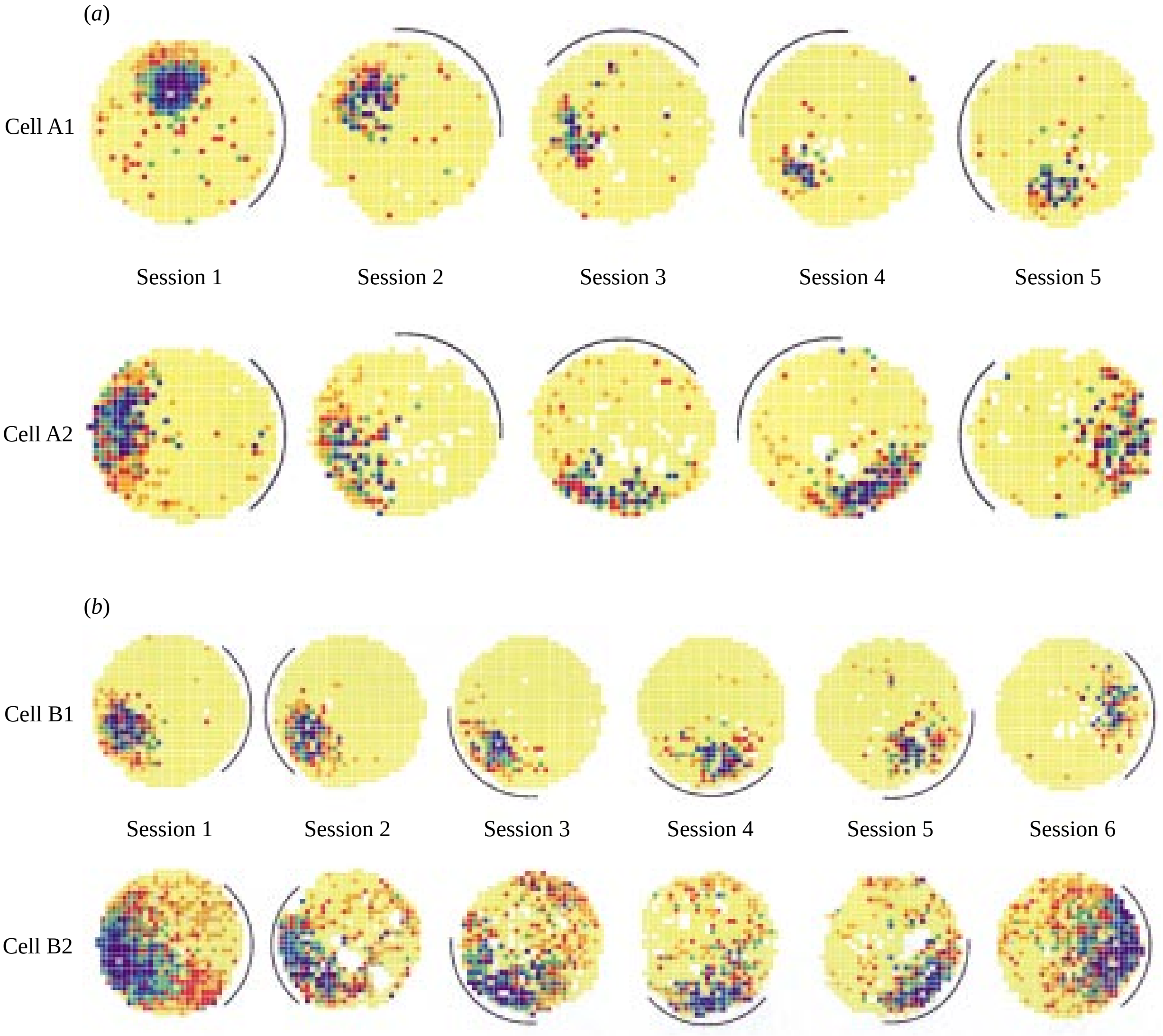

Figure 3. (*a*) Outcome of experimental variant 3: the effects of a series of visible 45° cue-card rotations on two independently recorded place cells. The baseline positions of the firing fields were established during session 1 with the cue card at its standard position. The card was then rotated by 45° between each pair of subsequent sessions while the rat was in the cylinder and could see the card. Each 45° cue-card rotation caused an equal rotation of the firing field. The fields of both cells maintained a constant angular relationship to the cue card for the five consecutive sessions shown and for four additional sessions not included. By session 5, the cue card was 180° away from its standard position. The firing fields of both place cells also rotated by 180°. Note that the crisper appearance of the firing fields in session 1 is due to the longer recording time; the baseline sessions lasted 16 min whereas the rotations sessions lasted 4 min (see Muller *et al*. (1987)). (*b*) Outcome of experimental variant 4: the effects of combined visible 180° and 45° cue-card rotations on two independently recorded place cells. The baseline positions of the firing fields were established in session 1 with the cue card in its standard position. Between sessions 1 and 2 the cue card was rotated 180° while the animal was in the cylinder and could see the card. Between each pair of sessions after session 2 the cue card was rotated 45° with the rat in the cylinder. The fields of both cells stayed at their initial position after the 180° rotation. In contrast, the fields followed the subsequent 45° card rotations. Note that by session 6 the cue card was back to its standard position, but the firing fields were 180° away from the positions seen in session 1. Thus, place cells can fire in two different ways in response to a single, continuously viewed stimulus. As in figure 4, the crisper appearance of the fields in session 1 is because that session lasted 16 min whereas the other sessions lasted only 4 min.

It is, however, unclear why a path integrator should be reset if self-motion cues indicate stability. It is not as if the system *must* reset: field position does not jump when the card rotation is large. We conclude that the results of visible 45° and 180° rotations are as hard to fit into a pattern-integration scheme as they are into a sensory scheme.

(**b**) ***The effects of combined visible 180° and 45° rotations suggest that place cells are part of a perceptual system***

Is it really proper to conclude that the idiothetic and static background cues are ignored if small cue-card rotations cause equal field rotations? This possibility seems implausible on at least the grounds that the flow of idiothetic information is uninterrupted. It is more satisfactory to imagine that a new binding is made between place cells and idiothetic cues. In path integration terms, one would say that the integrator was reset, but we suggest instead that idiothetic information is just a kind of sensory information that is used when external information is lacking or in great conflict with previous external information.

Similarly, it is tempting, but not necessarily correct, to conclude that the cue card is ignored if large card rotations do not alter field positions. Whether the card is ignored is testable; the results with subsequent small rotations indicate that the card continues to play a role in controlling firing fields. The notion is that the card is rebound in a new position in the angular coordinate of the place-cell system. Moreover, the rebinding is instantaneous within the temporal resolution of our measurements. The process is much faster than the 3–5 min it seems to take to establish a new map (Hill 1978; Bostock *et al.* 1991; Wilson & McNaughton 1993); this difference in speed suggests that different synaptic or cell-level mechanisms are involved in building a map than are required to link the map to external stimuli.

The difference in effectiveness of visible 180° and subsequent visible 45° rotations brings us back to our main theme, that place cells act as if they are part of a perceptual system. This can be seen most clearly when four 45° rotations are made after a single 180° rotation. The surprise is that after the rotatation sequence the card is back in its initial state whereas the field is 180° away from its initial position. In those cases in which some of the visible 45° rotations in a sequence failed to cause a 45° field rotation, other card rotations were successful. Therefore, in every repeat of the combined visible 180° and 45° rotations individual cells fired in two different ways relative to an identical cue configuration. This satisfies the criterion that was set out in § 1 to demonstrate that place cells reflect the operation of a perceptual system.

It is of interest whether the preferred directions of head-direction cells would stay in register with the angular locations of firing fields or whether the positional and directional systems would be dissociated in these circumstances. It is our belief that preferred directions in the directional system would show just the same variable coupling to the cue card, so that it would stay in register with the positional system.

We end by suggesting an additional experiment to test the validity of our conclusion. The basic idea for this experiment is similar to the elegant study by Logothetis & Schall (1989) in which monkeys were asked to report the currently perceived direction of motion of a visual pattern under circumstances in which the pattern could be seen to move in either of two ways. When single-cell recordings were made from units in the superior temporal sulcus, most units reflected properties of the retinal light pattern. In contrast, the activity of a fraction of the units shifted in time register with the report of movement direction by the monkey. Logothetis & Schall concluded that the superior temporal sulcus may be involved in the processing of visual movement perception. Note, however, that the changing cellular activity could be coupled to the response itself (if short-term memory of the response is registered) rather than to the subjective perception. In our experiment, it is hard to argue that the altered cell activity is due to altered motor activity, because the behaviour is indistinguishable before and after the visible 180° rotation.

The present work, on the other hand, suffers from the deficit that there is no way for the rat to report that it knows that the environment is different before and after the visible 180° card rotation. It would therefore be interesting to train the rat to go to a certain location on hearing an auditory signal. If the rat went to the original location in the laboratory frame, it would suggest that the place cells and the behaviour were in register. If the rat went to a rotated image of the original location it would indicate that place cells are dissociated from behaviour. It is our prediction, however, that the rat will go first to the original correct position and then to the rotated image; this result would indicate that the rat is aware that two almost equally good interpretations of the environment are available.

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