

Rat anterodorsal thalamic head direction neurons depend upon dynamic visual signals to select anchoring landmark cues

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Keywords: cue control, dynamic motion parallax, hippocampus, limbic system, single unit recordings, spatial orientation

Abstract

Head direction cells, which are functionally coupled to 'place' cells of the hippocampus, a structure critically involved in spatial cognition, are likely neural substrates for the sense of direction. Here we studied the mechanism by which head direction cells are principally anchored to background visual cues [M.B. Zugaro *et al.* (2001) *J. Neurosci.*, **21**, RC154,1–5]. Anterodorsal thalamic head direction cells were recorded while the rat foraged on a small elevated platform in a 3-m diameter cylindrical enclosure. A large card was placed in the background, near the curtain, and a smaller card was placed in the foreground, near the platform. The cards were identically marked, proportionally dimensioned, subtended the same visual angles from the central vantage point and separated by 90°. The rat was then disoriented in darkness, the cards were rotated by 90° in opposite directions about the center and the rat was returned. Preferred directions followed either the background card, foreground card or midpoint between the two cards. In continuous lighting, preferred directions shifted to follow the background cue in most cases (30 of the 53 experiments, Batschelet *V*-test, $P < 0.01$). Stroboscopic illumination, which perturbs dynamic visual signals (e.g. motion parallax), blocked this selectivity. Head direction cells remained equally anchored to the background card, foreground card or configuration of the two cards (Watson test, $P > 0.1$). This shows that dynamic visual signals are critical in distinguishing typically more stable background cues which govern spatial neuronal responses and orientation behaviors.

Introduction

Head direction (HD) neurons discharge selectively as the head is oriented in cell-specific preferred directions in the horizontal plane (Ranck, 1984; Taube *et al.*, 1990; Robertson *et al.*, 1999). They are found in an interconnected network of brain structures which is functionally coupled (Knierim *et al.*, 1998) to place-responsive cells of the hippocampal system (O'Keefe & Dostrovsky, 1971). Spatial responses of HD cells are anchored to visual cues but only when these are in the background (Zugaro *et al.*, 2001a). Background cues can also prevail over foreground cues for controlling hippocampal place responses (Cressant *et al.*, 1997). But how do HD cells select background cues? The psychophysical literature shows that relative depth in the visual field can be detected on the basis of several different stimulus attributes, including accommodation, occlusion (objects blocked by others are more distant), texture contrast, shadows, vergence and mechanisms like dynamic motion parallax (during displacements more distant objects appear to move less rapidly). Known brain systems specialized for detecting optic field flow could automatically confer the latter sensitivity on the HD system; for example, the optokinetic system is more sensitive to optic

flow at low, rather than high, velocities (Hess *et al.*, 1989). The present experiments were designed to test the hypothesis that anterodorsal thalamic HD cells distinguish anchoring background cues on the basis of dynamic visual processes like motion parallax and optic field flow detection.

Materials and methods

Experimental subjects

Seven male Long-Evans (pigmented) rats (250–300 g; Centre d'Élevage René Janvier, Le Genest-St-Isle, France) were put on a restricted food schedule to avoid excessive weight gain (about 14 g of rat chow per day). The animals were maintained on a 12 h light : 12 h dark cycle in an approved animal facility. All animal care and experimental protocols were in accord with institutional (CNRS Comité Opérationnel pour l'Éthique dans les Sciences de la Vie) and international (NIH guidelines) standards and legal regulations (Certificat no. 7186, Ministère de l'Agriculture et de la Pêche) regarding the use and care of animals.

Electrode implantation

The rats were implanted with electrodes in the anterodorsal nucleus of the (right or left) thalamus. (No differences were noted between left

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Received 14 October 2003, revised 4 May 2004, accepted 26 May 2004

and right recordings.) Electrode bundles consisted of eight formvar-coated nichrome wires (diameter 25 μm). Each bundle of wires was inserted in a 30-gauge stainless steel cannula and mounted on one of two independently advanceable connector assemblies on a single headstage (Wiener, 1993). Before surgery, the animals were tranquilized with xylazine and then deeply anesthetized with pentobarbital (40 mg/kg). The electrodes were implanted above the antero-dorsal thalamic nucleus (antero-posterior -1.4 to -2.0 mm and medio-lateral ± 1.1 to ± 1.4 mm relative to bregma, 4.2 mm ventral to brain surface) using conventional surgical techniques. The electrode descender assembly was permanently fixed to the skull with dental acrylic and seven tiny screws. A ground screw connector assembly was implanted in the cranial bone.

Signal processing

During the recording sessions, electrode signals passed through FETs were differentially amplified ($10\,000\times$) and filtered (300–5 kHz, notch at 50 Hz). The signal was then passed to a computer for automatic data collection. The acquisition software (DataWave® Discovery) digitized and collected 32 data points (at 20 kHz) for each signal that crossed a user-set threshold. Single unit activity was discriminated post-hoc using this system's spike-sorting techniques based on a maximum of eight different waveform parameters.

When a well-isolated neuron was successfully recorded, the electrodes were not advanced at the end of the session, in order to permit further recordings from the same neuron. The rationale for this was that existing studies are remarkably consistent in showing that, in simultaneous recordings of HD cells, all neurons respond coherently to cue manipulations (also see Results and Discussion). Thus, the responses would be the same in the well-isolated neuron as in its neighbor, which might prove difficult or impossible to isolate. A neuron was assumed to be recorded again in a subsequent session on the basis of the appearance of a similar waveform on the same electrode and this was supported by similar initial directional preferences and peak firing rates in the recordings. Prior to recordings, a support with two small lamps (10 cm separation) was mounted above the headstage. The (sagittally oriented) positions of the two lamps were detected by a video camera mounted above the platform (using the DataWave® video tracking system) and sampled at a rate of 60 Hz. The heading direction of the animal was later computed using the positions of the two lamps. Inversions of the lamps due to tracking errors were corrected with our own interactive software. Counter-clockwise rotations are considered positive here.

Recording protocol

Anterodorsal thalamic HD cells were recorded while the rat was on a small (22-cm diameter) elevated platform in a 3-m diameter cylindrical enclosure. The experimental cues were two freely standing cards, a small one in the foreground (height 60 cm, width 11 cm, distance 36 cm) and a larger one in the background (height 240 cm, width 44 cm, distance 144 cm) (Fig. 1a). The cards were identically marked, proportionally dimensioned and subtended identical (non-overlapping) visual angles from the central viewpoint. The equivalence of the intensity of reflected light from the two cards was controlled regularly with a luminance meter (LS-100; Minolta). The goal here was to make the relative distances of the cards constitute their major distinguishing difference rather than, for example, salience or apparent size. Initially the cards were separated by 90° from the viewpoint of the central platform. (The field of vision of rats is 270° .) The preferred directions

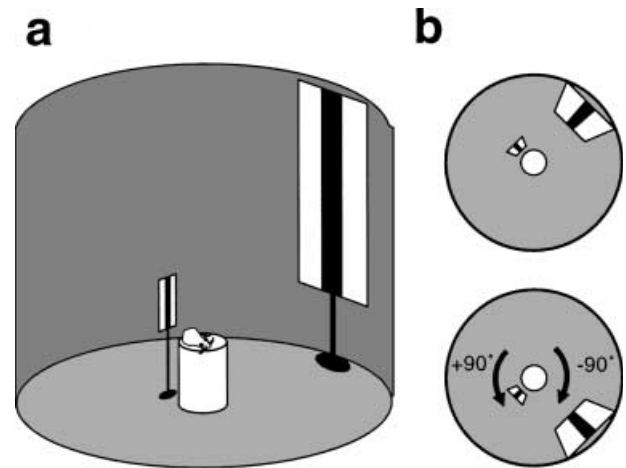


FIG. 1. Experimental protocol. (a) The rats freely foraged for food pellets on an elevated platform (diameter 22 cm) located in the center of a cylindrical black curtain (diameter 3 m). A foreground card (height 60 cm, distance 36 cm) and a background card (height 240 cm, distance 144 cm), bearing two vertical white stripes, served as principal orienting cues. The cards' respective sizes and distances to the platform center were proportioned so that they occupied the same visual angles. They were separated by 90° . (b) After an initial recording (top panel), the animal was removed from the platform and the two cards were rotated in opposite directions (bottom panel). The rat was then disoriented in complete darkness and returned to the platform as the light was turned back on and a second recording began. Recording sessions including baseline and double cue rotations were conducted in continuous or stroboscopic light (flashes at 1.5 Hz).

of HD cells were compared before and after we rotated the background card by 90° in one direction and the foreground card by 90° in the other direction around the platform (Fig. 1), thus providing conflicting orienting cues. After this rotation the cards were again separated by 90° but inverted in their left–right relation. The rats were removed from the apparatus prior to each recording, including during cue rotations, and were disoriented in a completely dark container as the experimenter rotated it erratically while walking about the room. After the disorientation procedure, the experimenter held the animal with its head oriented toward the midpoint between the two cards. The experimenter then asked a colleague to switch on the room light and placed the animal on the platform in a forward linear translation. In this way the animal was immediately exposed to both cues simultaneously while it was in motion (providing dynamic visual information). The difference in apparent angular velocity of the two cards is estimated as between 5 and $10^\circ/\text{s}$. This procedure was first carried out under continuous lighting to permit normal visual processing. It was then repeated under stroboscopic lighting at 1.5 Hz to disturb neural processing of image velocity (Wells *et al.*, 2001), which we hypothesized would provide cues for distinguishing background from foreground.

The results were interpreted as follows. If the preferred directions were anchored: (i) to the background card, they would rotate by 90° in the same direction as the card; (ii) to the foreground card, they would rotate by the 90° in the other direction, following that card; (iii) to the configuration of both cards, they would rotate by 180° (following the midpoint between the cards) and (iv) to uncontrolled room cues, they would remain unchanged. Finally, should no environmental cue exert control over the preferred directions, the latter would rotate by a random angle (as the rats were disoriented between successive recordings). The initial positions and directions of rotations of the foreground and background cards were varied among sessions. In

order to test for possible effects of the order that the manipulations were executed, in nine sessions, the protocol was repeated again immediately without unplugging the headstage or removing the animal from the experimental room (in one of these cases the protocol was repeated twice and in another three times). In two sessions the stroboscopic condition was presented first, in three others only the stroboscopic condition was tested and in one session, only the continuous light condition was presented four times.

Analyses

Methods for computing tuning curves for the HD cells are detailed in Zugaro *et al.* (2001b). Briefly, the software counted the number of spikes for each position sampling interval (16.6 ms) and associated the resulting frequency with the corresponding head angle. This was used to compute a histogram, for which each bin height was the average of all the frequencies associated with head angles within the range of the bin. To calculate preferred direction, we used a discretized adaptation of the Gaussian fit. A best-fit approximation to this curve was obtained via Matlab® (The MathWorks, Natick, MA, USA) software. Circular statistics are from Batschelet (1981). Although, for clarity, the data are shown as histograms in Fig. 4, none of the statistical tests actually relies on these binned values; instead, they use continuous random variables and thus our results are completely independent of the histogram bin sizes.

Histology

At the end of the experiments, a small electrolytic lesion was made by passing a small cathodal DC current (20 μ A, 10 s) through one of the recording electrodes to mark the location of its tip. The rats

were then deeply anesthetized with pentobarbital. Intracardial perfusion with saline was followed by 10% formalin–saline. Histological sections were stained with cresyl violet. Recording sites were reconstructed by detecting the small lesion and the track of the 30-gauge cannula, taking into account the distance that the microelectrode driver had been advanced from the point of stereotaxic placement of the electrodes. The recording sites were calculated by interpolation along the electrode track between the lesion site and the implantation site. Two HD cells from a fifth animal were excluded from analyses because the recording site was in the hippocampus.

Results

Seventeen anterodorsal thalamic HD cells were recorded in seven rats in 34 sessions which included 53 experiments in continuous light and 51 under stroboscopic lighting (an experiment is considered a comparison of directional responses prior to and after cue rotation.) In six sessions, multiple HD cells with different preferred directions were recorded simultaneously (two cells in three of the sessions, three cells in two sessions and four cells in the other session). In each of these cases, all of the neurons had the same responses to cue shifts in the continuous light and stroboscopic conditions (see, for example, Fig. 2). This indicates that the results from individual neurons are representative of all of the neurons of the anterodorsal nucleus of the thalamus in each of these sessions.

As shown by the typical examples in Fig. 3, in the majority (57%, i.e. 30 of 53) of the recording experiments the preferred directions of the HD cells stayed anchored to the background card after card rotations when recorded in continuous light (Fig. 3, left column). This disproportionately outnumbers the experiments where preferred

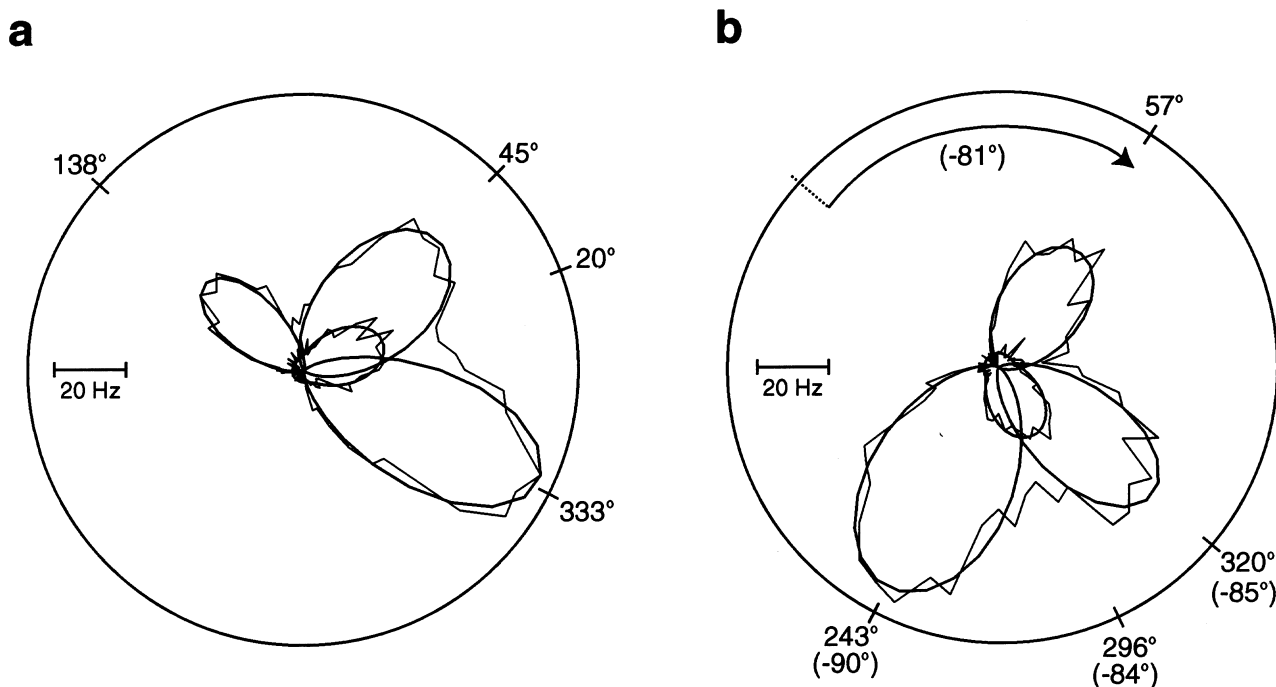


FIG. 2. Polar plots of directional responses of four anterodorsal thalamic neurons recorded simultaneously in continuous light conditions. Three were recorded simultaneously on the same electrode while the fourth (with the lowest peak firing rate) was recorded from another electrode. The thin jagged traces are the actual firing rate histograms (binwidth 6°, calibration bar to left). The thicker lines are Gaussian best-fit approximations of the individual response curves. (a) Responses prior to cue rotation. (b) Responses after cue rotation show a coherent shift of all of the preferred directions by about the same angles (–81, –85, –84 and –90°).

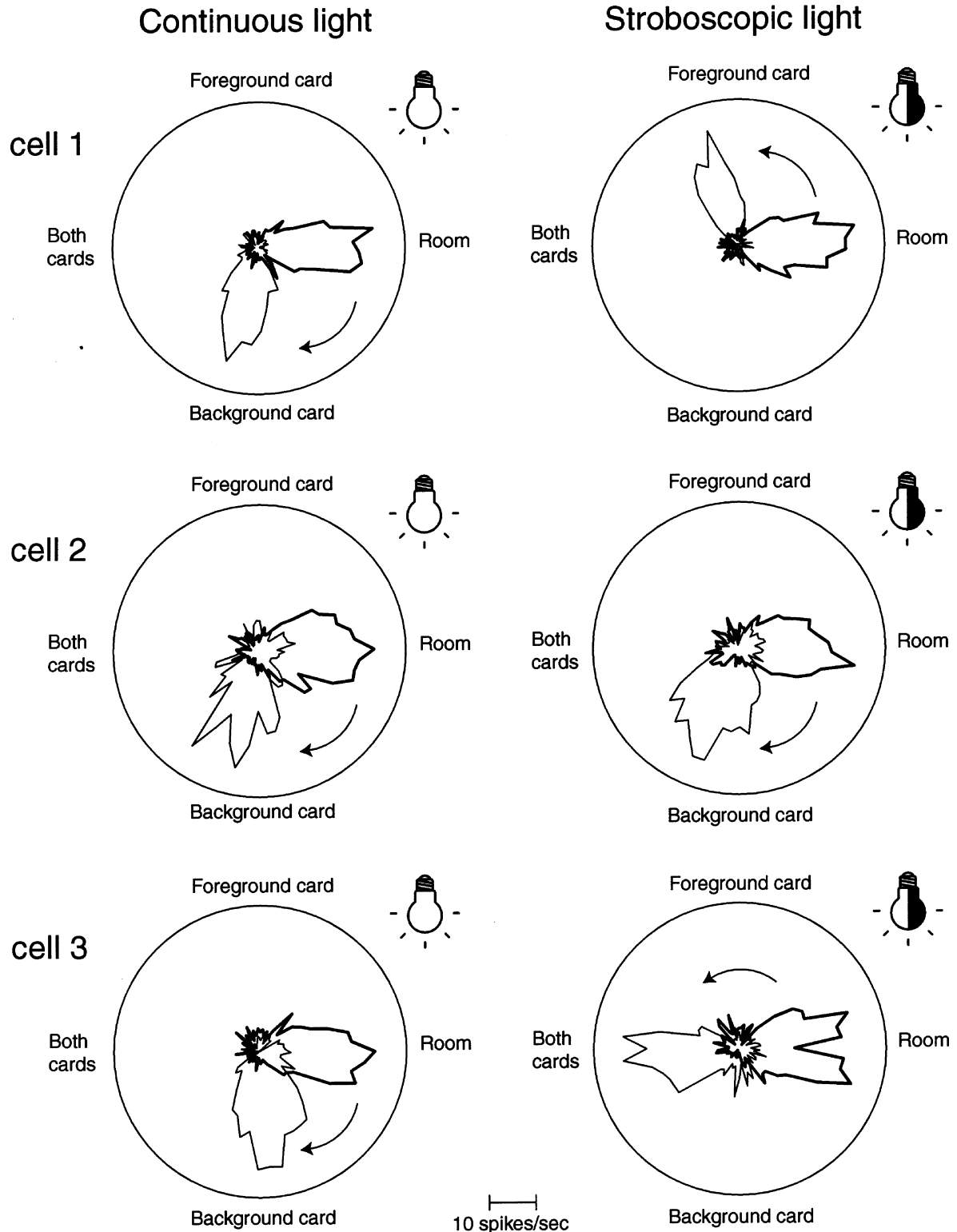


FIG. 3. Typical shifts in preferred directions after card rotations. The response curves of these head direction (HD) cells (recorded during three different sessions) were sampled during the recording preceding (thick curves) and following (thin curves) the rotation of the background card by -90° and the foreground card by $+90^\circ$ around the platform. The polar plots show the firing rate as distance of the trace from the central point (calibration bar at bottom center). The initial directional response curve has been oriented to point to the right (3 o'clock position) to facilitate comparisons. (a) Under continuous light conditions, the preferred directions of the HD cells always shifted by approximately 90° clockwise, following the card in the background. (b) Under stroboscopic light conditions, the preferred directions of the HD cells could shift 90° counterclockwise, following the foreground card (cell 1 in row 1), follow the background card (cell 2 in row 2) or shift by 180° , following the midpoint between the two cards (cell 3 in row 3). The labels 'Foreground card', 'Background card' and 'Both cards' show the predicted angle of rotation of the preferred direction if the respective cues had dominantly influenced the anchoring of the preferred direction. Data have been rectified to compensate for the fact that background and foreground cards were rotated in different directions among sessions.

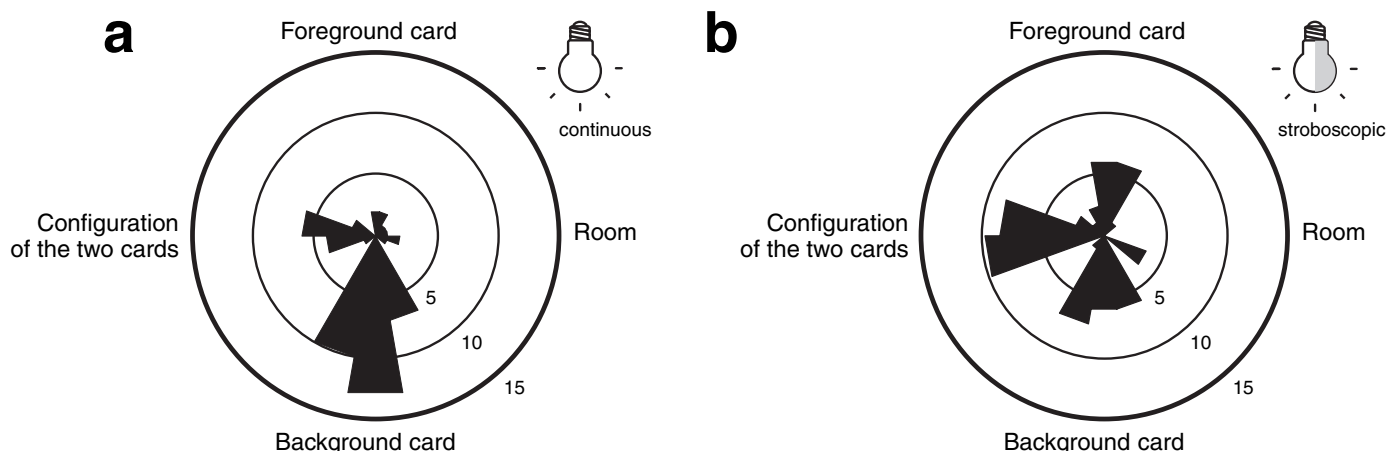


FIG. 4. Incidence of preferred direction shifts after foreground and background card rotations in (a) continuous and (b) stroboscopic light. The data are shown in the form of a circular histogram (bin size 20°) where the number of sessions corresponding to the respective shifts in preferred direction is indicated by the radius of the concentric circles that serve as calibration bars. The preferred directions after cue rotations are presented according to the same formalism as in Fig. 3 to facilitate comparisons: no shift (equivalent to dominance of room cues) is indicated at the 3 o'clock position ('Room') and shifts following the background cue are at 9 o'clock, etc. (a) Under continuous light conditions, the preferred directions of the head direction cells followed the background card in the majority of the recording sessions. (b) Under stroboscopic light conditions, the preferred directions were equally likely to follow the background card, foreground card or the configuration of both. Data have been rectified to compensate for the fact that background and foreground cards were rotated in different directions among sessions.

directions followed the foreground card in continuous light (9% of the cases, i.e. five of 53; Fig. 4a). The remaining experiments are inconclusive as the preferred directions followed the configuration of the two cards (25% of the cases, i.e. 13 of 53; as if the two cards were but a single cue) or did not shift (9% of the cases, i.e. five of 53). A V -test (Batschelet, 1981) showed that the data were clustered around the background cue orientation (6 o'clock position in Fig. 4a) under continuous illumination ($n = 53$, $V = 4.6521$, $P < 0.01$).

To test whether the selection of anchoring cues depends upon dynamic visual cues (such as motion parallax or optic field flow), we then repeated these experiments in stroboscopic light (flashes at 1.5 Hz). This was intended to disrupt continuous visual inputs and block the processing of fine time-scale spatial changes in retinal stimulation triggered by self motion, such as the relative shifts of images of the respective cards. Thus, under these conditions, if dynamic visual cues were of critical importance, the preferred directions of the HD cells would no longer be controlled by the background card.

Consistent with this prediction, Fig. 3 right column shows the response curves of three typical HD cells (recorded during three different sessions) before and after rotation of the cards under stroboscopic lighting. Each of the three principal responses was observed. Over all recording sessions (Fig. 4b), the preferred directions followed the background card in 33% (17 of 51), the foreground card in 27% (14 of 51) and the configuration of both in 33% (17 of 51) of the recording experiments. In three experiments the preferred directions did not shift. Thus, the preferred directions were equally likely to follow the background card, the foreground card or the configuration of both (Watson U^2n test against the normalized sum of three Gaussians centred at 90° , 180° and 270° with SDs of 10° , $U^2n = 0.11703$, $n = 51$, $P > 0.1$). The distributions of responses in the continuous and stroboscopic lighting condition (shown in Fig. 4a and b) were compared and proved to be significantly different (Watson U^2 test, $U^2 = 0.2151$, $n = 104$, $P < 0.05$).

To avoid possible interference of attentional processes with the results, the rats were introduced to the environment in a special manner described in Materials and methods. In those sessions where a continuous light condition session immediately followed a recording under stroboscopic light, the results were similar to those that occurred

at the beginning of the session (the background card was selected in 10 of 16 experiments while the foreground card was followed only twice; for both cards $n = 2$ and for the room cues, $n = 2$). Thus, there is little support for the different distribution of responses under stroboscopic lighting being due to its novelty or generalized disorienting effects as no systematic differences were found between responses in early versus late sessions within series in individual animals.

Discussion

The principal result is that stroboscopic lighting at a frequency disturbing certain dynamic visual processes interferes with the preferential anchoring of HD responses by background cues. This is consistent with the hypothesis that, under continuous lighting, this anchoring would occur by neural processing of fine time-scale spatial changes in retinal stimulation triggered by self motion, specifically the shifts of images of the respective cards. The relative velocities of retinal slip of the two cards would be detected during head movements. The image of the more distant card would shift more slowly and this would anchor the HD system by mechanisms as yet unknown (although anatomical pathways have been demonstrated that link these neural systems, rendering this interpretation parsimonious). Note that this requires estimation only of relative, not absolute, distance. This is supported by the absence of preferential anchoring by the background cue in stroboscopic lighting, which disrupts continuous visual inputs and blocks the use of visual motion signals (such as motion parallax) from helping to distinguish background from foreground cues. This also confirms and extends our previous findings showing that updates of the preferred directions of HD cells are dominated by background, rather than foreground, visual cues (Zugaro *et al.*, 2001a).

Although the background cue significantly dominated in the continuous light condition, the results varied from one experimental session to the next, even with repeated recording of the same individual neuron or same animal. This may be because the actual available dynamic visual cues for detecting relative distance consisted of low magnitude differences in relative velocity (estimated at $5\text{--}10^\circ/\text{s}$). As preferred directions can be reset very rapidly in the HD cell network (Zugaro *et al.*, 2003), it is not surprising that this automatic

mechanism would show variability as relative distance information was sparse and liminal. This is supported by the substantial numbers of sessions in both conditions where the preferred direction followed the midpoint between the two cues, indicating that they were not easily distinguishable. In any case, the suppression of this significant bias toward the background cue under stroboscopic lighting argues for the vital role of dynamic visual cues under continuous light, as the stroboscopic lighting deters velocity detection while not affecting other possible relative distance cues.

There are several arguments against other relative depth cues influencing the HD cells here. The experimental design and poor visual discrimination capacities of rats (Hughes, 1977; Hughes & Wässle, 1979) eliminated or dramatically reduced the risk of interference from certain other possible cues, like relative size, luminance, occlusion and texture. The two cues were positioned at the limits of the binocular viewing field of the rat visual system (Lashley, 1932), thus making vergence unlikely. Accommodation (which remains to be demonstrated in the rat) is also considered unlikely as HD cell responses are set within 80 ms while accommodation requires at least twice that time in humans (e.g. Kasthurirangan *et al.*, 2003). Nevertheless, it remains possible that under, other experimental conditions, HD cells could also be demonstrated to engage some of these other mechanisms in order to select anchoring background cues.

Each of the individual responses is considered to represent the activity of all of the neurons in the anterodorsal thalamus within that session. This is supported by our present results in four sessions with multiple cell recordings and by virtually all published reports of simultaneous recordings of HD cells (e.g. Taube *et al.*, 1990; Chen *et al.*, 1994; Goodridge & Taube, 1995; Dudchenko *et al.*, 1997; Knierim *et al.*, 1998; Zugaro *et al.*, 2001a) which consistently observe that these neurons respond coherently to changes of the orientation of the environmental cues. This binding is also a vital property permitting all existing computational models of HD cells to successfully replicate the properties of the actual neurons (Skaggs *et al.*, 1995; Blair, 1996; Redish *et al.*, 1996; Zhang, 1996; Goodridge & Touretzky, 2000; Sharp *et al.*, 2001; Xie *et al.*, 2002). This contrasts with some studies of hippocampal place responses where disparate responses among simultaneously recorded cells have been reported.

As HD cell responses varied across experiments rather than among individual cells, the relevant parameter for evaluating the results is the number of experiments (53 in continuous light and 51 in stroboscopic light) and data have been grouped together for multiple cells recorded within a single session. The absence of any apparent patterns in the session-to-session variations in the responses of individual neurons argues against any dependence of successive measures within individual animals and the same pattern of results is apparent for each animal.

In summary, dynamic visual signals play a critical role in selection of anchoring cues by HD cells. Such inputs could include dynamic motion parallax-related signals. These would permit background visual cues to be discriminated from those in the foreground during head translation movements as more distant objects appear to move at lower velocities. Alternatively, HD cells could receive critical information for this from the visual pathways specialized for detecting optic field flow; these are most sensitive to slow movements of large areas of the visual field, as provided by the image of background cues on the retina.

There is a clear adaptive advantage to selecting background cues as they are often more stable and reliable as the animal moves about. This complements the well-known role of optic flow information for updating heading information during movements (Lappe, 2000). While the latter concerns situations where the initial heading direction has already been established, the present work shows that dynamic visual cues are also important in the elaboration of these initial settings.

Acknowledgements

Thanks to Professor A. Berthoz for support and discussions, Dr J. Droulez for discussions, F. Maloumian for illustrations and M.-A. Thomas and S. Dautremer for histology. This work was supported by CNES, ACI du Ministère de la Recherche. M.B.Z. received a grant from the Fondation pour la Recherche Médicale and A.A. received a grant from the EU Marie Curie Programme.

Abbreviations

HD, head direction.

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