PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. Lond. B 1997 **352**, 1515-1524
doi: 10.1098/rstb.1997.0138

Dissociation of exteroceptive and idiothetic orientation cues: effect on hippocampal place cells and place navigation

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SUMMARY

Navigation by means of cognitive maps appears to require the hippocampus; hippocampal place cells (PCs) appear to store spatial memories because their discharge is confined to cell-specific places called firing fields (FFs). Experiments with rats manipulated idiothetic and landmark-related information to understand the relationship between PC activity and spatial cognition. Rotating a circular arena in the light caused a discrepancy between these cues. This discrepancy caused most FFs to disappear in both the arena and room reference frames. However, FFs persisted in the rotating arena frame when the discrepancy was reduced by darkness or by a card in the arena. The discrepancy was increased by 'field clamping' the rat in a room-defined FF location by rotations that countered its locomotion. Most FFs dissipated and reappeared an hour or more after the clamp. Place-avoidance experiments showed that navigation uses independent idiothetic and exteroceptive memories. Rats learned to avoid the unmarked footshock region within a circular arena. When acquired on the stable arena in the light, the location of the punishment was learned by using both room and idiothetic cues; extinction in the dark transferred to the following session in the light. If, however, extinction occurred during rotation, only the arena-frame avoidance was extinguished in darkness; the room-defined location was avoided when the lights were turned back on. Idiothetic memory of room-defined avoidance was not formed during rotation in light; regardless of rotation, there was no avoidance when the lights were turned off, but room-frame avoidance reappeared when the lights were turned back on. The place-preference task rewarded visits to an allocentric target location with a randomly dispersed pellet. The resulting behaviour alternated between random pellet searching and target-directed navigation, making it possible to examine PC correlates of these two classes of spatial behaviour. The independence of idiothetic and exteroceptive spatial memories and the disruption of PC firing during rotation suggest that PCs may not be necessary for spatial cognition; this idea can be tested by recordings during the place-avoidance and preference tasks.

1. INTRODUCTION

The discovery of hippocampal place cells (PCs) by O'Keefe & Dostrovsky (1971) and the ensuing systematic study of their properties (McNaughton *et al.* 1983; O'Keefe & Recce 1993; O'Keefe & Burgess 1996; Muller *et al.* 1987; Sharp *et al.* 1990; Bostock *et al.* 1991) created an extremely fruitful approach to the study of the cellular substrate of cognition. The idea that a PC firing in a specific region of a familiar environment participates in the neural processes that enable an animal to recognize its position in the charted world has inspired a deluge of ingenious experiments, highlighted by the papers in this volume.

One consequence of the putative correspondence of PC activity and animal behaviour is that principles used in behavioural studies have been applied to the investigation of single cells. Although PC personification should be avoided, examination of PC activity under certain organism-defined conditions proved to be useful (Markus *et al.* 1995; Gothard *et al.* 1996). This is particularly true for the separation of two sources of information that contribute to spatial representation: exteroceptive inputs derived from environmental features and idiothetic inputs used in path integration (O'Keefe & Nadel 1978; Gallistel 1990).

The same classification presumably applies to PC mapping. Exteroceptive control of PCs has been demonstrated repeatedly (O'Keefe & Conway 1978; Knierim *et al.* 1995; O'Keefe & Burgess 1996). In one experiment a shift of a cue card on the wall of the

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recording chamber caused a corresponding displacement of firing fields (Muller & Kubie 1987). Idiothetic information must also be able to control PCs: firing fields (FFs) established in light persist in darkness even though in light they are controlled by visual cues (Quirk *et al*. 1990; Markus *et al*. 1994; O'Keefe 1976; McNaughton *et al*. 1989*b*). Thus location-specific PC activity is determined both by exteroceptive and idiothetic information; after elimination of the exteroceptive component, path integration alone can support sustained PC mapping (McNaughton *et al*. 1996). This is in good agreement with behavioural findings that show that place navigation can be directed to new locations by changing the position of extramaze landmarks (Biegler & Morris 1993; Fenton *et al*. 1994) and that sudden darkness does not prevent successful homing (Alyan & Jander 1994; Mittelstaedt & Mittelstaedt 1980).

The equivalence of exteroceptive and idiothetic orientation applies to a stable world where both navigation modes yield the same information and can, therefore, substitute for each other. Thus, exteroceptively based navigation can be supported by path integration in track segments from which no remote landmarks are visible (Liu *et al*. 1994). It is conceivable that equivalence of these two classes of input can be disrupted when the relationship between extramaze landmarks and the animal's locomotion becomes unpredictable. This paper reviews several attempts to assess the changes in PC activity caused by such conditions.

The contribution of PC activity to place navigation is usually implied but only rarely verified by PC recordings in navigation experiments. Because such investigations require distributed exploration of the experimental arena as well as place-directed locomotion, another aim of the research described here was to develop tasks that meet these requirements.

2. GENERAL METHODS

(*a*) *Subjects and apparatus*

Adult male Long–Evans rats were trained to forage for randomly located food pellets in one of several circular arenas (80–100 cm in diameter). The pellets were dispensed by a computer-controlled feeder either at regular 10 s intervals or after the animal fulfilled some computer-evaluated criteria. The arena was also computer-controlled and could be rotated around its axis at angular velocities ranging from 6 to $30^\circ\,s^{-1}$. The arenas were placed in a room that provided many extramaze visual cues when the light was switched on, but was completely dark when the light was switched off.

(*b*) *Tracking system*

The rat's position was recorded by tracking an infrared light-emitting diode (LED) with an infrared-sensitive television camera connected to a computer-based tracking system. The infrared LED was in the recording head stage (see below) in the electrophysiological experiments and between the rat's shoulders in the purely behavioural studies. The custom-made tracking system operated with a spatial resolution of 0.4–0.5 cm and a temporal resolution of 100 ms. The software permitted interactive control of the experiment. For example, on fulfilment of various behavioural criteria, such as entering and staying in a specified region or moving for a criterion distance or duration, the system could switch the room lights on or off, rotate the arena, apply an electric shock, deliver food pellets, etc.

The position of the rat was plotted in two coordinate systems, either in the x–y coordinate system of the room or in the polar system of the arena where the origin is at its centre. Position in the arena frame was calculated by correcting the room coordinates by the coordinates of a second infrared LED on the arena wall (Bures *et al*. 1997). The arena projection corresponds to a view obtained from a virtual television camera fixed above the centre of the arena and rotating with it. Thus, tracks in the two reference systems are identical when the arena is stationary, but different when the arena is rotating. In the latter case, the track in the room frame records a combination of the animal's active locomotion and the movement of the arena, whereas tracking in the arena frame eliminates the rotation to reflect only the active locomotion.

(*c*) *Unit recording*

Under pentobarbital anaesthesia ($40\,mg\,kg^{-1}$) a driveable bundle of eight Formvar-insulated nichrome electrodes 25 μm in diameter was implanted about 1 mm above the CA1 cell layer of the dorsal hippocampus (3.0 mm caudal from bregma, 2.5 mm lateral from the sagittal suture (Paxinos & Watson 1986)). After several days of recovery the electrodes were slowly advanced until single CA1 units could be isolated. Recording sessions lasted 10 min. Extracellular potentials were first amplified with high-impedance preamplifiers (10 × gain) in the recording headstage, then amplified another 1000 times and filtered (300–10 000 Hz) before being digitized (32 kHz) and stored in a computer-based system (DataWave, USA).

(*d*) *Analysis of PC activity*

Unitary waveforms were discriminated offline with a template-matching algorithm that used a least-square fit to score the match between digitized spike-like events and a waveform template. Those waveforms sufficiently close to only one template were classified as belonging to a single neuron. The discriminated-spike time series for each unit, along with the position time series, were used to construct two-dimensional histograms of the session-averaged firing-rate distribution in 5 cm × 5 cm pixels. The mean firing rate in a pixel was calculated as the number of spikes recorded in the pixel divided by the total time spent in the pixel. Firing-rate distributions were displayed as grey-scale-coded firing-rate maps. White pixels represented undefined firing rate because the rat was never there. The lightest grey pixels were visited but had a firing rate of zero. The five remaining shades of grey increased in darkness to represent, in increasing order, 31, 25, 19, 14 and 11% of the non-zero firing rates.

Numerical methods were used to describe and compare the averaged firing-rate distributions. A firing field (FF) was defined as an area of at least four pixels ($100\,\mathrm{cm}^2$) where the firing rate was at least two standard deviations above the overall mean firing rate. The pixels included in a field had to share at least one side with another pixel of the same FF. The FF location was defined as the firing rate-weighted average of the x and y coordinates of the pixels included in the field. The distance between FFs observed in two sessions, i.e. the displacement (D), was used to assess the FF location change. The location was considered changed if the displacement exceeded 5% of the distance from the reference location to the most distant point of the arena. The quality of the location-specific firing was expressed by calculating spatial coherence, concentration and dispersion (Muller & Kubie 1989; Bures *et al*. 1997).

3. PC DISCHARGE ON A ROTATING ARENA

While foraging on a featureless rotating arena, a rat can perceive its position in relation to the immobile surroundings, i.e. to the room cues, or in relation to the surface of the arena, e.g. to the starting point of the movement. Although spatial knowledge is more or less irrelevant for successful pellet chasing, both exteroceptive and idiothetic spatial information is probably recorded automatically because in natural situations this information allows the animals to go straight to a chosen goal or to return to the safe haven of the home. A fundamental difference between exteroceptive-based and idiothetic-based navigation is that the former can generate trajectories to any location of the charted environment, whereas the latter can only generate paths to already-visited locations or projected locations along the current track. Whereas the exteroceptive-based navigation requires estimation of the current position and computation of the shortest direction to the goal, the return azimuth to home (or to another point of the current path) is continuously available from the path-integration system and can probably be obtained with shorter latency. This is a vital advantage in case of sudden danger.

Whether either or both classes of information are being utilized can only be verified in behaviourally relevant situations; recording PC activity during pellet chasing can examine how each contributes to PC mapping. A FF characterized on a stationary arena might be activated by one or both classes of information because they are equivalent. In contrast, this equivalence breaks down when the arena rotates. Thus, during slow constant rotation of the arena (one revolution per minute), an FF can (i) remain stable in the room frame, i.e. the PC fires when the rat moves into the FF either owing to passive rotation of the arena or by a combination of active and passive movements; (ii) remain stable in the arena frame, i.e. the PC fires when the rat enters a definite region of the arena irrespective of its position in the room; or (iii) disappear or be smeared in both the room and the arena frames. The first two possibilities indicate that the particular PC responds mainly to exteroceptive or to idiothetic inputs, respectively. The third suggests that such a PC is activated by the coincidence of exteroceptive and idiothetic information. This situation may only occur during the short interval when rotation of the arena brings its surface into the position corresponding to a match between both projections.

Figure 1 shows examples of PCs recorded in a cylindrical arena 1 m in diameter with walls 40 cm high. In the first session the arena was stable; in the next, it was rotated (1 rpm) to cause a disagreement between exteroceptive and idiothetic information, and in the third session it was stable again. The rat was not removed from the arena between sessions. In the rotation sessions, the firing-rate distributions were calculated for both the room frame and the arena frame. Figure 1*a* is an example of the most common finding. Although pellet chasing appeared unaffected, an FF characterized on the stationary arena disintegrated in both reference frames during rotation. There was no 'remapping' (Muller & Kubie 1987; Bostock *et al*. 1991; Markus *et al*. 1995) as might be expected for 20% (Thompson & Best 1989) to 50% of PCs (O'Keefe 1979; Wilson & McNaughton 1993).

It was uncommon for FFs to persist during rotation in the light. The few FFs preserved in the room frame (figure 1*b*) or in the arena frame (figure 1*c*) indicated, however, that exteroceptive or idiothetic information alone may be sufficient to maintain such PCs. In contrast, most PCs retained their FFs when the light was switched off; such FFs were preserved in the arena frame even during rotation in darkness (figure 2*a*). It seems that in the rotating arena once darkness diminished exteroceptive information the conflict with idiothetic information was removed and most PCs continued to fire in the arena frame. The above effect of darkness suggests that PCs are disturbed not by rotation alone but rather by the rotation-induced conflict between the two sources of information.

This conflict can be reduced by cues on the rotating cylinder wall. Indeed, the incidence of FFs in the arena frame was markedly increased when a white card was pasted on a 60° segment of the rotating arena wall (figure 2*b*). In this situation idiothetic orientation is reinforced by a prominent environmental feature that partly restores the correspondence between idiothetic and exteroceptive information. Although the information from the stable extramaze landmarks in the room continues to disagree with expectations corresponding to idiothetic information, the presence of a visual stimulus confirming these predictions seems to increase the animal's trust in the arena-frame view of the world. Thus, both darkness and visual cues enhance the significance of idiothetic input to the PCs, but the enhancement is achieved by different mechanisms. Darkness eliminated the conflicting salient exteroceptive input, whereas the salient cue card made enough exteroceptive information consonant with the idiothetic input.

4. FIELD CLAMP

The disagreement between idiothetic and exteroceptive orientation had no apparent effect on the rat's

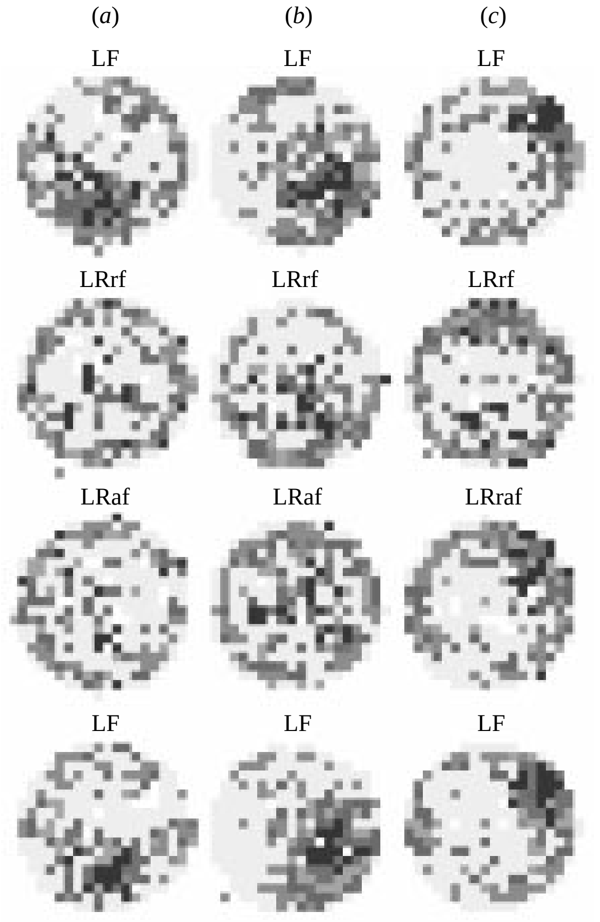

Figure 1. Examples showing three effects of rotating the arena (see text). Firing-rate maps of PCs recorded during 10 min of pellet chasing in light (L) on a fixed arena (F) and on a rotating arena (R). The maps from rotation sessions are presented in either the room reference frame (rf) or in the arena reference frame (af). The grey-scale code increases from the lightest grey (zero rate) to black through five rate-related levels corresponding to 31, 25, 19, 14 and 11% of the non-zero firing rates. (*a*) An FF characterized in the south on the stable arena disintegrated on the moving arena in both frames and returned to its original form when the rotation stopped. (*b*) An FF characterized in the south-east on the stable arena is detectable on the rotating arena in the room frame but not in the arena frame. During rotation the FF was somewhat disorganized but was stronger and in the same room-frame position after the rotation. (*c*) An FF characterized in the north-east on the stable arena disintegrated during rotation in the room frame but was preserved in the arena frame; the post-rotation FF is closely similar to the initial FF. Black category peak and median firing rates (action potentials per second, AP s^{-1}) from top to bottom: (*a*) LF 20.0, 6.0; LRaf 10.0, 3.0; LRaf 10.0, 3.0; LF 20.0, 10.0. (*b*) LF 8.9, 6.2; LRrf 8.3, 4.3; LRaf 8.3, 4.3; LF 27.8, 13.0. (*c*) LF 13.0, 7.0; LRrf 20.0, 3.0; LRaf 30.0, 5.0; LF 8.4, 6.0.

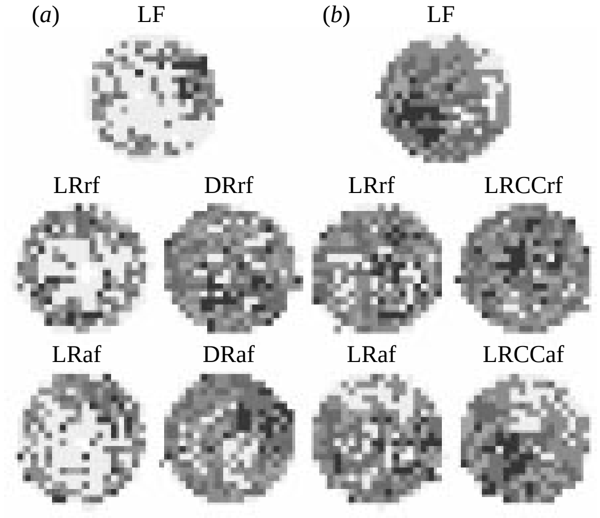

Figure 2. Changes that reduce the conflict between exteroceptive and idiothetic orientation stabilize FFs in the arena frame. (*a*) An FF in the north-east on the stable arena was abolished by rotation in the light but could be restored in the arena frame during rotation in darkness. (*b*) An FF in the south-west on the stable arena disintegrated in both frames during rotation in the light but was restored in the arena frame when a cue card (CC) was placed on the wall of the rotating arena. Other conditions as in figure 1. Black category peak and median firing rates (AP s^{-1}): (*a*) LF 10.0, 3.0; LRrf 3.3, 2.3; LRaf 10.0, 2.0; DRrf 11.1, 6.0; DRaf 16.7, 6.0; (*b*) LF 67.5, 32.0; LRrf 2.0, 8.0; LRaf 15.7, 10.0; LRCCrf 70, 13; LRCCaf 30.0, 15.0.

performance in the pellet-chasing task; this is probably the reason why prolonged rotation of the arena is tolerated by the PCs. After the rotation stopped, PC mapping returned immediately to the control stationary state. A more serious disturbance of PC mapping can be produced by the field-clamp technique (Zinyuk *et al*. 1996; Bures *et al*. 1997). The pellet-chasing task was used in a ring-shaped arena (25 cm wide, 1 m diameter of the outer wall, 40 cm height of the outer wall). Rotation of the arena in this experiment was used to enhance the disagreement between exteroceptive and idiothetic orientation by confining the animal to a fixed position in the room frame while allowing it to move freely in the arena frame. The field-clamp program controlled the rotation of the arena so that whenever the animal left a specific 30° sector of the ring (e.g. the southwest) the arena moved (30° s^{-1}) to return the rat to the region of the lock. In this way, the animal can travel all over the surface of the ring but nevertheless remain in the same room–frame position. Perhaps this makes the disagreement between the two modes of orientation more conspicuous: idiothetic perception tells the rat it has visited all parts of the arena, but visual perception of the room indicates that it has not moved, or that its attempts to leave the place were frustrated by some strange force. The rats' notorious dislike of restraint might have added emotional distress to the above perceptual disagreement. The slow search that is characteristic for foraging would have required only brief intervals of rotation to bring the animal back to the lock sector, but most rats occasionally ran out of the sector so fast that it sometimes took several seconds to rotate them back into the clamped area.

Changes of PC activity observed in 100 PCs tested in the field-clamp experiments extend the results obtained in the continuously rotating arena. When the field clamp confined the rat to a sector corresponding to the FF previously established in the stationary arena, the FF disappeared in most cases. This suggests that the exteroceptive orientation, asserting that the animal did not leave a definite location in the room could not resist the more persuasive idiothetic experience telling the animal that it could not be in a place from which it was trying so hard to escape. After termination of the clamp, an FF often appeared in a different location and returned to the original position only after an hour or on the next day. Only 15 PCs had the same FF location during the clamp and afterwards. Seventy PCs showed transient changes of FF location after the clamp; no FF recovery was seen in 15 PCs.

5. PC ACTIVITY DURING BEHAVIOURAL TESTING

Experiments on radial mazes studied how PC activity is controlled by goal locations but did not reveal how PC firing was related to navigation (O'Keefe & Conway 1978; Olton *et al*. 1978; O'Keefe & Speakman 1987; McNaughton *et al*. 1989*a*). The relation between PC mapping and cognitive behaviour might be examined in experiments that combine standard pellet chasing with place navigation. The well-established characteristics of FFs can then be compared during random foraging and goal-directed locomotion. The effect of conditions that differentially affect the importance of exteroceptive and idiothetic information could be compared as well as the potential influence of appetitive and aversive motivations. The two tasks described on the following pages were developed with the aim of understanding the relationship between PC firing and spatial cognition.

6. PLACE AVOIDANCE

One of the most widely used techniques in memory research, the passive avoidance task, is actually a cued spatial avoidance. In the step-down, step-through or two-compartment tasks (see Bures *et al*. (1983) for a review), the rat learns to inhibit visits to a part of the apparatus because it is punished by mild footshock at this location. The region to be avoided is easily discernible and the learned response is to stay in the start compartment. This classic model can be modified into place avoidance when the unmarked region to be avoided is defined by its relation to remote extramaze cues and when the learned response leads to continued foraging on the safe part of the arena and avoidance of the footshock zone (Sacchetti *et al*. 1997).

(*a*) *Method*

Under thiopental anaesthesia, a low-impedance silver wire (200 μm diameter, 4 cm long) connected to a miniature socket was implanted under the skin at the back of the neck. The socket was fixed to the skull with anchoring bolts and acrylate. After recovery, the animal was trained to forage for scattered pellets on an elevated circular arena with a metal floor. Through the socket a computer-controlled relay could deliver 0.6 mA of 50 Hz current between the implanted wire and the paws of the animal contacting the grounded metal floor. The infrared LED for tracking was positioned between the rat's shoulders with a latex harness. The rats were first trained for several days in the pellet-chasing task with pellets dispensed at 10 s intervals. A semicircular 'prohibited' area was then designated in one quadrant. Its centre was at the periphery and its radius corresponded to 20% of the arena's diameter. The rat received a mild 0.5 s electric shock whenever it entered the prohibited region for more than 0.5 s. The shock was repeated after 3 s if the animal did not leave the punishment area. Training continued until the animal displayed no apparent fear and continued to forage while avoiding the punishment zone. This initial 'pretraining' was followed by retrieval tests performed under extinction conditions, i.e. in the absence of electric shocks.

(*b*) *Results*

The place-avoidance task was used to learn how spatial memories based on distal visual information interact with memories based on path-integration information. Do these two types of information produce independent memories? And if so, how do they interact to mediate spatial behaviour?

Each experimental session began with an 'acquisition' period when footshock punished entries into a rat-specific prohibited area. Acquisition was always in the lit room with the punishment zone defined by room cues. Acquisition training in the light was on either a fixed ($n = 16$) or rotating arena ($n = 22$). Acquisition continued until the animal succeeded in avoiding shock during five consecutive epochs of 2 min duration. Retrieval testing under extinction conditions was then begun by switching off the electric shock, switching off the lights, and setting the rotation condition to either fixed or rotating. Testing continued until the rat regularly entered the prohibited zone. This was measured in each 2 min epoch by calculating the percentage of time spent in the prohibited zone compared with the total time spent in the prohibited zone and corresponding areas of the three other quadrants. An analogous calculation was made for the percentage of the total path length in the prohibited zone. The extinction criterion was met when measures of both time and path length were at least 13% in three consecutive 2 min epochs. If this criterion was not reached within 1 h, the rat was given a 60 min to-criterion score. The session continued by switching the lights on and testing for extinction the second time without removing the animal from the arena and without changing the rotation condition.

The results are shown in figure 3. When both training and testing proceeded on the stable arena, both exteroceptive and idiothetic memories of the place to be avoided were formed during acquisition and the idiothetic memories could support effective place avoidance during extinction testing in darkness (figure 3*a*). In this case, extinction attained in darkness transferred to the subsequent light condition.

The place avoidance acquired on a fixed arena could also be retrieved during testing performed on the rotating arena in darkness. Tracks recorded during a typical experiment (figure 4*b*) show that avoidance

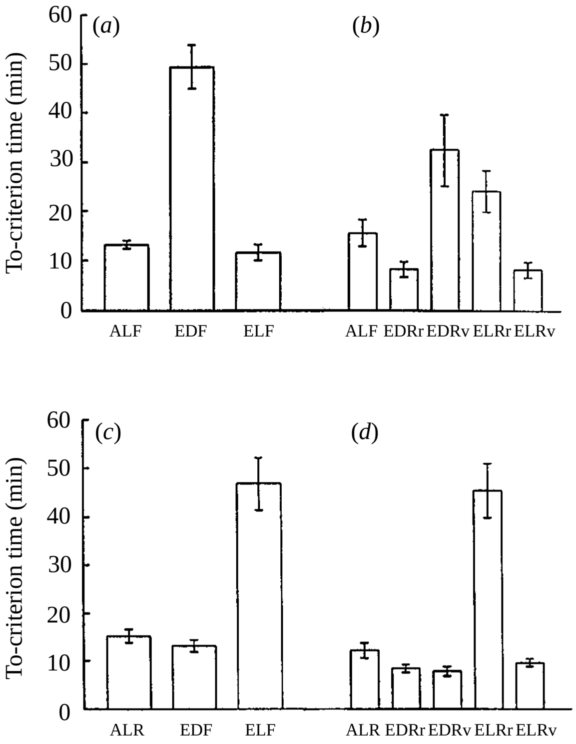

Figure 3. Mean (±s.e.m.) times to acquisition (A) or extinction (E) criteria of place avoidance. Column labels indicate the experimental conditions: D, darkness; L, light; F, fixed arena; R, rotating arena; r, real camera view (room frame); v, virtual camera view (arena frame). The experiments shown in (*a*), (*c*) and (*d*) were performed on 11 rats each. Five rats were used in the remaining experiment (*b*). Note that extinction in darkness is slow after acquisition on the fixed arena (*a*, *b*) and fast after acquisition on the rotating arena (*c*, *d*). Note also that place avoidance acquired on the fixed arena, when tested on the rotating arena, led to avoidance of an arena-frame location in darkness and of a room-frame location in the light (*b*).

was seen by the virtual camera in the arena reference frame and not in the room reference frame monitored by the real camera (figure 3*b*, $\mathrm{EDRv} > \mathrm{EDRr}$, $t_4 = 3.5$, $p < 0.025$). The opposite pattern was seen when the light was switched on in the second testing phase (figure 3*b*, $\mathrm{ELRv} < \mathrm{ELRr}$, $t_4 = 3.7$, $p < 0.025$). In contrast to extinction in the dark on the stable arena (figure 3*a*), extinction in the dark on the rotating arena did not transfer to the light phase. Clear avoidance in the room frame must have been supported by exteroceptive memory traces that were not extinguished in the dark. Although extinction appears accelerated, it was not significantly different from the idiothetic extinction in the previous dark phase (figure 3*b*, $\mathrm{EDRv} > \mathrm{EDRr}$, $t_4 = 1.2$, n.s.)

Acquisition of place avoidance on the rotating arena resulted in the formation of exteroceptive memories alone. Because any attempts to avoid a region defined in the arena frame may lead to footshock, formation of idiothetic memories for avoidance was probably suppressed. This suppression is manifested by the absence of place avoidance in darkness on either fixed (figure 3*c*) or rotating (figure 3*d*) arenas. As soon as the light was switched on, avoidance reappeared in the room frame. When both acquisition and retrieval testing proceeded on the rotating arena, avoidance in darkness was seen neither in the room frame (because no room cues were available) nor in the arena frame (because no idiothetic memories were formed during acquisition), but avoidance of the prohibited location defined in the room frame reappeared in the light (figures 3*d*, 4*d*).

These results indicate that place-avoidance training has independent exteroceptive and idiothetic components that can be dissociated. During place-avoidance training on the fixed arena the animal learns to avoid a specific location in the room that is identical with a definite sector of the arena. The independence of these two traces makes it possible to solve the task in two different ways: by using just the idiothetic memory in darkness or by using just the exteroceptive memory in light, provided that the idiothetic memory has been eliminated during the preceding extinction in darkness.

The dissociation of exteroceptive and idiothetic place-avoidance memories raises a not immediately apparent prediction. If place avoidance is acquired on a stable arena in the light, its extinction on a rotating arena in the light may lead to an ambiguous solution. This would be manifest as simultaneous avoidance of an exteroceptively defined location (e.g. of the north-west section of the arena) and of an idiothetically defined location (corresponding to the floor region that was in the north-west section of the stable arena during acquisition), which could be seen by the real and virtual cameras, respectively.

The place-avoidance results, compared with the activity changes in PCs induced by rotation, suggest that the PC mapping that is preserved in darkness on both fixed and rotating arenas can be the basis of continued avoidance of idiothetically defined locations. On the other hand, the disappearance of most location-specific firing during rotation in the light contrasts with the good retrieval of place avoidance on the rotating arena in the light, albeit after previous extinction of the idiothetic memory. It is conceivable that place-avoidance training may increase the percentage of exteroceptively dependent PCs; this increase could support the exteroceptive solution of the task. This is particularly probable in rats that acquire the task on a rotating arena in the light because the importance of exteroceptive input is enhanced by the disutility of idiothetic inputs. The other possibility, that striking exteroceptive place avoidance proceeds in the absence of exteroceptive PC mapping, would require a thorough reappraisal of the role of PCs in place navigation.

7. PLACE-PREFERENCE TASK

An obvious disadvantage of the place-avoidance task is that the avoided part of the arena remains unvisited. This drawback is removed in the place-preference task, which permits unlimited exploration of the whole arena (Rossier *et al.* 1997). The task is actually an operant procedure, which requires the animal to visit a specific location on the arena to activate the feeder. After a

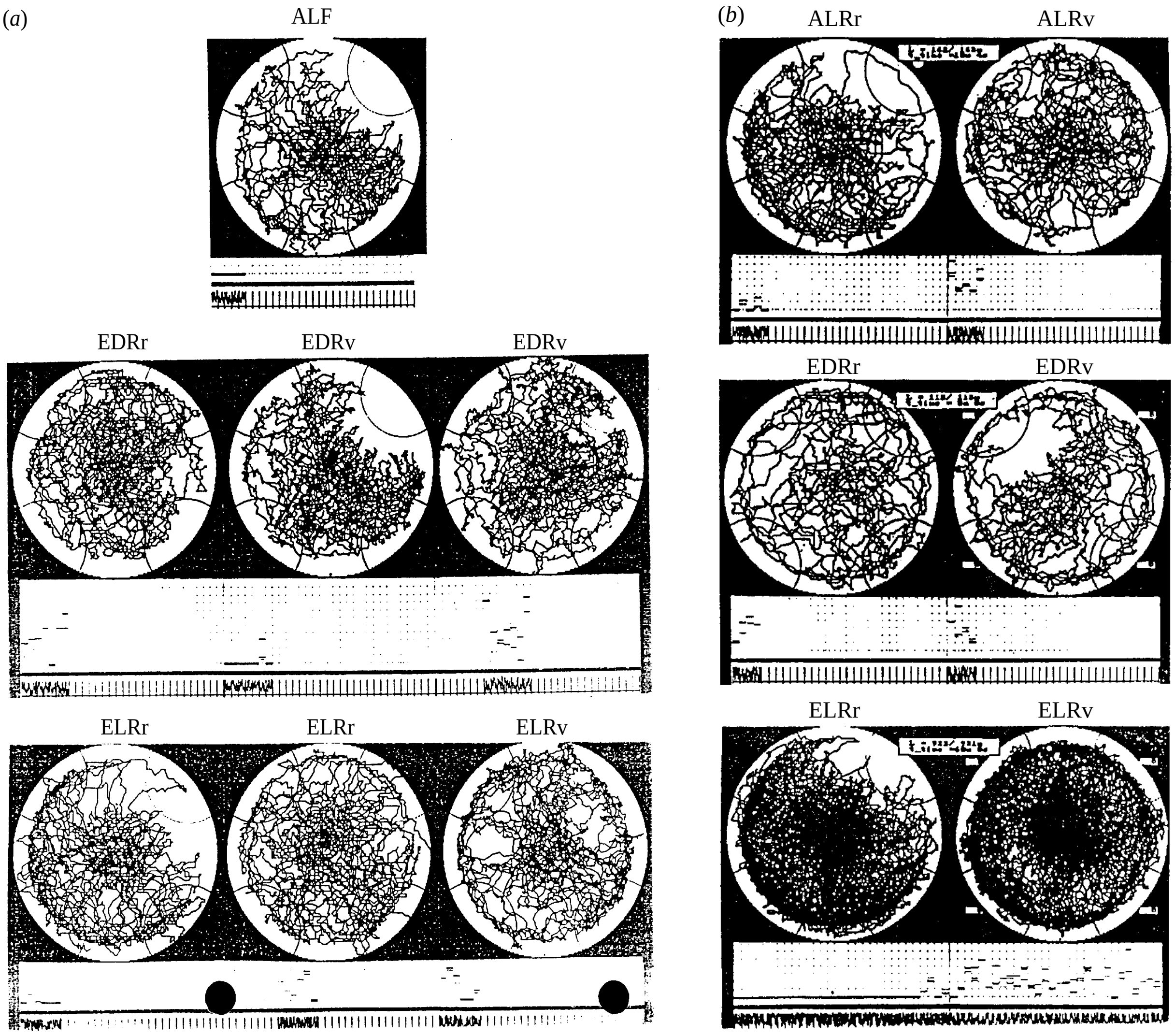

Figure 4. Representative tracks from experiments (*b*) and (*d*). (*a*) and (*b*) correspond to data in figure 3*b* and 3*d*, respectively. Tracks on the rotating arena are plotted either in the room frame of the real camera view (r) or in the arena frame of the virtual camera view (v). The arcs at the circumference of the arena indicate the prohibited and the three control areas. In each 2 min epoch, two measures of avoidance were calculated: percentage of time and track length in the prohibited area related to the totals for the prohibited and the three control areas. These measures are plotted for each epoch below the tracks. The bottom curve expresses the rat's movement by plotting the rat's distance from an arbitrary point in the reference frame. The rat learned to avoid the north-east region of the rotating arena in (*d*) and of the fixed arena in (*b*). Because no idiothetic memories of the shock region were formed in experiment (*d*), there was no avoidance in darkness in either reference frame. However, when the light was switched on, the avoidance reappeared in the room frame and lasted for more than 50 min. In experiment (*b*) avoidance was acquired on the fixed arena and both types of memory were formed. The idiothetic memory was manifested on the rotating arena by avoidance of the prohibited region in the first 12 min and by the gradual development of extinction later. No avoidance was seen in the real camera view. After the light was switched on, the rat avoided the north-east sector of the arena for more than 10 min before extinction set in. This is documented by the real camera view, whereas the virtual camera indicated no avoidance of the part of the arena where the shocks were administered.

pellet falls into the arena, the rat leaves the trigger location to search for it. After the pellet is retrieved, the rat runs more or less directly to the trigger area. Thus there is alternation of two modes of spatial behaviour: goal-directed place navigation and random searching.

(*a*) *Method*

Five rats were trained to search for pellets in the arena used in the place-avoidance experiments. The pellets were released by the computerized tracking system only when the animal had entered a circular target area (20–36 cm in diameter). Once the pellet was dispensed, the rat had to search for it and stay outside the target area for at least 3 s before the next visit to the target area was rewarded. The rat was placed near the centre of the arena to begin a session that lasted 30 min. The rat's position was recorded every 100 ms. The number of entries into the trigger annulus and the time spent there were compared with control values from analogous annuli in the other three quadrants of the arena. In addition, lengths of the approach and departure trajectories during the 3 s

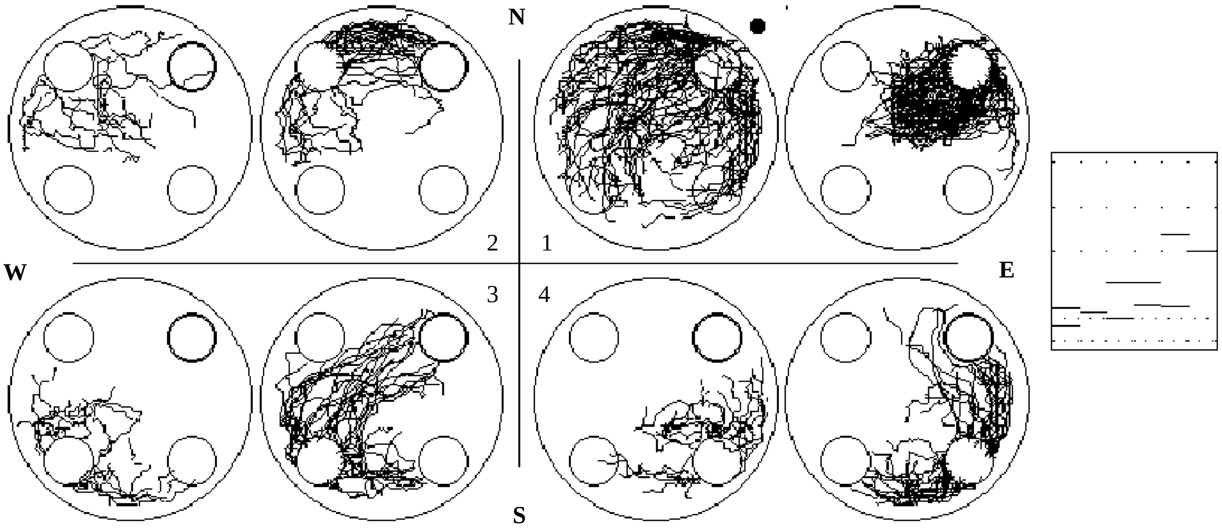

Figure 5. Tracks from an overtrained rat generated during 30 min in the place-preference task. The trigger area was in the northeast quadrant of the arena. Tracks are shown for the 3 s before entering (left maps) and after leaving (right maps) the trigger zone (1) and the equivalent regions in the other quadrants (2–4). The histogram on the right shows the development of the above values in 5 min bins during the course of the 30 min session.

Table 1. *The number of entrances, the approach path length and the time spent in these locations in six subsequent 5 min epochs*

(The percentage column indicates the contribution of the trigger area to the total entries or time. In the path-length section, the percentages indicate the excess of the approach path over the departure path; food deliveries = 94.)

	entrance					path length					time				
No.	1	2	3	4	%	1	2	3	4	%	1	2	3	4	%
1	13	6	4	11	38	33	35	26	25	16	16	5	6	17	36
2	22	8	10	7	47	44	34	24	33	51	16	11	13	10	31
3	16	9	8	11	36	47	32	22	27	66	12	9	11	14	25
4	16	5	6	10	43	50	45	31	20	66	15	5	6	13	39
5	18	3	8	9	47	48	—	14	25	118	20	2	16	15	37
6	19	6	9	7	46	50	—	24	26	100	24	5	9	9	51

preceding annulus entry were compared in the same way. Analogous values were also compared in the 3 s after departure from an annulus.

(*b*) *Results*

After two weeks of shaping, the rats were able to release about 100 pellets per session by entering a circular area 36 cm in diameter. A further two weeks of training were necessary to maintain this performance while gradually decreasing the diameter of the trigger annulus to 20 cm, i.e. to 6.25% of the surface of the arena.

Figure 5 and table 1 are an example from the place-preference task at the asymptotic performance level. During the 30 min trial the rat ran 447 m and obtained 94 pellets. The trigger annulus in the north-east quadrant of the arena was visited 104 times. The maps show the tracks generated in the 3 s preceding and 3 s following each visit of the trigger annulus in the north-east quadrant and in the control annuli. Note that the approach paths to the trigger annulus are longer and the departure paths shorter than those leading to the other annuli. This reveals that goal-directed place navigation generates less tortuous and faster locomotion than the random searching that is characteristic of pellet chasing. As soon as the rat hears the pellet fall, locomotion changes from directed to random. This is why the shortest departure paths correspond to the rat's leaving the trigger annulus. Departure paths from the control annuli are often longer because some of them may overlap with approach paths to the trigger annulus that went through a control annulus.

Figure 6 summarizes the results after four weeks of training. The trigger annulus was visited more frequently (55%) and more time was spent there (58%) than in the other annuli ($F_{3,12} = 82$, $p < 0.001$). The approach paths to the trigger annulus were 56% longer than the departure paths, whereas the departure paths from the control annuli were longer by about 10 % than the corresponding approach paths.

PC recordings during this task should help to reveal how PC mapping is related to the rat's behaviour. Because both the random search trajectories and goal-directed trajectories cover the whole arena, it would be possible to compare place-cell activity during these two modes of locomotion that probably reflect different categories of spatial behaviour. It will also be possible

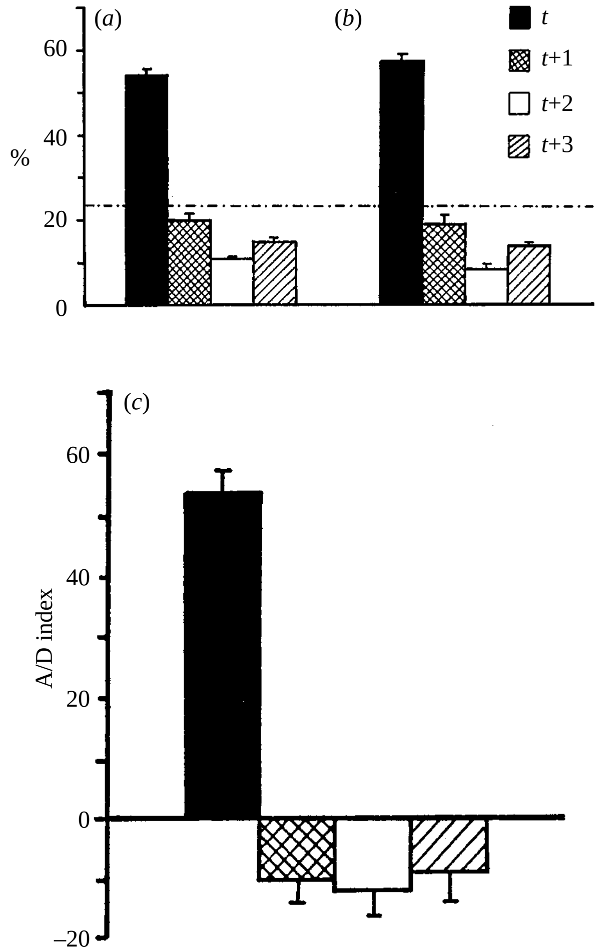

Figure 6. Mean (±s.e.m.) values of the percentage of entries (*a*) and of the time (*b*) spent in each annulus of the arena. *t*, Target annulus; *t*+1 to *t*+3, remaining annuli in an anticlockwise sequence. (*c*) Mean (±s.e.m.) values of the approach/departure (*A*/*D*) index calculated according to the equation $(L_1/L_2 - 1) \times 100$, where L_1 and L_2 are the lengths of the 3 s approach and departure tracks for individual visits to the respective annulus.

to learn how PCs are affected when only exteroceptive (on a rotating arena in the light) or only idiothetic (in darkness) information is useful for finding the location of the trigger annulus.

8. CONCLUSION

Place navigation in a stable environment is implemented by two cooperating memory mechanisms: one dependent on environmental features (referred to as exteroceptive) and the other dependent on proprioceptive and vestibular cues (referred to as idiothetic). Slow rotation of the experimental arena seems to disrupt the correspondence of the two memories and the animal's position becomes ambiguous: the rat cannot be simultaneously at the two different locations, corresponding to an exteroceptively defined fixed position in the room frame and to an idiothetically defined (or intramaze cue-dependent) fixed position in the arena frame. This conflict probably accounts for the disorganization of the FFs of most PCs on the rotating arena. The place-avoidance and place-preference tasks make it possible to create situations that increase the behavioural significance of either source of information on a rotating arena. If PC activity is necessary for spatial cognition, then PCs recorded during place-learning tasks should have FFs depending on the behaviourally relevant spatial orientation input. The alternative is either that spatial cognition can be mediated by extra-hippocampal structures or that the location specificity of PCs does not reflect a map-like representation of space in the hippocampus.

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