A Navigational Guidance System in the Human Brain

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ABSTRACT: Finding your way in large-scale space requires knowing where you currently are and how to get to your goal destination. While much is understood about the neural basis of one’s current position during navigation, surprisingly little is known about how the human brain guides navigation to goals. Computational models argue that specific brain regions support navigational guidance by coding the proximity and direction to the goal, but empirical evidence for such mechanisms is lacking. Here, we scanned subjects with functional magnetic resonance imaging as they navigated to goal destinations in a highly accurate virtual simulation of a real city. Brain activity was then analyzed in combination with metric measures of proximity and direction to goal destinations that were derived from each individual subject’s coordinates at every second of navigation. We found that activity in the medial prefrontal cortex was positively correlated, and activity in a right subicular/entorhinal region was negatively correlated with goal proximity. By contrast, activity in bilateral posterior parietal cortex was correlated with egocentric direction to goals. Our results provide empirical evidence for a navigational guidance system in the human brain, and define more precisely the contribution of these three brain regions to human navigation. In addition, these findings may also have wider implications for how the brain monitors and integrates different types of information in the service of goal-directed behavior in general. © 2007 Wiley-Liss, Inc.

KEY WORDS: navigation; goals; virtual reality; subiculum; medial prefrontal cortex; posterior parietal cortex

INTRODUCTION

The hippocampus is widely held to store or access the spatial representation of an environment and so facilitate navigation to unseen goals (O’Keefe and Nadel, 1978). Compelling evidence for this includes the spatially localized activity of hippocampal place cells that code for an individual’s current position in the environment (O’Keefe, 1976; Ekstrom et al., 2003). While knowledge of current position is clearly crucial, it is not sufficient for effective navigation in large-scale space. The primary purpose of navigation is to reach specific locations or goals. Despite goals being the raison d’être of navigation, we know surprisingly little about how the brain represents goal locations or guides navigation to them.

While hippocampal place cells can show modulation of their spatially localized activity by future goals (Breese et al., 1989; Kobayashi et al., 1997; Frank et al., 2000; Wood et al., 2000; Hollup et al., 2001; Ferbinteanu and Shapiro, 2003; Lee et al., 2006), they do not appear to directly code for goal locations (Speakman and O’Keefe, 1990; Lenck-Santini et al., 2002). Several computational models have instead suggested that brain regions downstream from the hippocampus guide navigation by integrating the spatial information from many hippocampal place cells with additional goal-related information. Two variables in particular have been identified as important, namely the distance to the goal location or goal proximity and the direction to the goal location (Burgess et al., 2000; Trullier and Meyer, 2000; Bilkey and Clearwater, 2005). In these models, goal proximity is coded by maximal activity of neurons at the currently sought goal location, which then decreases as a function of the distance in every direction from the goal, independent of any barriers in the environment. Separate brain regions are thought to signal the egocentric direction to the goal by coding the angle between the current heading direction and the ideal direction to the goal (Burgess et al., 2000).

Despite having detailed predictions about the computational mechanisms guiding navigation, empirical evidence about which brain areas subserve goal location is lacking. It is thought that regions coding goal proximity might integrate spatial information from the hippocampus with reward-related information. Reward-related information has been highlighted, because it might be useful for signaling the importance of goal locations. The subicular region (subiculum and presubiculum), nucleus accumbens, and medial prefrontal cortex (mPFC) have been suggested to code for goal proximity, because they receive both spatial information from the hippocampus and reward-related information via dopaminergic inputs (Kelley and Domesick, 1982; Amaral and Witter, 1989; Jay et al., 1989; Gasbarri et al., 1994). While there is some evidence that the activity of cells in certain regions can be modulated by navigational goals (Jung et al., 1998; Martin and Ono, 2000; Ekstrom et al., 2003), only one study examining the rodent mPFC has found evidence of goal proximity coding (Hok et al., 2005). However, the activity was not selective for the goal being sought, as would be expected of a guidance signal. No evidence of cells coding the egocentric direction to goals has been reported, although the posterior parietal cortex has been implicated because of its known role in egocentric spatial processing (Burgess et al., 2000; Andersen and Buneo, 2002).

In summary, while precise predictions have been made about how the activity in a number of brain regions might code information about goals during...
navigation, no study has directly tested these predictions. Furthermore, very little is known at all about goal coding in the human brain during navigation. Here, we examined directly the neural bases of goal proximity and goal direction in humans during active navigation. We used the video game “The Getaway” (© Sony Computer Entertainment Europe 2002) to present subjects with a highly accurate ground-level first person perspective of a simulation of central London, UK. Subjects’ navigation in virtual London was recorded during functional magnetic resonance imaging (fMRI), and their proximity and direction to goal destinations at every second along every route were calculated. These data were then combined with the fMRI time series, allowing us to establish the brain regions that maintained and updated goal signals during navigation.

**MATERIALS AND METHODS**

**Subjects**

Twenty healthy, right-handed male licensed London taxi drivers participated in the experiment (mean age 49.8 yr, SD 8.5 yr, range: 27–59 yr). Taxi drivers were employed as subjects to ensure consistent and accurate navigation performance. The average time spent working as a licensed taxi driver was 18.3 yr (SD 10.9 yr, range: 1–38 yr). All subjects had lived in London their entire lives or for the vast majority of it, and were naïve to the experimental stimuli. All subjects gave informed written consent to participation, in accordance with the local research ethics committee.

**The Virtual Environment**

The video game The Getaway (© Sony Computer Entertainment Europe 2002) run on a Sony PlayStation2 (© Sony Computer Games) was used to present subjects with a ground-level first person perspective view of a simulation of central London, UK (Fig. 1, and Spiers and Maguire, 2006a for a movie of navigation through the environment). In the game, over ~110 km (~70 miles) of drivable roads have been accurately recreated from Ordinance Survey map data, covering ~50 sq. km (~20 square miles) of the city center. The game designers decided to truly recreate the city, and a large team of photographers walked the streets of central London for 2 yr recording details of the city. Buildings, shops, the one-way systems, working traffic lights, the busy London traffic, and an abundance of Londoners going about their business are all included. The “Free Roaming” mode of the game was used, permitting free navigation with the normal game scenarios suspended. Subjects moved through the environment in a virtual London taxi cab controlled using a modified MRI-compatible game controller, consisting of two joysticks providing analogue control of acceleration, braking, and steering left and right. To avoid constant collisions with other vehicles in the environment, Action Replay Max software (© Datel Design and Development Ltd. 2003) provided a “cheat” modification to the game, permitting subjects to drive through other vehicles if necessary. Subjects were instructed to drive “legally” as they would in actual London. All of the taxi drivers confirmed that the game was very reminiscent of their experience of driving in central London.

**Pre-scan Training and Familiarization**

Two weeks prior to scanning, subjects were given 2 h of practice with the game controls, by asking them to navigate to various locations in areas of the environment not used in the experimental task. To avoid crashes with other vehicles and waiting for long periods at red traffic lights, subjects were familiarized with being able to drive through cars and red traffic lights, but were otherwise required to comply with all other road traffic regulations in the UK. Thirty minutes before the scan subjects were again given further practice in an area not used in experimental tasks. During this practice session subjects were trained to respond to a set of recorded customers’ requests to take them to goal destinations in London. Finally, inside the MRI scanner, the
Subjects were given practice in an area of London not tested in the experimental tasks and with the MRI-compatible game control for between 2 and 3 min prior to the start of the experimental task. They were also given experience of hearing voices of customers over the noise of the scanner through head phones worn during the scan. Prior to scanning subjects were told the locations they would be starting from in the experimental tasks, but not the order.

**Experimental Tasks**

During the fMRI scan, subjects responded to customers’ requests (heard via headphones) by delivering them to their required destinations within virtual London, while driving a London taxi. When the game came on the screen (view angle of 27.6°), subjects were given between 3 and 5 s to orient themselves in the environment. Following this they heard a customer request a destination (mean duration 2.0 s). For all routes, at some point during navigation the subjects heard customers request a change of destination (mean duration 3.0 s). For three of the routes an additional request to avoid a location (one route) or go via a location (two routes) was made by the customer (mean duration 3.7 s). Seven routes were tested (3–6-min duration). Two subjects completed only four routes, in one case due to discomfort, the other due to a technical problem. Each block of navigation ended when either the subject reached the destination or when a predetermined period of time elapsed. Each block of navigation was separated by a period of rest in which the subjects viewed a blank white screen for 60 s. Total mean functional scanning time was 31 min 35 s (SD 4 min 9 s). Subjects’ navigation performance was recorded onto videotape for later analysis.

**Calculation of Goal Proximity and Egocentric Direction to the Goal**

We focused our analysis on goal proximity (shortest linear distance) and egocentric direction to the goal, because models of navigation specifically predict that populations of neurons in particular brain regions would code this information in their firing rate (Burgess et al., 2000; Trullier and Meyer, 2000; Bilkey and Clearwater, 2005). The brain may track other variables during navigation such as the path distance to the goal. However, unlike proximity and direction information, path distance does not provide the means of navigational guidance. People may not choose to take the most direct path to a goal destination, for example, in order to avoid traffic congestion points or road works. Also, in a city like London, path distance is often affected by one-way systems, thus weakening its relationship with goal proximity. This is clearly evident in our task where there were instances on every route, where subjects were in close proximity to the goal (e.g., location B on the route in Fig. 2) but still had a long path ahead of them in order to reach the goal.

Proximity and direction data were derived as follows. Each subject’s navigation performance was analyzed in order to create a record of which street junctions were entered and when they were entered for each route. Information about where and when...
subjects stopped moving or made U-turns was also incorporated into this record. The latitude and longitude of each of the street junctions and stop/U-turn locations (totaling 582 locations) were determined using the program Google Earth (© Google 2005) and converted into Euclidean coordinates corresponding to Northings and Eastings on a transverse Mercator projection using software from DMAP (© Alan Morton). Matlab (© Mathworks) was used to provide a linear interpolation over these coordinates to create an estimate of each subject’s spatial position for every second of every route. A corresponding record of each subject’s goal proximity and egocentric direction to the goal was then calculated from each of these coordinates and the coordinates of the goal locations (Fig. 2).

Goal proximity was calculated by finding the shortest linear distance between a subject’s current location and the goal location, and then rescaling this between 0 and 1, where a value of 1 corresponded to being at the goal and a value of 0 to being at the location furthest from the goal. Customers requested a change in goal destination at some point along each route. The goal coordinates changed to the new goal at that moment on each route. For two of the routes, the subject was also asked to go via a location. These “via” locations were treated as goal locations.

To calculate the egocentric direction to the goal, we first determined the current heading direction and the heading direction pointing to the goal at each location on each route. The current heading direction was determined by finding the phase angle between current location and the location of the subject 1 s later on the route. Because there was no future location for each final location, we assumed the subject was heading in the same direction at the final location as the location occupied 1 s previously. The heading direction pointing to the goal was determined by finding the phase angle between the current location and the goal location. To determine the egocentric direction to the goal, we first subtracted the current heading direction from the heading direction pointing to the goal. In this study, our main focus was on measuring the overall variation in the egocentric direction toward the goal, thus we collapsed across left and right directions. This meant that values greater than 180° were then subtracted from 360° to bring all values into a range between 0° (goal directly in front of the subject) and 180° (goal directly behind the subject).

A measure of the total distance traveled for every second of every route was also calculated to examine the independence of goal proximity and egocentric direction from this additional changing variable. Distance traveled was calculated by initially determining the shortest distance between the current location and the location occupied 1 s previously. This was then added to the sum of the previously calculated distances traveled.

fMRI Image Acquisition and Analysis

T2-weighted echo planar images (EPI) with blood oxygen level dependent contrast were acquired on a 1.5-T Siemens Sonata MRI scanner. We used standard scanning parameters to achieve whole brain coverage: 44 slices, 2 mm thickness (1-mm gap), TR 3.96 s, TE = 50 ms. The first 4 volumes from each session were discarded to allow for T1 equilibration effects. A T1-weighted structural MRI scan was acquired for each subject. Images were analyzed in a standard manner using the statistical parametric mapping software SPM2 (www.fil.ion.ucl.ac.uk/SPM). Spatial preprocessing consisted of realignment, unwarping, normalization to a standard EPI template in MNI space with a resampled voxel size of 3 × 3 × 3 mm³, and smoothing using a gaussian kernel with full width at half maximum of 10 mm. Following preprocessing, statistical analysis was performed using the general linear model. A regressor consisting of events sampled once every second during the navigation periods was specified using a stick function and convolved with the hemodynamic response function. These events were parameterically modulated by two variables of interest: the goal proximity and the direction to the goal, to create regressors of interest. Rest periods were modeled with boxcar functions and auditory events (customer requests), and turning events were modeled with stick functions, and all convolved with the hemodynamic response function to create the regressors of no interest. Second-order parametric modulations (square of the goal proximity and cosine of the direction to the goal) were also modeled as regressors of no interest to account for nonlinear effects. All parametric regressors were orthogonalized with respect to each other within SPM2 (Buchel et al., 1998). Subject-specific parameter estimates pertaining to each regressor (betas) were calculated for each voxel. The parameter estimates were entered into a second-level random-effects analysis using t tests.

We report results in a priori regions of interest at P < 0.001 uncorrected for multiple comparisons, with an extent threshold greater than seven contiguous voxels. A priori regions of interest were based on predictions from models of navigation (Burgess et al., 2000) and previous neuroimaging studies of navigation (Hartley et al., 2003). These included the mPFC (Hartley et al., 2003; Yoshida and Ishii, 2006) the subiculum region (including: subiculum, presubiculum, and parasubiculum, see Duvernoy, 2002), nucleus accumbens, hippocampus (area covering CA1–CA3 and dentate gyrus), and posterior parietal cortex. Activations in other regions are reported if they survive correction for multiple comparisons across the whole brain at P < 0.05.

In order to verify the orthogonality of the current analysis from that previously reported (Spiers and Maguire, 2006a), we expanded the model described earlier by including regressors representing the conditions identified in the previous reported analysis. The same significant results of t-contrasts for goal proximity and egocentric direction to goals were found in this second model, thus confirming the orthogonality of the two research questions. In addition, we also created a model in which the distance traveled was included as a regressor, and another model in which the time periods when the goal was visible were removed from the goal proximity measure. Again similar results of t-contrasts for goal proximity and egocentric direction to goals were found, confirming that our current findings were independent from changes associated with the distance traveled in each route, and seeing the goal (for the latter model, P < 0.005 for mPFC).
In order to plot parameter estimates for different levels of goal proximity (Fig. 3), a new model was created in which goal proximity was modeled by eight regressors. Each regressor reflected \( \frac{1}{8} \) of the total range of goal proximity in steps of 0.125 from 0 to 1. Thus, the first of these regressors reflected changes in goal proximity when the subject was far from the goal, while regressor eight reflected changes in goal proximity when the subject was close to the goal. The same procedure was applied to the egocentric direction to the goal (Fig. 4).

**RESULTS**

**Behavioral**

As expected, all subjects completed the task successfully with 94% (SD 9%) of their routes being efficient. An efficient route was one where the subject moved continually closer to the goal given the constraints of London’s one-way system and occasional obstructed streets that were included in the game. The mean...
speed traveled was 41.9 virtual \( \text{km/h} \) (SD 7.6), and the mean total distance covered was 16.9 virtual \( \text{km} \) (SD 3.4).

Functional Magnetic Resonance Imaging

Aspects of the findings from this rich and flexible data set relating to different questions have been reported elsewhere (Spiers and Maguire, 2006a,b). We now report new analyses focused on the orthogonal issue of goal coding.

Goal Proximity

Details of the brain areas, where activity was significantly correlated with goal proximity, can be found on Table 1 and Figure 3 (see also Fig. 5). Activity in just two brain regions was correlated with goal proximity. A significant positive correlation was observed in the mPFC, and a significant negative correlation was observed in a region extending from the right subiculum to the right entorhinal cortex (EC). No significant positive or negative correlations were observed in the hippocampus or nucleus accumbens even at liberal thresholds \((P < 0.01 \text{ uncorrected})\), or elsewhere in the brain \((P < 0.05 \text{ corrected})\).

Egocentric Direction to the Goal

As with goal proximity, activity correlated positively with goal direction in very specific and focal brain regions, this time in bilateral posterior parietal cortex (see Table 1 and Fig. 4; see also Fig. 5). No negative correlations were observed. As before, no significant positive or negative correlations were observed in the hippocampus or nucleus accumbens even at liberal thresholds \((P < 0.01 \text{ uncorrected})\), or elsewhere in the brain \((P < 0.05 \text{ corrected})\).

Distance and Time Spent Traveling to the Goal

Because driving speed was relatively constant for all subjects, distance traveled to the goal and time to the goal increased linearly within each route. No positive or negative correlations with distance traveled during a route/time spent traveling to the goal were observed in any brain region \((P < 0.05 \text{ corrected})\).

DISCUSSION

In this study we used fMRI and an accurate and interactive VR simulation of a complex real city to explore the brain regions in humans that support navigational guidance. We measured on a second-by-second basis the precise proximity and direction to specific goal destinations. This allowed us to test the prediction

**TABLE 1.**

<table>
<thead>
<tr>
<th>Brain regions</th>
<th>Z-score</th>
<th>x</th>
<th>y</th>
<th>z</th>
</tr>
</thead>
<tbody>
<tr>
<td>Goal proximity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Positive correlation:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Medial prefrontal cortex</td>
<td>3.98</td>
<td>3</td>
<td>30</td>
<td>39</td>
</tr>
<tr>
<td>Negative correlation:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Right subicular/entorhinal region</td>
<td>4.87</td>
<td>21</td>
<td>-18</td>
<td>-36</td>
</tr>
<tr>
<td>Egocentric direction to the goal</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Positive correlation:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Right posterior parietal cortex</td>
<td>3.70</td>
<td>24</td>
<td>-78</td>
<td>51</td>
</tr>
<tr>
<td>Left posterior parietal cortex</td>
<td>3.47</td>
<td>27</td>
<td>-87</td>
<td>36</td>
</tr>
<tr>
<td>Negative correlation:</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>No regions active</td>
<td></td>
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</tbody>
</table>

Activations statistically significant at \(P < 0.001 \text{ uncorrected}\). MNI coordinates are listed (see Materials and Methods, and Fig. 5 for parameter estimates).
from computational models that, during navigation, the relationship to goal locations is continuously tracked by brain regions whose activity encodes either goal proximity (shortest linear distance) or egocentric direction to the goal. Our results revealed that activity in a select set of brain regions codes for goal destinations during navigation. Specifically, activity in the mPFC was positively correlated with goal proximity, while activity in the right subicular/entorhinal region was negatively correlated with goal proximity. By contrast, activity in bilateral posterior parietal cortex was significantly correlated with the egocentric direction to the goal. These results provide evidence for neural signals that could flexibly guide navigation over large distances to specific goals in familiar real world environments.

A Medial Prefrontal Code for Goal Proximity

In contexts other than navigation, the prefrontal cortex is known to play an important role in processing future goals to guide actions (Miller and Cohen, 2001; Genovesio et al., 2006). The medial region in particular is thought to be involved in processing goal-related information when the relationship between our actions and our goals is liable to change (Matsumoto et al., 2003; Matsumoto and Tanaka, 2004). Our finding that mPFC activity correlates with goal proximity during navigation is consistent with this view, since coding goal proximity requires monitoring the spatial relationship between current location and the goal while negotiating obstacles in the environment. In addition, since reaching a goal is likely to be a rewarding experience, this result also accords with the suggestion that the mPFC is important for integrating information about future rewards (Knutson et al., 2005). Our results now show that in the context of goal processing the mPFC can integrate information from long-term memory about the Euclidean distances between locations in a familiar environment.

Several computational models have suggested that a neural code for goal proximity may be used to guide an animal to its goal (Burgess et al., 2000; Trullier and Meyer, 2000; Bilkey and Clearwater, 2005). Our results provide direct empirical support for this prediction and indicate that it is the mPFC which codes goal proximity, responding maximally near the goal. This finding is consistent with the suggestion that the mPFC is important for guiding navigation (Poucet et al., 2004; Hok et al., 2005). Lesions to the mPFC in rodents can impair navigation when behavioral flexibility is required (Lacroix et al., 2002), and cells in the mPFC have been found to code for goal locations during navigation tasks (Jung et al., 1998; Hok et al., 2005). In open environments, these cells appear to have large place fields often peaked at goal locations (Hok et al., 2005). However, whether the cells could provide information aiding navigational guidance was not clear, as they responded whenever the animal was near a goal irrespective of whether that goal was the focus of current navigation or not. Modulation of activity by the current goal of navigation has been observed in cells of the frontal cortex in humans navigating in a VR environment (Ekstrom et al., 2003). However, no evidence of goal proximity coding was observed in the activity of those cells. Our results extend these previous studies by revealing that a neural representation exists in the mPFC, which is both goal-selective and modulated by a spatial proximity code. In addition, our findings shed light on why activity in a similar region of mPFC region may have been observed to be active during previous neuroimaging studies of navigation (Gron et al., 2000; Hartley et al., 2003; Yoshida and Ishii, 2006). Our data suggest that the increased mPFC activity in navigation epochs may have derived in part from the processing of goal proximity.

A Complementary Goal Proximity Code in the Right Subicular/Entorhinal Region

A wide body of evidence indicates that the hippocampal formation is critical for spatial memory and navigation (O’Keefe and Nadel, 1978; Morris et al., 1982; Taube, 1998), but the contribution of different subregions to navigation is not well understood. Several computational models have proposed that goal proximity is coded by the subiculum or presubiculum (Burgess et al., 2000; Trullier and Meyer, 2000). Our observation
that activity in an area encompassing these regions is correlated with the goal proximity supports this proposal. The negative correlation with goal proximity indicates that activity in this region increases with the Euclidean distance from the goal. Such a signal could be used for navigational guidance based on gradient descent, where the navigator moves toward the location in the environment with the lowest firing rate.

The combination of two complementary goal proximity signals, one increasing (mPFC) and the other decreasing (subicular/entorhinal region) with proximity, might provide a more efficient code than a single signal. This is because a single signal increasing with goal proximity would have a low firing rate whenever the animal is at large distances from the goal. Since low firing rates would be more susceptible to interference from background noise (Dayan and Abbott, 2001), such a signal would be poor at guiding navigation at large distances. Conversely, a signal decreasing with goal proximity would be poor at guiding navigation when the animal is near the goal. However, if navigation is guided by both signals, it will be efficient across a whole range of distances.

An alternative explanation for why a negative correlation with goal proximity was observed might be that the subicular/entorhinal region could be sensitive to retrieval demands. In this view, retrieval demands are related to the size of the region to be navigated. Because this might decrease the nearer to the goal, retrieval demands might have a negative relationship with goal proximity. In our study the routes often contained segments where subjects were close to the goal but, because of London’s one-way systems, still had navigate through another substantial region of the city to reach the goal (e.g., location B on the route in Fig. 2). This would mean that during these route segments both retrieval demands and goal proximity would be high, while during other segments one might be low while the other was high. Thus, we believe it unlikely that the subicular/entorhinal finding is due solely to retrieval demands. However, future studies are required aimed specifically at dissociating retrieval demands from goal proximity.

In the present study, the activated area covers both the EC and the subicular region, which may reflect the strong anatomical connections between these regions (Amaral and Witter, 1989) and similar electrophysiological responses (Sharp, 1999). Both regions have been found to signal location in a manner that is less environment-specific than the hippocampus proper (Sharp, 1997, 1999, 2006; Frank et al., 2000). Recently, medial entorhinal cells have been found to code a conjunction of distance, direction, and speed in their firing rate, covering the environment with a grid-like pattern of firing peaks (Hafting et al., 2005; Sargolini et al., 2006). Such information may be important for spatial updating during navigation. Notwithstanding these exciting findings, how entorhinal and subicular representations are related to goal locations has received little attention. Subicular cells have been found to alter their activity during navigation to a goal (Martin and Ono, 2000), but it was not clear what was being encoded by such responses. Our data now suggest that goal proximity might be represented by cells in the subicular/entorhinal region.

The hippocampus and nucleus accumbens were not involved in coding goal proximity. The absence of a correlation with hippocampal activity is consistent with the predictions from computational models (Burgess et al., 2000; Trullier and Meyer, 2000), which suggest that this function is served by other regions. The hippocampus and nucleus accumbens were found to be active specifically during periods of initial route planning in VR London (Spiers and Maguire, 2006a).

**CONCLUSIONS**

These results provide empirical evidence for a navigational guidance system in the human brain. Our findings support and refine computational models, where signals of goal proximity and egocentric direction to the goal are posited to guide navigation. We show that activity in regions of the mPFC and right subicular/entorhinal area are directly linked to a spatial metric. Furthermore, we provide evidence that the posterior parietal cortex can code and monitor egocentric spatial information concerning distant locations beyond current sight during active navigation toward a goal. In summary, our findings reveal that an integrated system comprised of brain areas with complementary responses allows us to adapt to challenges in the environment in order to reach our goals.

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