Thoughts, behaviour, and brain dynamics during navigation in the real world

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How does the human brain allow us to interact with and navigate through a constantly changing world? Whilst controlled experiments using functional brain imaging can give insightful snapshots of neuronal responses to relatively simplified stimuli, they cannot hope to mirror the challenges faced by the brain in the real world. However, trying to study the brain mechanisms supporting daily living represents a huge challenge. By combining functional neuroimaging, an accurate interactive virtual simulation of a bustling central London (UK), and a novel means of 'reading' participants' thoughts whilst they moved around the city, we ascertained the online neural correlates underpinning navigation in this real-world context. A complex choreography of neural dynamics was revealed comprising focal and distributed, transient and sustained brain activity. Our results provide new insights into the specific roles of individual brain areas, in particular the hippocampus, retrosplenial, and frontal cortices, as well as offering clues about how functional specialisations operate within dynamic brain systems.
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Introduction

How the human brain processes the continuous and highly complex inputs from the external world to produce a seamless reality and an integrated sense of who and where we are remains a fundamental mystery in neuroscience. Whilst controlled experiments can give snapshots of neuronal responses to simplified stimuli, they cannot hope to mirror the challenges faced by the brain in the real world (Burgess et al., 2002; Hasson et al., 2004). Thus, several recent functional magnetic resonance imaging (fMRI) studies have examined brain activity elicited by viewing more naturalistic stimuli, such as Hollywood movies (Bartels and Zeki, 2004; Hasson et al., 2004; Zacks et al., 2001). Analyses using subsequent ratings of various attribute intensities (Bartels and Zeki, 2004), subsequent classification of event boundaries (Zacks et al., 2001), or events detected from the BOLD signal itself (Hasson et al., 2004) enabled the segregation of neural activity linked to specific events within the overall continuous stream of complex naturalistic stimulation. Whilst studies such as these are starting to provide clues about how functional specialisations might operate within dynamic brain systems, a fundamental limitation remains. Passively watching a movie is substantially different from most of our everyday activities that involve engaging interactively with the world around us. However, trying to ascertain the 'online' neural correlates of functioning in the real world represents a huge challenge.

One field where attempts have been made is in relation to arguably the most ubiquitous of our everyday activities, navigation. Previous functional neuroimaging studies using interactive virtual reality (VR) environments have identified a distributed network of brain regions engaged during active navigation including the hippocampus, parahippocampus, caudate nucleus, parietal and retrosplenial cortices, and regions within prefrontal cortex (PFC) (Aguirre et al., 1996; Ekstrom et al., 2003; Gron et al., 2000; Hartley et al., 2003; Maguire et al., 1998; Shelton and Gabrieli, 2002; Voermans et al., 2004). The functional role of some of these structures has been probed further by correlating their activity with measures such as navigational accuracy, typically averaged over epochs of 30–60 s (Hartley et al., 2003; Maguire et al., 1998). However, even in these experiments with more naturalistic interactive settings, unitary temporally gross measures fail to capture the multi-faceted and highly dynamic operation of the human navigation system.

We set out to extend the previous passive, and the temporally insensitive studies by integrating three factors (see below) in a novel way in the context of fMRI. We chose to focus on navigation, a prime example of the human brain operating in a real-world context. Our approach permitted a remarkably detailed characterisation of the unfolding navigation process that has eluded previous studies. Accompanying this, we were able to pinpoint the transient and highly specific engagement and disengagement of particular brain regions, such as the hippocampus, revealing the choreography of neural dynamics underlying this complex behaviour, whilst also providing new insights into the function of individual brain areas.

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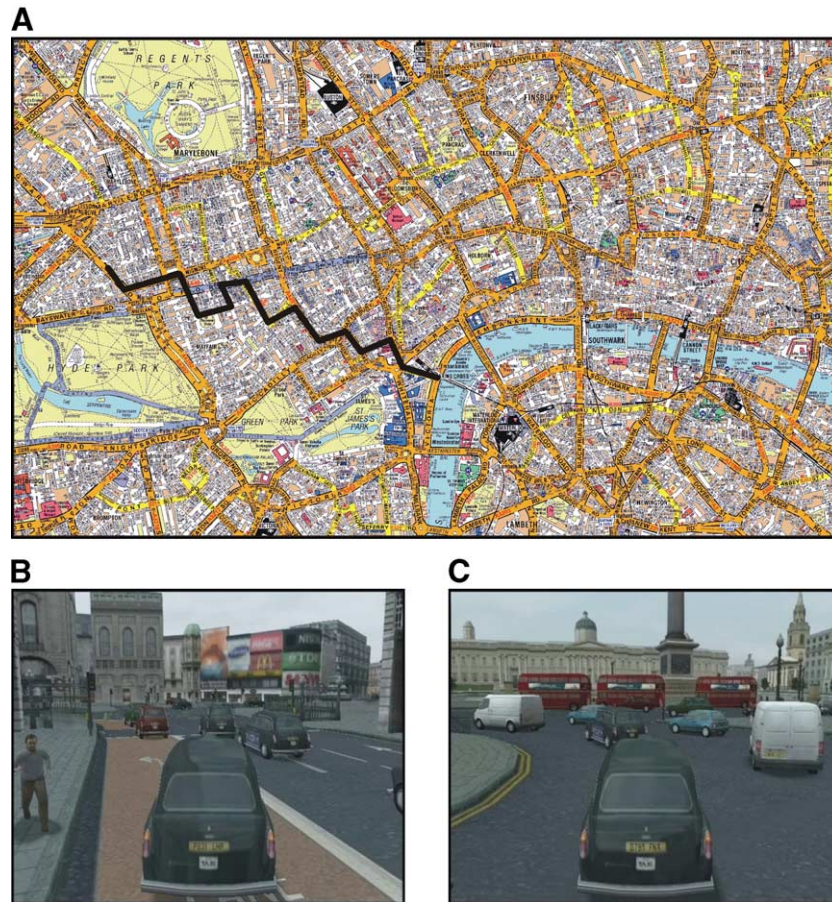**Available online on ScienceDirect (www.sciencedirect.com).**

Fig. 1. Panel A shows the area of London simulated (not all the minor streets shown were included), with an example route overlaid. Reproduced by permission of Geographers' A–Z Map Co. Ltd. © Crown Copyright 2005. All rights reserved. License number 100017302. Panels B and C show example views from within the video game "The Getaway" © 2002 Sony Computer Entertainment Europe. Panel B shows a view at Piccadilly Circus, panel C shows a view at Trafalgar Square. These images are reproduced with the kind permission of Sony Computer Entertainment Europe. See also Movie 1, Appendix C.

The first key factor required for this approach is a truly realistic context in which behaviour can occur. Although VR is now in common use in cognitive neuroscience, even the best environments have a somewhat deserted, stark, and simplistic quality (Ekstrom et al., 2003; Gron et al., 2000; Hartley et al., 2003; Iaria et al., 2003; Maguire et al., 1998; Shelton and Gabrieli, 2002; Voermans et al., 2004; Wolbers and Buchel, 2005). By contrast, we identified a commercially available video game that overcame these constraints. 'The Getaway' (© Sony Computer Entertainment Europe) is set in London (UK). Over 110 km (70 miles) of drivable roads have been accurately recreated from Ordinance Survey map data, covering 50 km^2 (20 square miles) of the city centre. The one-way systems, working traffic lights, the busy London traffic, and an abundance of Londoners going about their business are all

included (see Fig. 1 and Movie 1, Appendix C). Conveniently, one can simply navigate freely around the city using the game console, with a normal ground-level first person perspective, in a car of one's choice.

The second vital ingredient in our experiment was the choice of subjects. Navigation ability is variable (Maguire et al., 2003), particularly in a large city. Thus, in order to ensure a consistent and accurate level of performance as a platform for our analyses, licensed London taxi drivers participated. In London (UK), taxi drivers engage in extensive training and have to pass examinations set by the Public Carriage Office in order to obtain a license to operate.

The third, and most crucial element of the study was the means by which we 'read the thoughts' of subjects as they navigated in
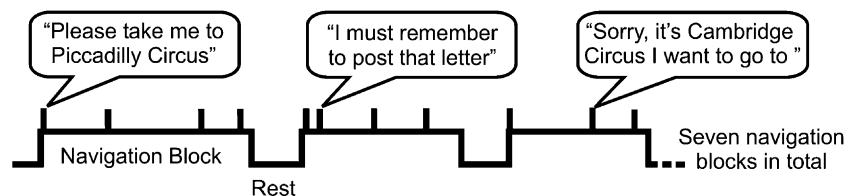

Fig. 2. A schematic illustration of the task structure. Navigation blocks were 3–6 min in length. During 1 min rest periods, subjects were presented with a blank screen. Speech callouts provide examples of customers' initial requests, irrelevant statements, and requests for a change in destination. Seven blocks were tested in total (see Materials and methods for more details).

London. We achieved this in the following way. During the fMRI scan, subjects responded to customers' requests (heard via headphones) by delivering them to their required destinations within virtual London, whilst driving a London taxi. They also heard customers make navigationally irrelevant statements, and request new destinations en route (see Materials and methods and Fig. 2). Subjects' navigation performance during scanning was recorded onto video tape. Immediately postscan, and without prior warning, subjects watched the video replay of their performance and were interviewed using a verbal report protocol (Ericsson and Simon, 1980). Simply put, this involved getting subjects to review their performance and report on what they had been thinking whilst they had been doing the task in the scanner. If carried out in a stringent manner and with a pre-established protocol (ours was established from piloting with taxi drivers), verbal reports can give remarkable access to cognition (Ericsson and Simon, 1980; Jack and Roepstorff, 2003). Our plan was to analyse the transcribed thoughts of the subjects and use this to model every second of the fMRI time series (see Appendix A). During scanning, subjects' eye movements were also recorded. The veridicality of the verbal reports was further tested using these independent eye-tracking data.

Materials and methods

Participants

Twenty healthy right-handed male licensed London taxi drivers participated in the experiment (mean age 49.8 years, SD 8.5 years, range: 27–59 years). The average time spent working as a licensed taxi driver was 18.3 years (SD 10.9 years, range: 1–38 years). All had either lived in London their entire lives or for the vast majority of it and were naive to the stimuli used in the experiment. All subjects gave informed written consent 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 Inc.) was used to present subjects with a ground-level first person perspective view of a simulation of central London (see Fig. 1 for still pictures from the game, and Movie 1, Appendix C for example of navigation in the game). The game designers decided to truly recreate the city and a large team of photographers walked the streets of central London for 2 years recording many streets, shops, and other details. The area covered in the game (see Fig. 1) stretches from Hyde Park in the west to Shoreditch and Bethnal Green in the east; from the Angel in the north to Lambeth Bridge in the south. There are no readable street signs in the game, so one has to rely on extant knowledge to navigate. Breaking all speed limits and ignoring all red traffic lights, it takes 15 min to travel between the furthest points east to west. All of the taxi drivers confirmed that the game was very reminiscent of their experience of navigating in central London. Subjects moved through the environment by controlling a virtual taxi cab using a modified MRI-compatible game controller, consisting of two joysticks providing analogue control of acceleration, braking, and steering left and right. Subjects were instructed to navigate 'legally' as they would in actual London. The 'Free Roaming' mode of the game was used, permitting free navigation with the normal game scenarios suspended. 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.

Prescan training and familiarisation

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 environment not used in the experimental task. To avoid crashes with other vehicles and waiting for long periods at red traffic lights, subjects were familiarised 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 destinations in London. They also heard navigationally irrelevant statements which they had to listen to carefully but did not need to respond to. 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 headphones 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 fMRI scanning, navigation was tested in blocks where subjects responded to customers' requests (heard via headphones) by delivering them to their destinations. During each block, one route was tested. The routes were (in order): Kings Cross to the Middlesex Hospital (initially to Guy's Hospital), Trafalgar Square to the Royal Courts of Justice (initially to the Old Bailey), St. Giles Circus to Peter Street in Soho (initially to Paddington Station), St. Martin's Place to Leicester Square (initially to Covent Garden), Piccadilly Circus to Leicester Square (initially to St. James's Square), Buckingham Palace to the American Embassy (initially to Sheperd Market), and the American Embassy to Cavendish Square (initially to Manchester Square). When the game came on the screen, 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) and on a separate occasion make a navigationally irrelevant statement (mean duration 2.0 s). The latter were played when the experimenters thought that subjects were most likely to be engaged in a period of 'coasting'. This was later confirmed to be the case in the verbal reports. For three of the routes, an additional request to avoid a location or go via a location was made by the customer (mean duration 3.7 s). Requests for a change of destination or requests to go via another location occurred at time points that varied along each route and were unknown to the subject but predetermined by the experimenters. Seven routes were tested. Two subjects completed only four routes, in one case due to discomfort, the other due to a technical problem. The first route began after the collection of the first four dummy scans. Each block of navigation ended when either the subject

reached the destination or when a predetermined period of time elapsed. The maximum time taken to get to each of the routes was between 3 and 6 min (mean 3.8 min SD 1.1 min). 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).

Video recording

In order to debrief subjects and create an independent record of eye-tracking, two videos were recorded during the scan. Video output from the Playstation2 was split three ways: (1) to a projector presenting stimuli in the MRI scanner (view angle of 27.6 degrees), (2) to a VHS video recorder for debriefing, (3) to a video mixer to create an eye-tracking video. Video output going into the video mixer was mixed with camera footage of the scan console and a stopwatch manually synchronised with the time stamp on debriefing video. By noting the time on the stopwatch when the scanner finished, it was possible to convert the time in the debriefing video into time from the onset of scanning. Gaze position cross hairs collected via an ASL504LRO infra red eye-tracker (Applied Science Laboratories, Bedford, MA) were overlaid onto the video sent to the mixed video recording in 14 subjects. Accurately calibrated eye-gaze tracking was achieved in nine subjects.

Verbal report protocol

Immediately postscan, the subjects were taken from the scan room to a separate room where they were given a surprise debriefing with a verbal report protocol (Ericsson and Simon, 1980). In this debriefing, subjects watched the video of their performance during scanning. They were carefully instructed to describe what they remembered thinking, step-by-step, during their original performance. The interview proceeded at a pace determined by the subject, with the video being paused and rewound by the interviewer where necessary to capture the details provided by the subject. A new copy of the original video was recorded during the interview with the voices of the subject and interviewer collected by a microphone overlaid. In accordance with the methods described by Ericsson and Simon (1980) and others (Jack and Roepstorff, 2003), the interviewer followed a predetermined protocol during the interview. The subject's report was interrupted as little as possible, the interviewer intervening only to improve the subject's specification of the onset and duration of thoughts where possible, and on occasion where clarification was required to latter aid analysis. The mean duration of the collection of the verbal reports was 108.9 min (SD 16.9 min).

Analysis of the verbal reports

Anonymised audio information from the verbal report interviews was transcribed by a professional transcription agency, who was blind to the purpose of the experiment. By comparing the transcript with the time stamp from the original performance video, information about the timing of the thoughts was incorporated into the transcripts and any errors or unclear statements rectified. Each statement in the transcript was then classified into one of a set of categories (see Table 1), and its onset and duration recorded to create a segmented timeline of the

subject's experiences in order to model the fMRI data. Unambiguous categories were predetermined by analysis of common repeated statements in the verbal reports of four subjects who took part in an in-depth pilot study outside of the scanner. The pilot study also served to create a guide to aid classification and generate a protocol for the verbal report collection. The independent eye-tracking video was used to aid the identification of onsets and durations where the subjects reported looking at a feature in the environment, and served as an external measure to validate the procedure. For each report of looking at a feature in the environment, the eye-tracking video corresponding to that time point was examined to determine when, to the nearest second, a saccade to the feature was made and how long fixation of the feature occurred in seconds. Of note, it is not just taxi drivers who were able to produce such detailed retrospective verbal reports. Several non-taxi driver subjects who navigated in the game through areas of the city they were familiar with were able to produce reports as accurate as those of the taxi drivers.

fMRI image acquisition and analysis

T2-weighted echo planar (EPI) images with BOLD (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 analysed in a standard manner using the statistical parametric mapping software SPM2 (http://www.fil.ion.ucl.ac.uk/SPM). Spatial preprocessing consisted of realignment, unwarping, normalisation to a standard EPI template in MNI space with a resampled voxel size of $3 \times 3 \times 3$ mm, 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. We used coasting as the baseline to which we compared each of the other categories (see Table 1). Since we wished to compare categories represented as events and categories represented as epochs to coasting, two separate models were created. In one model, coasting was modelled as epochs (mean duration 15.0 s, SD 2.6 s), and in the other as events. The coasting events were specified at the middle of each period of coasting rather than at the start or end to avoid temporal correlation of the other events/epochs in the other categories. In both models, categories consisting of epochs were modelled with a boxcar function (duration determined by the subject's verbal report) and categories consisting of events were modelled with a stick function. These functions were then convolved with the canonical haemodynamic response function to create regressors of interest. For the three categories modelled as epochs, the mean durations were: expectation = 9.6 s (SD = 2.2 s), visual inspection = 17.2 s, (SD = 8.5), and monitoring traffic = 6.4 s (SD = 1.7 s). Turning (left and right combined, mean number of events = 77.0, SD 13.5) and rest periods were convolved with the canonical haemodynamic response function to create regressors of no interest. Within each model, the 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

Table 1
Category definitions and their mean number of occurrences

Category	Definition	Mean number of occurrences (SD)
Customer-driven Route Planning	Planning a route to a given destination	16.6 (1.8)
Subtypes: Initial plan	Planning from the initial request	6.8 (0.8)
Change in plan	Planning after an en route request from a customer to alter the destination	9.8 (1.0)
Spontaneous Route Planning	Further planning en route, independent of customers	34.3 (10.9)
Subtypes: Filling in	Planning the next stage of the journey	17.7 (6.6)
Re-planning	Altering the current plan to adapt to the environment	16.7 (5.7)
Action Planning	Planning future movements with the vehicle	45.8 (15.1)
Expectation Confirmation	Detecting the presence of an expected environmental feature	28.6 (9.9)
Expectation Violation	Detecting the absence of an expected environmental feature	31.6 (10.5)
Expectation	Looking out for the next expected environmental feature	24.5 (8.5)
Visual Inspection	Visual inspection of an environmental feature	36.0 (11.8)
Monitoring Traffic	Watching moving traffic in the environment	11.4 (5.9)
Coasting	Navigating automatically without any directed thoughts	25.8 (7.5)
Customers' Navigationally-Irrelevant Statements	Navigationally-irrelevant statements by customers, (a control for Customer-driven Route Planning)	6.6 (0.9)

The categories listed were used to model the fMRI time series. SD = standard deviation. The order of the categories in the table does not indicate their order of occurrence in the task. See Appendix A for example of classified extracts taken from a subject's report. The categories were sufficiently uncorrelated in the time series to model them as separate regressors. Other less frequent categories of thought were identified but did not occur in every subject and did not co-occur consistently with any category modelled. Examples include theory of mind, emotions, spontaneous recollection, regret, and logical reasoning. Importantly, the infrequent spontaneous recollection did not co-occur with route planning.

threshold of >5 contiguous voxels. These regions were identified from previous neuroimaging studies of spatial navigation (Burgess et al., 2002; Hartley et al., 2003) and form the basis of our discussion and interpretation of the data. For completeness in our result tables, we also report other areas active at the same threshold of $P < 0.001$ uncorrected for multiple comparisons; however, these later activations should be interpreted with caution.

Results

How does navigation unfold in a real city?

The first question is whether subjects could review the video of their navigation performance postscan and provide information on what they had been thinking during the scan. Subjects were able to produce staggeringly detailed accounts of what they had been thinking during navigation. There was a high degree of consistency in the types of thoughts across the 20 subjects. Reviewing the transcriptions of all subjects, and aided by a classification guide developed during the piloting phase, 12,484 events or epochs were classified into distinct categories (see Appendix A). Sufficient event/epoch numbers of nine core navigational categories present in every subject were obtained and found to be suitably uncorrelated for statistical analysis (see Table 1). Not only was the level of detail in the retrospective verbal reports unprecedented, subjects reviewing the video of their navigation performance were quite clear about when exactly they had experienced particular thoughts. This enabled a complete specification of the fMRI time series in terms of onsets and durations of event/epochs (see Fig. 3A and Appendix A for details). The precision of the timings was further tested using the independent eye-tracking data acquired during the scan. In those subjects with accurate calibration, 94% (SD 6%) of reports of looking at a feature in virtual London whilst navigating, were corroborated by a saccade to its location at (or very near, ±2 s) the time retrospectively reported.

Previous psychological, environmental, and neuroscientific studies have focussed on many aspects of the navigation process in humans (Ekstrom et al., 2003; Golledge, 1999; Hartley et al., 2003; Maguire et al., 1998; Passini, 1984; Shelton and Gabrieli, 2002; Voermans et al., 2004), but surprisingly, no analysis of the core components of the navigation experience exists. We now provide a detailed breakdown of how navigation unfolds in a familiar city (see Table 1). We initially plan our route to a destination; en route we often see an opportunity to adjust our plan. Sometimes we plan our route only to an intermediate point and once reached, we then fill in the rest of the route plan. Often within a familiar environment, we are almost on automatic pilot, 'coasting' along without thinking. We also set up expectations, waiting to see a certain landmark to check if we are on the right track, occasionally inspecting the city around us as we travel through it. We monitor the surrounding traffic to achieve safe passage to our destination, and have to be able to plan our own actions, stay in a traffic lane, change lanes, and so forth. It is notable how recognisable the above aspects are to our everyday experience of urban navigation, and yet many of them have gone largely undocumented. What one truly appreciates from the retrospective verbal reports is how, second-by-second, the underlying cognition can dramatically change, and that a substantial amount of the thinking behind navigation in large-scale space is in fact not particularly spatial.

Do these diverse categories within navigation have distinct neural correlates?

The fMRI time series were modelled in terms of the categories described in Table 1, as deduced from the verbal reports (see Materials and methods and Appendix A). The condition coasting, where subjects reported navigating almost automatically without directed thoughts, was used as the baseline condition to which we compared the other navigation categories. Thus, we were able to discern what brain areas were engaged over and above those associated with basic factors such as movement in virtual London,
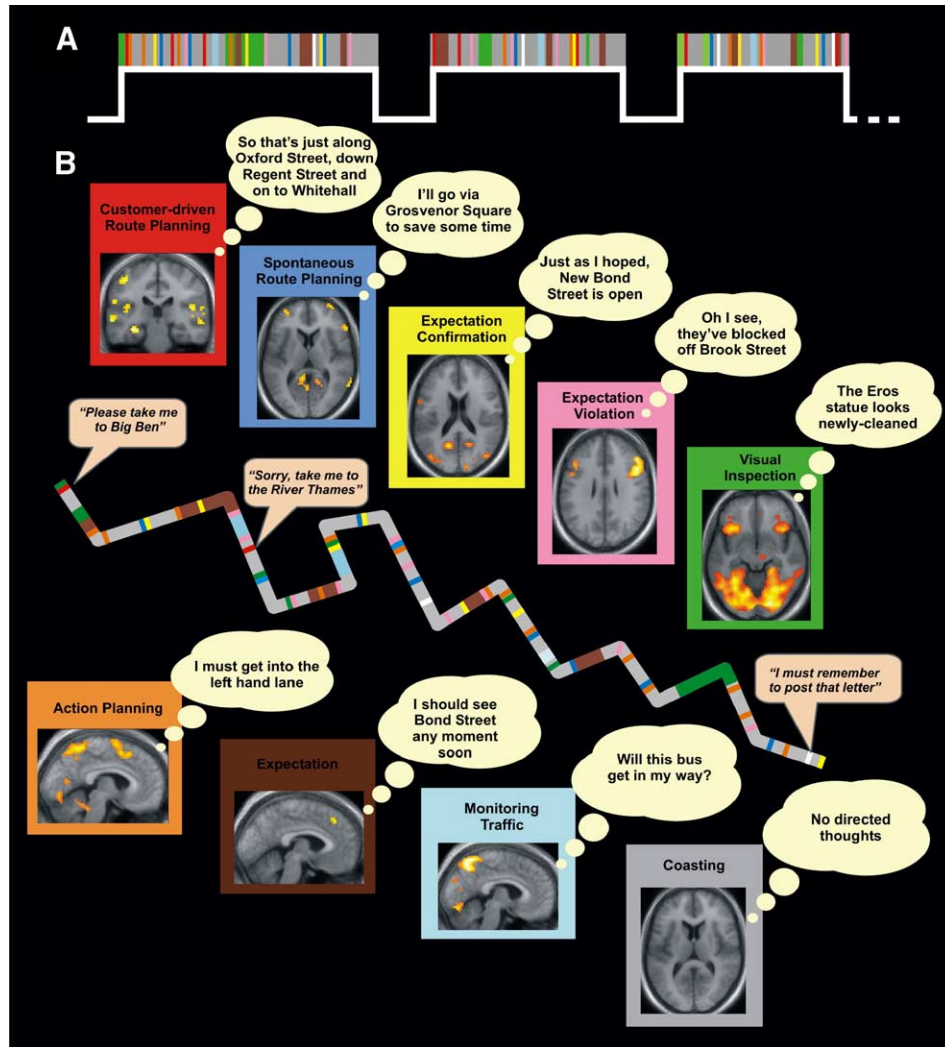
Fig. 3. Panel A shows a schematic example of an fMRI time series after classification of a verbal report, with the time series segregated into different events and epochs corresponding to the different categories present. Each subject's time series was unique. Panel B shows a cartoon of the route shown in Fig. 1A classified into a sequence of events and epochs of the different categories extracted from a verbal report. Routes chosen by the subjects were efficient, with the majority of destinations reached. Speech callouts provide illustrative examples of auditory presentations of customers' requests and statements. On either side of the route are shown the results of the statistical comparison of the brain activity in each category with the category coasting. Customer-driven route planning was compared with the response to customers' navigationally irrelevant statements. See Table 1 for definitions. Thought bubbles provide illustrative examples of thoughts described by subjects (see Appendix A for further examples from a subject). Examples of significantly active regions (*P* < 0.001 uncorrected for multiple comparisons) are shown overlaid on the mean structural scan of the 20 subjects and include: Customer-driven Route Planning: left hippocampus; Spontaneous Route Planning: anterior prefrontal cortex, retrosplenial cortex; Action Planning: precuneus, pre-SMA, cerebellum; Visual Inspection: cuneus to parahippocampal cortex, anterior insula/ventrolateral prefrontal cortex; Expectation Confirmation: retrosplenial cortex, middle occipital gyrus; Expectation Violation: right lateral prefrontal cortex; Expectation: dorsomedial prefrontal cortex; Monitoring Traffic: precuneus; Coasting: no regions more active than the mean activity. For full details of peak activations, see Appendix B: Tables B1–B9. See Movie 1, Appendix C for a dynamic presentation of the neuroimaging data along side footage of navigation through the environment.

visual stimulation, optic flow, and use of the games console that were also present during coasting. Relative to the session mean coasting was not associated with any significant activation in any brain region.

Remarkably, the thoughts that unfolded during navigation in London were associated with clearly distinct patterns of brain activity (see Fig. 3B, Movie 1 (Appendix C), and Appendix B: Tables B1–B14 for details of peak activations). The initial few seconds of route planning following specification of the goal destination by the customers were associated with increased activity in the right and left hippocampi, and other areas including left parahippocampal cortex, bilateral retrosplenial cortex, superior

and middle temporal gyri, and lateral and medial PFC. Interestingly, when subjects spontaneously decided to alter their route during navigation, the hippocampus did not activate, but rather several areas of prefrontal cortex, right parietal, and retrosplenial cortices were then engaged. In fact, the hippocampus was not significantly active during any other aspect of navigation besides customer-driven route planning to new destinations. Thus, we appear to have isolated a very specific and temporally discrete role for the human hippocampus in real-world navigation (considered in more detail below).

Navigation relies enormously on extracting useful visual information from the environment. During periods of general

visual inspection of fixed city features, there was activation of an expansive region running from posterior occipital cortex through the retrosplenial cortex to the parahippocampal cortex ventrally, to posterior parietal cortex dorsally, as well as activity in the dorsomedial, ventrolateral, lateral, and anterior prefrontal cortices. However, when observation was directed to moving entities, such as monitoring traffic, a more focal set of regions was involved comprising superior parietal cortex and precuneus. Interestingly, in contrast to observing the actions of other traffic, subjects' planning of their own actions (e.g. I need to turn left, change lane) activated pre-SMA, cerebellum, lateral occipital, superior parietal cortices, and precuneus.

Subjects also purposefully engaged the environment by setting up expectations about certain features they were waiting to see as they navigated. These expectations were associated with dorsomedial PFC, right anterior insula/ventrolateral PFC activity. Confirmation of expectations was associated with greater activity in the retrosplenial cortex, posterior occipital cortex, and posterior parietal cortex. However, expectations are sometimes violated when, for example, a route is blocked unexpectedly. On these occasions, a very different set of regions was recruited, namely the right lateral PFC, right parietal cortex, and anterior insula/ventrolateral PFC.

Route planning and the hippocampus

The hippocampus has long been associated with navigation in both animals and humans (Burgess et al., 2002; O'Keefe and Nadel, 1978). Having observed its engagement by customer-driven route planning but not spontaneous route planning, we sought to examine this in more depth (see Fig. 4 and Appendix B: Tables B9–B14 for full details). We first compared the route planning associated with customers' requests with the navigationally irrelevant comments of the customers, thus controlling for auditory and language processing. There was significantly increased activity in the left hippocampus, left parahippocampus, nucleus accumbens, bilateral retrosplenial cortex, posterior parietal cortex, dorsolateral, and ventrolateral PFC for customer-driven route planning compared with customers' irrelevant statements. We further investigated whether there were greater responses elicited during route planning to initial requests than to customers' requests for new destinations that occurred during navigation. Significantly greater activity was found in the nucleus accumbens, cuneus, fusiform, and ventral PFC for initial requests, but there was no statistical difference in terms of hippocampal activation. This confirms that the left hippocampus responds to the need to plan routes to new destinations at any point in the navigation process.

Direct comparison of customer-driven route planning and spontaneous route planning showed that the former indeed involved the left hippocampus compared with the latter. Further scrutiny of spontaneous route planning showed that it comprised two different subcategories, one where subjects reached an intermediate point in a route and then planned the next part in more detail, and another where they saw a previously unforeseen opportunity or found their path blocked and decided to alter the current route plan. When compared with each other, no hippocampal activations were apparent, and when either was compared with customer-driven route planning, the left hippocampus was more active for customer requests. To identify brain areas active in common for customer-driven route planning and spontaneous route planning, we performed a conjunction analysis which tested the conjunction of the comparisons of customer-driven route planning with the
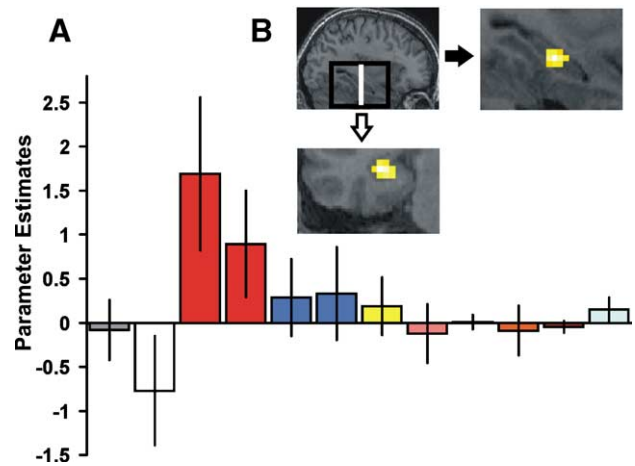

Fig. 4. Panel A shows the parameter estimates (betas) of the response in the left hippocampus ($x = -33$, $y = -27$, $z = -18$) in arbitrary units for each category (and subcategories) averaged across subjects relative to the session mean. The location was determined from an F contrast of all conditions of interest. Error bars are the 90% confidence intervals. Conditions from left to right are (1) coasting, (2) response to customer's irrelevant statements, (3) customer-driven route planning (initial goal), (4) customer-driven route planning (switch to new goal), (5) spontaneous route planning (replanning), (6) spontaneous route planning (filling-in), (7) expectation confirmation, (8) expectation violation, (9) visual inspection, (10) action planning, (11) expectation, (12) monitoring traffic. For clarity, only the parameter estimate for coasting sampled as events is shown. Coasting sampled from blocks in the epoch model resulted in a similar parameter estimate value. Panel B shows the left hippocampal activation for the comparison of customer-driven route planning (both initial and switch to a new goal) versus responding to customers' irrelevant statements overlaid on the structural of a randomly chosen subject. Threshold set at $P < 0.001$, uncorrected. See Appendix B: Table B9 for peak coordinates and Movie 1, Appendix C for a horizontal section.

navigationally irrelevant comments of the customers and the spontaneous route planning with the coasting events. This revealed dorsomedial PFC and retrosplenial cortex, but not the hippocampus.

Whilst the left and right hippocampi were active for customer-driver route planning compared with coasting, comparison with customers' irrelevant statements resulted in only a left hippocampal increase for route planning. Interestingly, comparison of the navigationally irrelevant customers' statements with coasting showed increased activity in the right hippocampus for the irrelevant statements. Thus, aspects of both route planning and hearing occasional snatches of a customer's conversation elicited response from the right hippocampus. By contrast, the left hippocampus was very specifically engaged by the temporally discrete planning of routes to specified goals. Route planning-related hippocampal activity, both right and left, peaked in the mid-posterior portion of the hippocampi, consistent with the idea that this region is particularly important for spatial memory (Maguire et al., 1998, 2000; Moser and Moser, 1998). The right hippocampal response to random customer remarks was more anterior, perhaps reflecting a type of oddball or novelty response (Strange and Dolan, 2001).

Discussion

In this study, we have explored the second-by-second nature of human thought processes and their underlying brain dynamics

during the interactive experience of navigating the city of London. Against a background of general visual, motor, and attentional processing, we observed a complex choreography of neural responses comprising focal and distributed, transient, and sustained brain activity, which fluctuated depending on specific circumstances and priorities. This fine-grained temporal characterisation of the unfolding navigation process permits new insights into the roles of specific brain regions that were inaccessible to previous studies with temporally gross unitary performance measures and less realistic VR environments.

We first consider the role of the hippocampus. Whilst previous neuroimaging studies have implicated the hippocampus in navigation (Ghaem et al., 1997; Gron et al., 2000; Hartley et al., 2003; Maguire et al., 1998; Voermans et al., 2004), none has sought to determine its precise role within the context of ongoing navigation in a familiar and real city. Here we provide new evidence that speaks directly to two questions: firstly, when might the hippocampus be most required during a period of navigation; secondly, which processes might it be most required for? We extend previous findings by showing that the hippocampal role in navigation seems to be primarily in facilitating the planning of routes to specified goals. Moreover, its engagement is brief, with increased activity occurring only when planning a route to a new destination, but not when further consideration of or alteration to the already specified route is made. Our finding is consistent with a view that during goal-specified route planning, the hippocampus activates, or retrieves from elsewhere, the information relating to the relevant region of space to be navigated from a stored cognitive map of the environment. Throughout the subsequent navigation, the relevant allocentric spatial information is available to the hippocampus and other neural structures, and no increased processing demands are made of the hippocampus unless a change in destination is made and the activation or retrieval of new information necessitated. Thus, spontaneous replanning or filling-in the next stage of the journey requires the manipulation of information held in a currently active representation and not the retrieval of additional spatial information, and so no increase in hippocampal activity is apparent. By contrast, our results seem to refute notions that activity in the hippocampus provides an unmodulated and tonically active signal throughout navigation.

Several computational models also provide some suggestions as to when increased activity in the hippocampal region during navigation might be expected (Banquet et al., 2005; Burgess and O'Keefe, 1996; Howard et al., 2005; Koene et al., 2003; Sharp et al., 1996; Touretzky and Redish, 1996; Trullier and Meyer, 2000; Voicu, 2003). These models commonly propose that the hippocampus, or a down stream output region, provides a heading vector to the goal location within an allocentric representation of the environment. It has also been suggested that activity in hippocampus and associated regions changes as the navigator moves closer to their goal or as the navigator optimises their current heading with respect to the goal (e.g. Burgess and O'Keefe, 1996). Thus, generating the initial vector, updating the most efficient route, and observing landmarks to update the current vector to the goal, might all be likely candidates to show increased activity in the hippocampus. Whilst the first prediction is borne out by the current results, the latter two are not. Thus, our results provide an empirical basis from which models of hippocampal processing might be refined.

Of note also in relation to the hippocampus, even though the subjects had been navigating in the city for more than 18 years on average, the hippocampus was nevertheless active, suggesting that environments learned long ago and used over many years still engage the hippocampus (Rosenbaum et al., 2000; Teng and Squire, 1999). The temporally discrete activity of the hippocampus also speaks against the hippocampal response in this study merely reflecting episodic encoding of the experience of navigating, as this would have resulted in sustained activation throughout.

Heavily interconnected with the hippocampal region, the retrosplenial cortex is one of the most often-activated brain areas in fMRI studies of both memory and navigation (Maguire, 2001). Given this prevalence, it is surprising that previous neuroimaging studies have failed to dissociate its function within navigation, making its precise role difficult to determine (Gron et al., 2000; Hartley et al., 2003; Maguire et al., 1998). Here we found that when navigating in the real world, the retrosplenial cortex was most active when planning a new route, but unlike the hippocampus, showed increased activity during spontaneous route planning, expectation confirmation, expectation violation, and sustained activity during periods of inspecting the environment. Thus, rather than being engaged throughout the process of navigation, its activity was increased when topographical representations needed to be updated, integrated, or manipulated for route planning, or when new topographical information was acquired. It has been proposed that retrosplenial cortex integrates and translates between egocentric representations in posterior parietal cortex and allocentric representations in the medial temporal lobe region (Burgess et al., 2001, 2002; Maguire, 2001; Wolbers and Buchel, 2005). Our results are consistent with such a role, but indicate that the processing is not tonically maintained during navigation within familiar environments, rather its activity alters to meet changing demands. Of note, the current results do not support the suggestion that the retrosplenial cortex plays a particular role in navigational motor planning (Cho and Sharp, 2001) as there was no increased activity in this region during action planning events.

The hippocampus was joined by the nucleus accumbens in supporting initial goal-directed route planning. Whilst a general association between the nucleus accumbens and goal-directed behaviour has been well established in numerous studies (e.g. Schultz et al., 1997), its specific role during navigation is less clear. Within navigation, the nucleus accumbens has been theorised to support the translation of the hippocampal information it receives via direct connections (Thierry et al., 2000) into a sequence of sensori-motor actions necessary to reach the destination (Poucet et al., 2004; Redish and Touretzky, 1997). Our results provide the first support in humans for a role of this region in goal-related aspects of navigation.

Previous imaging studies of navigation often elicited activity in the prefrontal cortex. This activity was attributed in somewhat general terms to executive functions, planning, decision making (Hartley et al., 2003; Maguire et al., 1998), or increased working memory demands (Gron et al., 2000) by reference to its know role in these functions. Again our current data are able to characterise more specifically the contributions of four distinct areas of prefrontal cortex to navigation. The presence of dorsomedial PFC activity, present to varying degrees in all conditions but most during route planning, is compatible with its suggested role in monitoring responses in situations of uncertainty and altering behaviour to adapt to the environment (Ridderinkhof et al., 2004). Deep right lateral PFC activity was specifically associated with expectation violations and is consistent with data showing greater response in this region during events containing a

violation of an expected previously learnt association (Corlett et al., 2004; Fletcher et al., 2001). Anterior PFC is thought to be critical for manipulating information whilst holding on-line goal related information (Koechlin et al., 1999). Such is the case when dealing with unexpected obstructions in the environment (expectation violation) and responding to meet them (spontaneous route planning). The anterior insula/ventrolateral PFC was active at many points throughout the navigation process, perhaps linked with arousal and a perception of 'internal state' (Craig, 2002) associated most with the sparse auditory cues, expectation violations, and spontaneous route planning.

Concordant with a role in egocentric spatial processing (Burgess et al., 2002) and spatial working memory (Rowe et al., 2000), the posterior parietal cortex was also active when subjects navigated. Interestingly, the results extend previous findings by showing medial parietal regions to play more of a role in aspects of processing movement through immediate space, with lateral parietal regions planning movement through space beyond the current view.

Our results show that the neural correlates of functioning in the real world are amenable to scrutiny using fMRI, and that allowing the brain to operate in its true context facilitates an appreciation of focal and distributed, transient, and sustained responses. Whilst acknowledging that it may not be suitable in all cases, we suggest that asking subjects about their experiences (in a controlled fashion) may provide useful insights into the cognition underpinning behaviour. We have revealed a breadth of thinking behind navigation in humans supported by a dynamic interplay between brain regions that adapts to meet the demands of an ever-changing environment. In the future it will be important to explore the neural systems supporting the wider realm of human interactions, both with the physical environment and the people that inhabit it.

Acknowledgments

Appendix A. Generation of the fMRI time series model from verbal reports

This appendix is split into 4 sections: (A.1) short extracts taken from a single subject's retrospective verbal report, (A.2) the same extracts classified into the different categories, (A.3) the incorporation of temporal information into the report, and (A.4) the generation of the model of the fMRI time series.

A.1. Extracts from a verbal report

Each extract is drawn from a different time point in the interview with subject seven.

A.1.1. Verbal Report

Extract 1

| INTERVIEWER | Okay. So when you saw that view, did you think anything then? |
| SUBJECT | No, it's just a straight, when you know it's like that, why think? |

Extract 2

| INTERVIEWER | What did you think here? |
| SUBJECT | Well I'm thinking well, if I go left and think of myself all the way up round there, you can't get into Wardour Street, Wardour Street's going out the wrong way, you can't miss it, so I've got to go down. I don't want to go right because I'm going towards Wardour Street. A lot of questions came to my head there. Do I want to go left? But you go left, you go left, that's Noel Street, left Wardour Street, but you're only at the top end, Peter Street's down the bottom end. And then I was thinking where is Wardour Street, is that definitely right? And then I don't want to do the right here because it's Great Marlborough Street. Is there anything off the Great Marlborough Street. I'm thinking, scanning my brains for everything on the Great Marlborough Street. I'm trying to scan my brain for actually exactly where Wardour Street and Peter Street is. |

Extract 3

SUBJECT	I'm just checking the street, and I could see the no entry arrow there. Could you see that sign?
INTERVIEWER	I saw that as well. And you saw that at this time?
SUBJECT	Yes.

Extract 4

| INTERVIEWER | Okay. And as you come here, what are you thinking? |
| SUBJECT | Well, I'm looking for Ryder Street, I realise it ain't there. |

Extract 5

INTERVIEWER	Okay, so you saw this and then-
CUSTOMER	Hi, could you take me to Shepherd Market, please.
SUBJECT	First of all I was thinking shall I reverse, spin round and go up Marlborough Gate, Marlborough Road and I thought no, I'll do it the way I would do it, and it's Constitution Hill, round Hyde Park Corner, Park Lane, Stanhope Gate. That's what we're looking for. Stanhope Gate, not to go into Deanery Street, Stanhope Gate to spin round to go back into Curzon Street.

Extract 6

| INTERVIEWER | So what are thinking now? |
| SUBJECT | I've got to get in the lane. |

Extract 7

INTERVIEWER	Are you thinking of anything?
SUBJECT	I'm looking at the taxi cabs over the other side in the bus lane.
INTERVIEWER	You're watching these taxi cabs?
SUBJECT	Yes. Then hopefully, then I see oh, Brook Gate yes, is there.

A.2. Statements classified into the different categories

Statements assigned to different categories are coloured in the following manner:
Coasting, Spontaneous Route Planning, Visual Inspection, Expectation, Expectation Violation, Customer-driven Route Planning, Action Planning, Monitoring Traffic and Expectation Confirmation. See Table 1 for definitions.

A.2.1. Verbal report - classified

Extract 1

INTERVIEWER	Okay. So when you saw that view, did you think anything then?
SUBJECT	No, it's just a straight, when you know it's like that, why think?

Extract 2

INTERVIEWER	What did you think here?
SUBJECT	Well I'm thinking well, if I go left and think of myself all the way up round there, you can't get into Wardour Street, Wardour Street's going out the wrong way, you can't miss it, so I've got to go down. I don't want to go right because I'm going towards Wardour Street. A lot of questions came to my head there. Do I want to go left? But you go left, you go left, that's Noel Street, left Wardour Street, but you're only at the top end, Peter Street's down the bottom end. And then I was thinking where is Wardour Street, is that definitely right? And then I don't want to do the right here because it's Great Marlborough Street. Is there anything off the Great Marlborough Street. I'm thinking, scanning my brains for everything on the Great Marlborough Street. I'm trying to scan my brain for actually exactly where Wardour Street and Peter Street is.

Extract 3

SUBJECT	I'm just checking the street, and I could see the no entry arrow there. Could you see that sign?
INTERVIEWER	I saw that as well. And you saw that at this time?
SUBJECT	Yes.

Extract 4

INTERVIEWER	Okay. And as you come here, what are you thinking?
SUBJECT	Well, I'm looking for Ryder Street, I realise it ain't there.

Extract 5

INTERVIEWER	Okay, so you saw this and then-
CUSTOMER	Hi, could you take me to Shepherd Market, please.
SUBJECT	First of all I was thinking shall I reverse, spin round and go up Marlborough Gate, Marlborough Road and I thought no, I'll do it the way I would do it, and it's Constitution Hill, round Hyde Park Corner, Park Lane, Stanhope Gate. That's what we're looking for. Stanhope Gate, not to go into Deanery Street, Stanhope Gate to spin round to go back into Curzon Street.

Extract 6

INTERVIEWER	So what are thinking now?
SUBJECT	I've got to get in the lane.

Extract 7

INTERVIEWER	Are you thinking of anything?
SUBJECT	I'm looking at the taxi cabs over the other side in the bus lane.
INTERVIEWER	You're watching these taxi cabs?
SUBJECT	Yes. Then hopefully, then I see oh, Brook Gate yes, is there.

A.3. Determining the onsets and durations of thoughts described in the report

Timing of the events was provided by the time stamp on the video used for the debriefing, and examination of the eye-tracking video (see Materials and methods). Subjects were never shown the eye-tracking video.

A.3.1. Time (Minutes · Seconds) verbal report and eye-tracking information

Extract 1

	INTERVIEWER	Okay. So when you saw that view, did you think anything then?
12.38	**SUBJECT**	No, it's just a straight, when you know it's like that, why think?

Extract 2

	INTERVIEWER	What did you think here?
13.08	**SUBJECT**	Well I'm thinking well, if I go left and think of myself all the way up round there, you can't get into Wardour Street, Wardour Street's going out the wrong way, you can't miss it, so I've got to go down. I don't want to go right because I'm going towards Wardour Street. A lot of questions came to my head there. Do I want to go left? But you go left, you go left, that's Noel Street, left Wardour Street, but you're only at the top end, Peter Street's down the bottom end. And then I was thinking where is Wardour Street, is that definitely right? And then I don't want to do the right here because it's Great Marlborough Street. Is there anything off the Great Marlborough Street. I'm thinking, scanning my brains for everything on the Great Marlborough Street. I'm trying to scan my brain for actually exactly where Wardour Street and Peter Street is.

Extract 3

21.14	**SUBJECT**	I'm just checking the street, and I could see the no entry arrow there.
		Could you see that sign?
	INTERVIEWER	I saw that as well. And you saw that at this time?
	SUBJECT	Yes.

(Eye-tracking shows fixation of the no entry sign at 21.14)

Extract 4

	INTERVIEWER	Okay. And as you come here, what are you thinking?
21.56	**SUBJECT**	Well, I'm looking for Ryder Street,
21.59		I realise it ain't there.

(Eye-tracking shows saccades along the street ahead to where Ryder Streeshould appear from 21.56 to 21.59)

Extract 5

	INTERVIEWER	Okay, so you saw this and then-
	CUSTOMER	Hi, could you take me to Shepherd Market, please.
23.58	**SUBJECT**	First of all I was thinking shall I reverse, spin round and go up Marlborough Gate, Marlborough Road and I thought no, I'll do it the way I would do it, and it's Constitution Hill, round Hyde Park Corner, Park Lane, Stanhope Gate. That's what we're looking for. Stanhope Gate, not to go into Deanery Street, Stanhope Gate to spin round to go back into Curzon Street.

Extract 6
24.49 **INTERVIEWER** So what are thinking now?
SUBJECT I've got to get in the lane.

Extract 7 Are you thinking of anything?
INTERVIEWER I'm looking at the taxi cabs over the other
25.27 **SUBJECT** side in the bus lane.
You're watching these taxi cabs?
INTERVIEWER
(Eye-tracking shows visual tracking of the taxi cabs from 25.27
to 25.29) Yes. Then hopefully, then I see oh, Brook
25.35 **SUBJECT** Gate yes, is there.

(Brook Gate appears in view at 25.35)

A.4. A schematic of the model of the subject's fMRI time series data
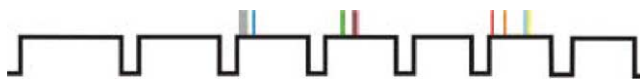
Black lines demarcate the task periods and shorter rest periods. Coloured lines represent the onsets and durations of the classified events and epochs generated from the extracts presented in section A.3.1 of this figure.

A schematic illustration of how the model of the subject's times series might appear when all statements in the subject's verbal report have been classified. Statements classified into categories not listed in Table 1, such as spontaneous recollection, were not modelled due to their low numbers of occurrence.

Appendix B. Tables B1–B14 of peak coordinates and *Z* scores

PFC = prefrontal cortex, PPC = posterior parietal cortex, L = left, R = right. Infinite *Z* score in Table B1 is due to the *P* value being so small that the *Z* score is effectively infinite. All activations are listed statistically significant at *P* < 0.001. For brevity, each region is listed only once; where several peaks were observed in the same region, the coordinates and *Z* scores refer to the strongest activation. MNI coordinates are listed. Specification of the location of the pre-SMA was guided by Picard and Strick (2001).

Table B1
Customer-driven route planning > coasting events

Brain regions	Z score	Coordinates of peak activation		
		x	y	z
L hippocampus	4.19	−30	−27	−21
R hippocampus	3.36	27	−24	−18
L parahippocampus	3.81	−27	−30	−24
L retrosplenial cortex	5.90	−6	−63	9
R retrosplenial cortex	5.85	9	−63	6
Superior frontal gyrus (dorsomedial PFC)	5.95	0	18	60
L inferior frontal gyrus (lateral PFC)	6.85	−48	24	−6
R inferior frontal gyrus (lateral PFC)	6.21	45	24	3
R superior/middle temporal gyrus	Infinite	60	−33	−3
L superior/middle temporal gyrus	7.77	−57	−21	3
Brain stem	4.57	3	−33	−39
Cerebellum	3.75	0	−54	−39
R fusiform gyrus	3.43	48	−54	−27

Table B2
Spontaneous route planning > coasting events

Brain regions	Z score	Coordinates of peak activation		
		x	y	z
R superior frontal gyrus (dorsomedial PFC)	5.00	9	18	48
R middle frontal gyrus (lateral PFC)	4.91	48	9	4
L middle frontal gyrus (lateral PFC)	4.14	−42	18	30
L superior frontal gyrus (anterior PFC)	4.04	−18	57	0
R middle frontal gyrus (anterior PFC)	3.94	36	63	6
L retrosplenial cortex	3.88	−15	−63	15
R retrosplenial cortex	3.54	18	−45	0
R superior parietal gyrus (PPC)	4.34	3	−75	51
R angular gyrus (PPC)	3.80	45	−69	27
L angular gyrus (PPC)	4.01	−36	−84	24
R superior parietal gyrus/precuneus	4.70	6	−54	57
L inferior parietal gyrus	3.55	−48	−51	51
R inferior parietal gyrus	3.72	42	−45	57
L anterior insula/ventrolateral PFC	4.58	−39	24	−6
R anterior insula/ventrolateral PFC	4.35	33	21	−15
L cerebellum	4.35	−36	−69	−33
R cerebellum	4.67	33	−60	−30
R middle temporal gyrus	3.90	63	−60	6
L superior frontal gyrus (posterior)	3.83	−21	12	57
R superior frontal gyrus (posterior)	3.45	30	0	60
L precentral gyrus	3.67	−51	−9	42
Brain stem	4.55	6	−18	−39
R superior temporal sulcus	3.64	54	−39	0
R inferior occipital gyrus	3.60	12	−84	−15
R anterior cingulate cortex	3.47	9	36	12

Table B3
Action planning > coasting events

Brain regions	Z score	x	y	z
R superior frontal gyrus (pre-SMA)	4.27	3	6	54
R cerebellum	5.28	36	−51	−30
L cerebellum	4.42	−30	−69	−30
L precuneus/superior parietal cortex	4.52	−3	−54	48
L middle occipital gyrus	4.65	−45	−75	12
R middle occipital gyrus	3.75	36	−81	6
R postcentral gyrus	3.31	63	−27	30
L postcentral gyrus	3.69	−45	−30	42
R middle frontal gyrus (dorsolateral PFC)	4.52	51	9	42
L middle frontal gyrus (posterior)	4.39	−33	−6	54
R superior frontal gyrus	4.34	12	27	51
L superior frontal gyrus	4.07	−21	9	60
L inferior frontal gyrus	3.74	−45	15	0
R middle temporal gyrus	4.23	57	−51	3
R superior temporal sulcus	3.64	57	−45	27
R insula	3.35	42	−6	−21

Table B4
Expectation confirmation > coasting events

Brain regions	Z score	x	y	z
L retrosplenial cortex	5.73	−15	−63	12
R retrosplenial cortex	4.37	18	−51	6
R middle occipital gyrus	4.11	42	−78	18
L middle occipital gyrus	3.87	−42	−81	21
R intraoccipital sulcus	4.09	15	−93	21
R inferior occipital gyrus	4.02	24	−78	−18
R inferior parietal sulcus (PPC)	4.07	27	−69	45
L intraparietal sulcus (PPC)	4.01	−27	−81	33
R superior parietal gyrus	3.95	9	−54	60
L superior parietal gyrus	3.42	−15	−66	57
R superior temporal sulcus	4.32	51	−51	6
R cerebellum	4.20	33	−45	−36
L cerebellum	3.62	−33	−54	−27
Mid cerebellum	4.96	0	−51	−27
R inferior frontal sulcus	4.08	51	12	30
L inferior frontal gyrus	3.99	−60	9	12
R superior frontal gyrus	3.84	24	6	57
Medial superior frontal gyrus	3.66	0	21	54

Table B5
Expectation violation > coasting events

Brain regions	Z score	x	y	z
R middle frontal gyrus (lateral PFC)	5.42	48	30	27
R superior parietal gyrus	4.00	18	−84	42
L retrosplenial cortex	3.51	−15	−63	18
Medial superior frontal gyrus	5.04	0	12	57
R intraparietal sulcus	4.26	36	−72	33
R paracentral lobule	4.44	6	−42	66
L superior parietal gyrus	4.34	−3	−63	54
L anterior insula/ventrolateral PFC	4.44	−36	24	−3
R superior temporal sulcus	4.31	63	−51	15

Table B5 (*continued*)

Brain regions	Z score	x	y	z
R anterior cingulate cortex	4.10	12	39	15
L inferior frontal gyrus	4.07	−39	36	9
R cerebellum	4.00	12	−72	−24
L inferior frontal gyrus	3.87	−57	9	12
L middle frontal gyrus	3.74	−45	24	24
R middle temporal gyrus	3.67	60	−36	−12
L cerebellum	3.62	−9	−75	−24
R isthmus of cingulate gyrus	3.60	12	−42	3
R angular gyrus	3.60	54	−48	36
R inferior frontal sulcus (anterior PFC)	3.60	27	54	6
R fusiform gyrus	3.58	42	−45	−24
L fusiform gyrus	3.52	−36	−63	−21
L superior frontal gyrus (posterior)	3.40	−24	−18	66
R postcentral gyrus	3.33	42	−51	54
L postcentral gyrus	3.26	−45	−45	48

Table B6
Expectation epochs > coasting epochs

Brain regions	Z score	x	y	z
L superior frontal gyrus (dorsomedial PFC)	3.67	−3	33	42
R anterior insula/ventrolateral PFC	3.55	39	24	−6
R inferior occipital gyrus	3.53	27	−87	−18
R parahippocampus	3.47	24	−39	−15
R middle frontal gyrus (anterior PFC)	3.39	36	63	0

Table B7
Visual inspection epochs > coasting epochs

Brain regions	Z score	x	y	z
R inferior occipital cortex	6.22	21	−87	−12
L inferior occipital cortex	5.85	−30	−81	−18
R retrosplenial cortex	5.00	15	−48	3
L retrosplenial cortex	4.87	−12	−54	0
R parahippocampal gyrus	4.87	21	−39	−12
L parahippocampal gyrus	4.49	−24	−42	−9
R middle occipital gyrus	4.94	39	−81	15
L middle occipital gyrus	4.87	−33	−87	12
L inferior parietal gyrus (PPC)	4.46	−30	−69	51
L intraparietal sulcus	3.96	−30	−57	42
L middle frontal gyrus (dorsolateral PFC)	5.85	−45	12	30
R middle frontal gyrus (dorsolateral PFC)	5.60	48	33	18
L anterior insula/ventrolateral PFC	5.19	−33	21	−12
R anterior insula/ventrolateral PFC	5.43	39	29	−15
L cingulate gyrus (ventromedial PFC)	4.09	−3	30	−21
R superior frontal gyrus (dorsomedial PFC)	5.17	6	15	57
R middle frontal gyrus (anterior PFC)	4.25	27	60	15
L middle frontal gyrus (anterior PFC)	4.17	−30	51	18
R collateral sulcus	4.17	30	−3	−33
R cingulate sulcus	4.13	3	−45	42
L middle frontal gyrus	3.76	−30	3	57
R middle frontal gyrus	4.65	33	6	57
L precentral gyrus	3.69	−45	−21	54
L mediodorsal thalamic nucleus	4.06	−9	−9	6
L amygdala	3.60	−18	−3	−21
L postcentral gyrus	3.56	−39	−36	45

Table B8
Monitoring traffic epochs > coasting epochs

Brain regions	Z score	Coordinates of peak activation		
		x	y	z
Medial superior parietal gyrus	5.37	0	−60	57
R precuneus	5.25	6	−54	60
R cuneus	4.54	12	−87	6
R intraparietal sulcus	3.37	51	−36	45
L superior parietal gyrus	4.46	−30	−57	54
L inferior occipital gyrus	4.81	−33	−84	−18
R inferior occipital gyrus	4.98	36	−81	−15
R middle occipital gyrus	3.75	24	−84	15
L middle temporal gyrus	4.07	−48	−69	6
R middle temporal gyrus	4.51	51	−54	9
R superior temporal gyrus	4.25	54	−42	21
L superior temporal gyrus	3.73	−60	−45	9
L inferior lingual gyrus	4.46	−21	−60	−1
R inferior frontal sulcus	4.51	42	24	27
L superior frontal gyrus (anterior PFC)	4.24	−24	51	18
R superior frontal sulcus (anterior PFC)	4.02	30	51	12
L superior precentral sulcus	3.90	−48	3	33
R superior precentral sulcus	3.90	39	0	39
R posterior orbital gyrus	3.85	33	24	−18
L anterior insula/ ventrolateral PFC	3.57	−33	30	−3
R middle frontal gyrus	3.54	39	0	57
L middle frontal gyrus	3.47	−27	−3	54

Table B9
Customer-driven route planning > response to customers' irrelevant statements

Brain regions	Z score	Coordinates of peak activation		
		x	y	z
L hippocampus	4.51	−33	−27	−18
L parahippocampus	3.68	−27	−30	−24
L middle frontal gyrus (dorsolateral PFC)	4.53	−48	6	39
R middle frontal gyrus (dorsolateral PFC)	3.60	48	27	24
R retrosplenial cortex	4.43	12	−54	6
L retrosplenial cortex	4.21	−9	−60	6
Superior frontal gyrus (dorsomedial PFC)	4.23	0	30	45
L nucleus accumbens	3.62	−9	12	−6
R nucleus accumbens	3.48	12	12	−6
R cuneus	4.46	9	−81	6
L posterior cingulate cortex/precuneus	4.08	−9	−48	45
L fusiform gyrus	4.15	−18	−84	−12
R fusiform gyrus	4.32	27	−72	−12
R superior parietal gyrus (PPC)	3.47	27	−72	45
L angular gyrus (PPC)	3.95	−36	−57	45
L intraparietal sulcus	3.95	−36	−57	45
L postcentral gyrus	4.30	−48	−33	45
L precentral gyrus	3.90	−57	−24	21
Brain stem	3.85	0	−36	−42
R superior temporal gyrus	4.47	63	−21	12
L superior temporal gyrus	4.36	−54	−18	−3
L middle temporal gyrus	3.76	−63	−51	−3
L superior occipital gyrus	3.76	−30	−84	39

Table B10
Customer-driven route planning (initial goal) > customer-driven route planning (switch to new goal)

Brain regions	Z score	Coordinates of peak activation		
		x	y	z
R nucleus accumbens	5.19	18	6	−9
L nucleus accumbens	4.88	−15	9	−12
R cingulate gyrus (ventromedial PFC)	4.00	3	18	−6
R cuneus	5.52	3	−84	0
R fusiform gyrus	5.32	27	−60	−15
L supramarginal gyrus	4.69	−45	−39	54
L precentral gyrus	4.44	−51	6	33
L superior parietal gyrus	4.34	−27	−72	54
L insula	4.18	−45	−3	15
L superior frontal sulcus	3.99	−21	12	51
R inferior occipital gyrus	5.07	36	−84	−12
L middle occipital gyrus	3.68	−24	−90	24
L medial superior temporal gyrus	3.66	−24	6	−42
L mid cingulate gyrus	3.41	−6	6	36

Table B11
Customer-driven route planning (switch to new goal) > customer-driven route planning (initial goal)

Brain regions	Z score	Coordinates of peak activation		
		x	y	z
L transverse temporal gyrus	4.03	−39	−30	9
L superior temporal sulcus	3.42	−60	−21	−9
R superior temporal sulcus	3.76	54	−27	−12
R superior temporal gyrus	3.65	63	−21	0

Table B12
Customer-driven route planning > spontaneous route planning

Brain regions	Z score	Coordinates of peak activation		
		x	y	z
R superior and middle temporal gyri	Inf	63	−36	0
L superior and middle temporal gyri	7.61	−51	−30	3
R nucleus accumbens	6.14	9	9	−3
L nucleus accumbens	4.65	−12	9	−6
L hippocampus	3.35	−30	−24	−21
L anterior superior frontal gyrus	5.15	−9	51	33
L mid superior frontal gyrus	4.80	−6	15	63
Anterior cingulate gyrus	5.08	0	33	18
L mid cingulate gyrus	5.12	−3	−21	30
R precuneus	5.02	9	−66	36
R cuneus	4.81	9	−78	9
Brain stem	4.74	0	−36	−42
L cerebellum	4.45	−18	−75	−30
R cerebellum	4.34	15	−72	−30
R inferior occipital gyrus	3.76	30	−81	−15
L inferior occipital gyrus	4.26	−24	−87	−12
R amygdala	4.30	27	−6	−21
L central sulcus	4.11	−45	−15	42
Gyrus rectus (orbito-frontal cortex)	4.05	0	45	−21
R precentral sulcus	3.54	39	−12	39
R precentral gyrus	3.40	57	0	45
L fusiform gyrus	3.69	−45	−54	−24

Note. The L hippocampus is significant at $P < 0.005$ uncorrected for multiple comparisons with our criterion of a minimum of 6 contiguous voxels active.

Table B13
Conjunction of customer-driven route planning > response to customers' irrelevant statements and spontaneous route planning > coasting events

Brain regions	Z score	Coordinates of peak activation		
		x	y	z
L retrosplenial cortex	4.11	−15	−63	18
R retrosplenial cortex	3.38	18	−57	15
Superior frontal gyrus (dorsomedial PFC)	3.74	0	18	51
L superior occipital gyrus	3.93	−42	−81	27
L precuneus	3.85	−6	−54	48
R middle temporal gyrus	3.76	66	−36	−9
L middle frontal gyrus	3.70	−48	27	24
R middle frontal gyrus	3.69	51	33	18
L precentral gyrus	3.58	−51	−9	42
L superior parietal gyrus	3.54	−36	−60	48
R fusiform gyrus	3.47	24	−72	−12
R anterior insula/ ventrolateral PFC	3.38	39	21	−18
L postcentral gyrus	3.37	−42	−45	48
L cerebellum	3.35	−39	−66	−33

Table B14
Response to customers' irrelevant statements > coasting events

Brain regions	Z score	Coordinates of peak activation		
		x	y	z
R superior/middle temporal gyrus	7.45	60	−15	−12
L superior/middle temporal gyrus	7.28	−60	−15	0
L amygdala	4.21	−24	−3	−27
R amygdala	3.76	24	−6	−24
R hippocampus	3.47	27	−12	−27
L middle frontal gyrus	4.93	−51	−6	48
R posterior superior frontal gyrus	4.70	9	24	57
R middle frontal gyrus	4.10	48	15	39
Medial superior frontal gyrus	3.69	0	48	39
Gyrus rectus (ventromedial PFC)	3.74	0	45	−21
Posterior cingulate cortex	4.34	0	−48	24
R precuneus	3.58	6	−75	33
R brain stem/cerebellum	3.92	6	−36	−30
L ventrolateral thalamic nuclei	3.40	−15	−21	0

Appendix C. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neuroimage.2006.01.037.

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