

# Detection of unexpected events during spatial navigation in humans: bottom-up attentional system and neural mechanisms

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## Abstract

Navigation is a complex cognitive ability requiring the processing and integration of several different types of information extracted from the environment. While navigating, however, an unexpected event may suddenly occur, which individuals are required to detect promptly in order to apply an appropriate behavioural response. The alerting mechanism that is integral to the detection of unexpected events is referred to as the bottom-up attentional system. Using event-related functional magnetic resonance imaging, we investigated the neural basis of bottom-up detection of unexpected events while individuals moved within a virtual environment. We identified activation within a right fronto-temporo-parietal network in response to unexpected events while navigating in this virtual environment. Furthermore, when an unexpected event requires an adjusted behavioural response, a region of the right ventrolateral pre-frontal cortex (areas 45 and 47/12) is selectively activated. Our data replicate earlier findings on the neural mechanisms underlying visual attention and extend these findings to the more complex real-life ability of spatial navigation, thereby suggesting that these neural mechanisms subservise the bottom-up attentional systems that are crucial for effective locomotion in real surroundings.

## Introduction

Visual attention in humans involves many factors (Knudsen, 2007). For example, the knowledge, expectations and aim of our behaviour may direct our attention to a selective frame of reference (Miller & Cohen, 2001; Miller & D'Esposito, 2005), allowing the selection of stimuli relevant to a specific cognitive demand; these factors are referred to, collectively, as 'top-down' attentional systems. Some information, however, does not need to be modulated by top-down signals in order to be processed (Egeth & Yantis, 1997). For instance, highly salient stimuli may be perceived as 'popping out' from the scene and may affect our ongoing cognitive activity (Bisley & Goldberg, 2003), sometimes by modulating top-down control (Miller & Cohen, 2001; Miller & D'Esposito, 2005). This stimulus-driven response is referred to as the 'bottom-up' attentional system, and allows individuals to detect unexpected events. In daily life, unexpected events may occur in different forms and, in some cases, they may substantially interfere with ongoing activity. Therefore, the prompt detection and evaluation of these events may be crucial (e.g. driving on the highway when an animal suddenly starts to cross in front of you).

It has been proposed that bottom-up attentional mechanisms in humans involve a selective neural network that includes the temporo-parietal junction (inferior parietal lobule and superior temporal gyrus) and the ventral frontal cortex (inferior and middle frontal

gyrus), and has been referred to as the right ventral frontoparietal network (Corbetta & Shulman, 2002). This neural network is strongly lateralized to the right hemisphere and it is suggested that it can function as an alerting mechanism for the detection of unexpected relevant stimuli while performing a task (Corbetta & Shulman, 2002).

Recent neuroimaging studies support the role of this neural network in processing both task-relevant and task-irrelevant unexpected stimuli. For instance, while performing target detection tasks, activity within the right ventral frontoparietal network has been reported when targets occurred at an unexpected location (Corbetta *et al.*, 2000; Perry & Zeki, 2000) or when changes occurred at the expected target location but referred to differences in the features of the stimulus (Kirino *et al.*, 2000; Marois *et al.*, 2000). Additional work has shown that activity within the same right ventral frontoparietal network is related to feature changes of a target stimulus independent of the sensory modality (visual, auditory or tactile) in which these changes occurred (Downar *et al.*, 2000). Altogether, these studies provide evidence that the right ventral frontoparietal network plays a critical role in the detection of unexpected events and confirm earlier studies that suggested that distinctive sensory stimuli attract our attention, especially when they are relevant to the task that we are performing as well as when they share common features with the stimuli for which we are actively searching (Folk *et al.*, 1992).

Although these studies lend credence to the proposed role of the right ventral frontoparietal network in the bottom-up system responsible for the detection of unexpected events during visual attention tasks, to our knowledge there is no evidence demonstrating how and if this bottom-up attentional mechanism is involved during a realistic

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task such as navigation. The extension of these visual attention findings to a more realistic spatial navigation task was the aim of the present study. We hypothesized that the 'bottom-up' ventral frontoparietal network of the right hemisphere would be responsible for alerting individuals to unexpected events that occurred while navigating. We tested this hypothesis by using event-related functional magnetic resonance imaging combined with a virtual reality paradigm that allows participants to perform a navigational task in simulated three-dimensional space. First, we assessed the neural mechanisms involved while individuals navigated along a familiar pathway and then we investigated the brain regions involved in processing unexpected events that did, or did not, require adjustments in behavioural response, thus disentangling the processes of perception and action in response to these unexpected events.

## Materials and methods

### Participants

Ten right-handed healthy subjects (five females, mean age 23.08 years, range 22–27 years) participated in this study. All subjects had normal or corrected-to-normal vision and no history of neurological disorders. All subjects provided informed consent, the protocol was approved by the institutional review board of the University of British Columbia and the experiment was conducted conforming to The Code of Ethics of the World Medical Association (Declaration of Helsinki), printed in the British Medical Journal (18 July 1964).

### Experimental protocol

Participants navigated within a virtual reality environment by using a three-button keypad, each button corresponding to movement in one of three directions: left, forward and right. All participants were familiar with virtual environments and had previous experience of playing three-dimensional video-games. Before scanning, all participants practiced the motor aspects of the task by moving within a virtual environment different from the one used during functional magnetic resonance imaging scanning. Both practice and experimental virtual environments were created with a three-dimensional game software editor (Game Studio A6, La Mesa, CA, USA). The virtual environments were composed of several buildings with the same texture and different streets, all leading to the same target location. In each street, a series of single barriers were randomly located in the middle of the road, with different locations on each trial, around which the subjects needed to move. The purpose of these barriers was to control for the acquisition of a purely standard motor pattern, which would not require active navigation each time the participants moved along the same route. Figure 1 provides a schematic outline of the environment (top view). The target location was indicated by the presence of an orange ball, which the subjects were instructed to take (by walking into the ball), thus ending the trial. As soon as the orange ball was taken, subjects were automatically transported back to the starting position and a new trial began.

Participants were instructed to reach the target location as many times as possible. They were asked to reach the target location by following the shortest path unless it was necessary to follow an alternative route. Note that following the shortest path would allow the completion of more trials, which was the goal of the subjects. In addition, the subjects were told that if there was no way to reach the target location, they could return to the starting position, where they would find the orange ball and be able to begin a new trial.

The scanning session consisted of two functional runs, namely a familiarization and an events phase. The duration of each run was 16 min. In both runs (phases), the virtual environment was the same, the starting position and target location were in the same places, and the instructions were identical. During the familiarization phase subjects were required to explore the virtual environment in order to find the target location, and follow the shortest path in order to reach the same target location as many times as possible for the entire duration of the run. Each time the target location was reached, subjects were automatically transported back to the same starting position and a new trial began. During the entire run, both starting position and target location were the same (Fig. 1). No unexpected events occurred in this familiarization phase.

During the events phase, which was performed immediately after the familiarization phase, the subjects performed the same task within the same environment but four different unexpected events could occur randomly during the task (Fig. 1). In one unexpected event the colour of a building was changed (green instead of the usual brown), which did not require an altered behavioural response (Fig. 1A and B); we refer to this event as the perceptual event. In a second unexpected event the location of two barriers was changed (Fig. 1C), forcing subjects to adopt a different motor sequence to move around them but not a different route. In a third event, the usual path to the target was blocked in such a way that subjects could still reach the target but had to use an alternative route (Fig. 1D). In the fourth event the usual path was blocked at a point that made it impossible to reach the target location (Fig. 1E) and therefore forced the subjects to go back to the starting position. We refer to these last three events as the action events as they all required an action response different from the one used in the usual path. The order of administration of all of these four events (the one perceptual and the three action events) was randomized across subjects but always occurred for all participants on trials 4, 11, 16 and 20 (out of about 28 trials). The reason for the selection of such a number of events and their identity is the following: in this study we investigated the detection of unexpected events suddenly occurring while performing the task; by definition, unexpected events occur rarely. We administered four events (one event per trial) occurring in a total of 20 trials; an increased frequency of events (greater than 20% of the trials) would result in the subjects being more alert to any upcoming change in the individual trials. In our experimental design, the reduced number of unexpected events kept subjects focused on the given task, which consisted of reaching the target location as many times as possible by following the shortest pathway, the same task as performed in the familiarization phase. A similar issue was addressed by the identity and nature of the events. Events are more unexpected when they are not repeated while performing a task. For this reason, our experimental design included three different action events that had the common feature of requiring a change in the usual/planned performance, i.e. a change in motor response following the same route or a change in motor response following a different route; this commonality of action change, irrespective of the nature of the change, was the aim of our investigation.

In the scanner, participants performed the experiment via a mirror retro-projection magnetic resonance imaging system connected to the laptop used to present the tasks. The laptop was located outside the scanner room and displayed the subjects' performance while they performed the experimental tasks. This allowed us to use a video-camera to record each individual's performance for the entire duration of the scanning session. For each participant, the video was analysed offline in order to assess time and accuracy of performance at each task and for each experimental condition. However, the analysis of the videos did not allow the assessment of the detection of the perceptual

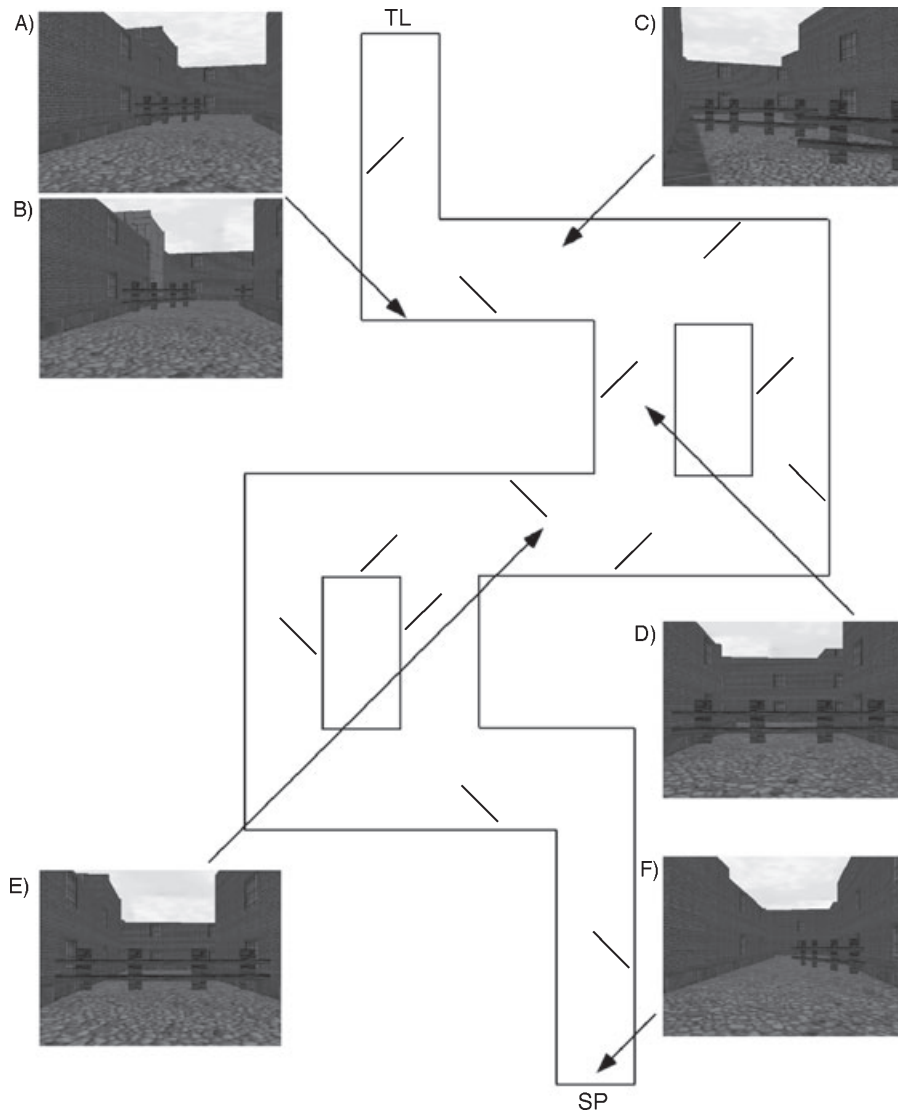


FIG. 1. Virtual environment and task design. The figure depicts a survey map of the environment (not shown to the participants) in which the subjects navigate from the starting position (SP) to the target location (TL). The figure shows: a view of the environment without (A) or with (B) the occurrence of the perceptual event; a view of the action event in which participants are required to adopt a different motor response (C); a view of the action event in which participants are required to reach the target location by following a different path (D); a view of the action event in which participants are required to go back to the starting position (E); and the participant's view when starting the trials (F).

event as this did not affect the behavioural performance. For this reason, after scanning, experimenters interviewed the subjects to gather information regarding the detection of the events that occurred during scanning; subjects were required to explicitly report which unexpected changes occurred in the environment while they were following the usual path.

#### *Functional magnetic resonance imaging data acquisition and analysis*

Images were acquired with a 3.0 Tesla Phillips scanner. Functional images were acquired parallel to the anterior commissure/posterior commissure line with a T2-weighted EPI sequence of 36 interleaved axial ascending slices (TR 2000 ms; TE 40 ms) of 3 mm thickness (1 mm gap) with an in-plane resolution of  $1.675 \times 1.675$  mm. Each functional run consisted of 480 volumes. Structural images were

acquired with a T1-weighted EPI sequence, recording 170 axial slices of 1 mm thickness (1 mm gap) with an in-plane resolution of  $1 \times 1$  mm (FOV 256).

The first volume of each functional run was discarded to allow for scanner equilibration. All magnetic resonance imaging data were analysed using BrainVoyager QX Version 1.8 (Brain Innovation, Maastricht, The Netherlands). Pre-processing of functional runs consisted of corrections for slice scan time acquisition, head motion (trilinear interpolation) and temporal filtering with a high-pass filter in order to remove frequencies less than 3 cycles/time course. Functional runs were individually coregistered to their respective anatomical scan, using the first retained functional volume to generate the coregistration matrix. For the familiarization phase, whole-brain analysis was carried out by contrasting the last 60 volumes (2 min) against the first 60 volumes (2 min) of the acquisition scan. Our rationale for selecting this specific number of volumes was based on the analysis of behavioural response times while subjects performed

the task. On average, subjects spent 131 s (SD 11 s) identifying the shortest pathway (see behavioural data in Results). The use of 120 s (mean of 131 s minus 1 SD), i.e. 60 volumes, ensured that we included only early performances in which all participants were still learning the shortest path in the functional contrast. We used the same number of volumes (60 volumes) in the late performances to obtain a comparable amount of dynamic data. For the events phase, whole-brain analysis regarding the perceptual event was carried out by contrasting the 5 volumes following the appearance of the perceptual event against the 5 volumes acquired while subjects performed the same part of the path during the previous trial, in which no unexpected events occurred. In this contrast, the reason for using the previous trial as baseline relies on the fact that in such a long acquisition scan (16 min) the level of the haemodynamic response is subject to decrease over time; thus, the use of trials close in time along the acquisition scan makes the comparison more reliable when subtracting BOLD signal changes directly. For similar reasons as in the familiarization phase, we kept the number of volumes included in the direct comparison equal (5 volumes; 10 s), which represented the length of time that subjects needed to detect the unexpected event and apply the appropriate behavioural response, as shown by the video-recordings. Whole-brain analysis of the action events was carried out by contrasting the 5 volumes acquired following the appearance of the action events against the 5 volumes acquired following the appearance of the perceptual event. In this manner, activity directly related to altered behaviour, in response to an unexpected event, could be evaluated.

In all cases, significant BOLD signal changes were determined at each voxel, based on a general linear model corrected for autocorrelations. To obtain the average group *t* maps, all individual magnetic resonance imaging data were first normalized to the Talairach stereotaxic space (Talairach & Tournoux, 1988) and were then combined using a mixed-effects linear model. The resulting *t* statistic images were thresholded using the random field theory to correct for multiple comparisons (Worsley *et al.*, 1996).

## Results

### *Neural mechanisms involved in performing a familiar route*

To assess that the familiarization phase was effective, we compared the number of trials (i.e. number of paths) executed by the participants during the first 2 min and the last 2 min of performance. The results showed that the number of trials performed in the last 2 min of the familiarization phase was statistically higher (average 4; SD 0) than the number of trials performed during the first 2 min of performance (average 1.5; SD 0.97), confirming that familiarity and learning occurred in all participants by the end of the familiarization phase ( $t_9 = 8.14$ ,  $P < 0.001$ ).

We contrasted the last 2 min of the familiarization phase (when subjects were highly familiar with the shortest path) with the first 2 min (when subjects were still unfamiliar with the shortest path). This contrast (last 2 min > first 2 min) yielded significant neural activity ( $P < 0.005$ ) within the frontal, temporal and parietal cortex, bilaterally (Fig. 2; Table 1). Within the frontal lobe, there was bilateral activity in the central region involving the motor cortex (Brodmann's areas 4 and 6), paracentral lobule (Brodmann's area 4), and in the middle and inferior frontal gyrus (right hemisphere, Brodmann's areas 9/46; left hemisphere, Brodmann's areas 44). Within the posterior cortex, there was symmetrical bilateral activity in the superior parietal lobe (Brodmann's area 7) and middle temporal gyri (Brodmann's areas 21 and 22). Finally, there was

bilateral activity in the hippocampus, in the striatum of the right hemisphere and the parahippocampal gyrus of the left hemisphere (Table 1). These regions of neural activity relate to the performance during the last 2 min of the familiarization phase, when individuals were highly familiar with the environment and the path. It is reasonable to believe, however, that neural activity within the same regions was gradually increasing and present to some extent even during the time of learning prior to the last 2 min, which was not modelled in our analysis.

### *Bottom-up attentional mechanisms during the occurrence of unexpected events*

Behaviourally, all participants performed the perceptual and action event trials in an identical manner, as expected and required by the task, with 100% accuracy. During the action event trials, they all performed the task perfectly by following an alternative path or adopting a different motor response in order to get to the target location. During the remaining trials in which there were no unexpected events all participants followed the usual (shortest) path, which they had learned during the familiarization phase. After scanning, all subjects correctly reported all unexpected events that occurred during the events phase, including the appearance of a green building (the perceptual event), even though this event did not affect their behavioural response.

To investigate the mechanisms involved in detecting a change in the environment that did not require modification of planned performance, we contrasted the BOLD signal change when a perceptual event occurred with the BOLD signal change when the same part of the path was followed in the previous trial when no unexpected events occurred. This contrast revealed increased BOLD signal ( $P < 0.005$ ) within frontal and temporo-parietal regions of the right hemisphere alone (Fig. 3). These included supplementary motor cortex (Brodmann's area 6), anterior cingulate cortex, temporo-parietal junction (Brodmann's areas 40/22), middle temporal gyrus (Brodmann's areas 37 and 39) and perirhinal cortex (Brodmann's area 36). There was also bilateral activity in the occipital cortex (Brodmann's areas 18 and 19), subcortical structures (thalamus and putamen) and cerebellum (Table 2).

To determine the mechanisms involved when unexpected events required a modification of planned performance, independent of the coincident perceptual processing, we compared brain activity during action events (i.e. when unexpected events required a change in movement, direction or plan) with activity during the perceptual event (i.e. when an unexpected event did not require a change in action). In this contrast, the action events were collapsed based on our *a-priori* hypothesis of testing the neural mechanisms involved in changing a planned performance in response to an unexpected event, irrespective of the nature of such an action change. This contrast resulted in a selective increase ( $P < 0.0005$ ) in activity within the ventrolateral prefrontal cortex (i.e. areas 45 and 47/12) of the right hemisphere (Fig. 4).

Finally, in order to have a more detailed description of the neural activity related to the different action events, we performed direct comparisons among the different action events (events B, C and D), and between these individual action events and the perceptual event (event A). Overall, among the different action events, we revealed several peaks of neural activity mainly within the frontal, parietal and temporal cortex (Table 3), whereas the direct comparisons of each individual action event with the perceptual event resulted in increased neural activity mainly located in the frontal cortex (Table 4).

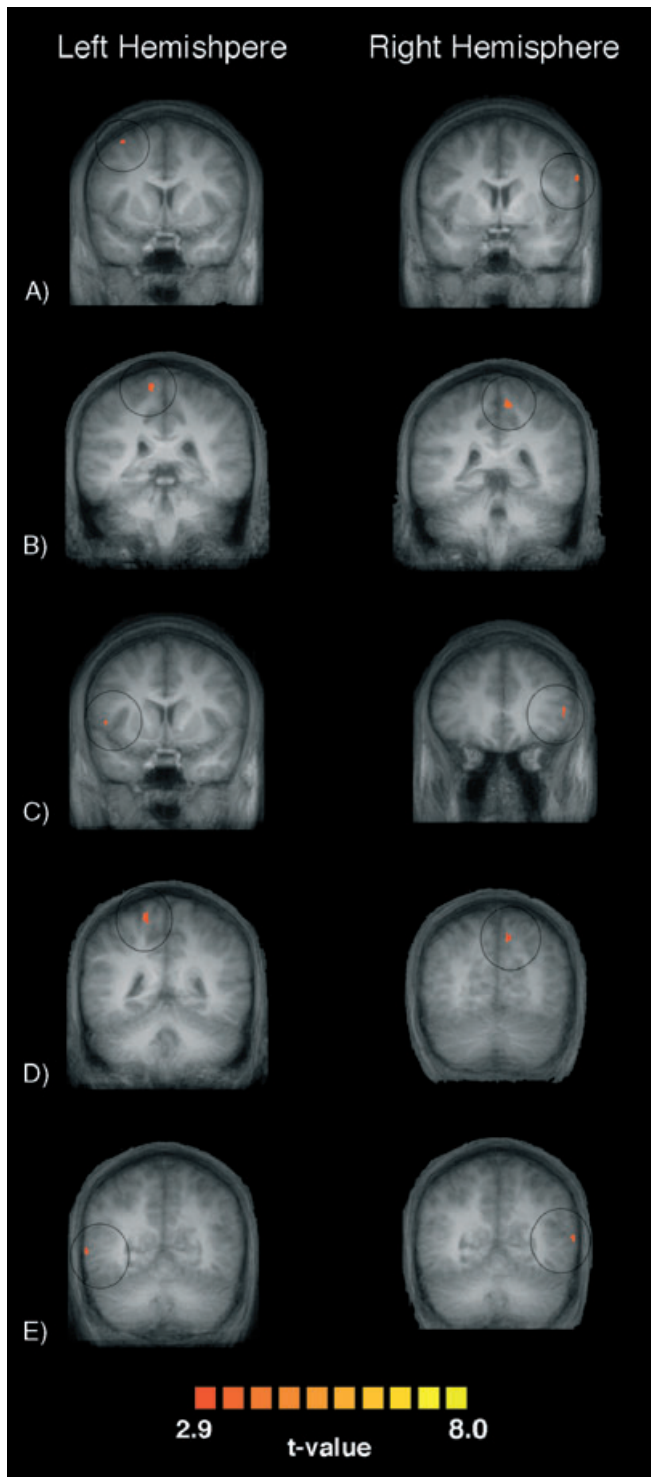


FIG. 2. Bilateral brain activity related to the performance of the familiar path. The neural activity resulted from the comparison between the last 2 min of performance (when participants were highly familiar with the pathway) minus the first 2 min of the task (when participants were still unfamiliar with the path). The figure displays in coronal section the bilateral significant increased BOLD signal within (A) the pre-motor cortex (left:  $x = -31$ ,  $y = 9$ ,  $z = 56$ ; right:  $x = 61$ ,  $y = 3$ ,  $z = 30$ ), (B) the paracentral lobule (left:  $x = -9$ ,  $y = -33$ ,  $z = 63$ ; right:  $x = 8$ ,  $y = -35$ ,  $z = 54$ ), (C) the inferior/middle frontal gyrus (left:  $x = -45$ ,  $y = 8$ ,  $z = 7$ ; right:  $x = 45$ ,  $y = 31$ ,  $z = 15$ ), (D) the superior parietal lobe (left:  $x = -16$ ,  $y = -43$ ,  $z = 59$ ; right:  $x = 10$ ,  $y = -63$ ,  $z = 38$ ) and (E) the middle temporal cortex (left:  $x = -60$ ,  $y = -55$ ,  $z = 5$ ; right:  $x = 49$ ,  $y = -13$ ,  $z = -15$ ).

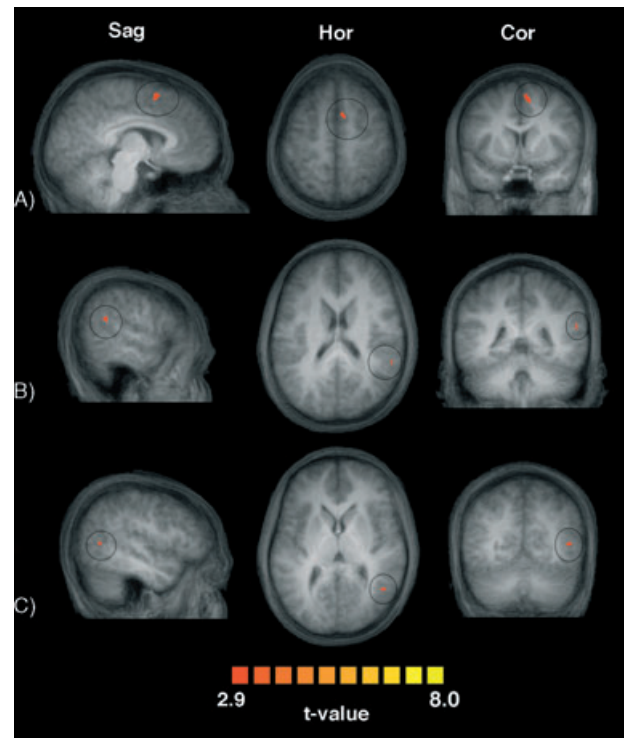


FIG. 3. Brain activity related to the perceptual detection of relevant environmental changes. The activity resulted from the comparison between the BOLD signal occurring when sudden unexpected stimuli were encountered on the path and the BOLD signal when no such stimuli occurred while the subject was on the same part of the path. Significant increase in the BOLD signal was seen within the supplementary motor cortex (A) ( $x = 7$ ,  $y = 8$ ,  $z = 52$ ), the temporo-parietal junction (B) ( $x = 54$ ,  $y = -40$ ,  $z = 20$ ) and the middle temporal gyrus ( $x = 45$ ,  $y = -57$ ,  $z = 7$ ) (C) shown in sagittal (Sag), horizontal (Hor) and coronal (Cor) sections.

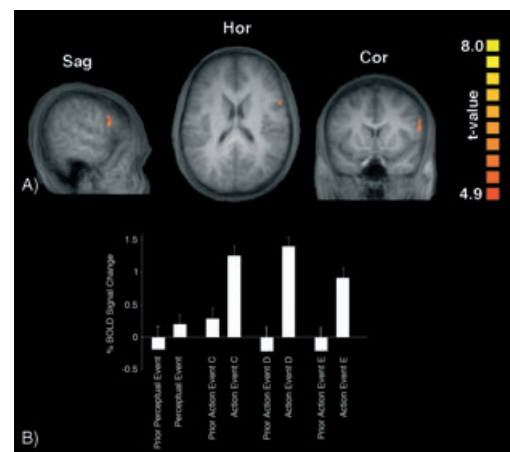


FIG. 4. The figure shows the brain activity resulting from the direct comparison between activity related to stimuli that required change in action (action events) minus activity related to stimuli that did not require action (perceptual events). The figure depicts activity within the right mid-ventrolateral pre-frontal cortex in areas 45 and 47/12 ( $x = 55$ ,  $y = 21$ ,  $z = 11$ ; peak  $t$ -value = 6.685; number of voxels 124) in sagittal (Sag), horizontal (Hor) and coronal (Cor) sections (A). In addition, the figure shows the BOLD signal change of this brain region during the different conditions of the task (B).

TABLE 1. Neural activity related to the performance of the highly familiar pathway

Anatomical region	Hemisphere	x	y	z	Voxels	t-value	BA
Pre-motor cortex	R	61	3	30	32	4.29	6
Somatosensory cortex	R	64	-11	28	39	4.04	43
Paracentral lobule	R	8	-35	54	145	4.40	4
Middle frontal gyrus	R	45	31	15	29	3.64	9/46
Superior parietal lobule	R	10	-63	38	65	4.07	7
Superior temporal cortex	R	58	-52	12	58	4.04	22
Middle temporal cortex	R	49	-13	-15	54	3.60	21
Hippocampus	R	34	-21	-17	22	4.14	
Putamen	R	21	-9	-2	141	5.26	
Pre-motor cortex	L	-31	9	56	16	3.37	6
Paracentral lobule	L	-9	-33	63	50	4.17	4
Inferior frontal gyrus	L	-45	8	7	17	4.15	44
Superior parietal lobule	L	-16	-43	59	42	3.85	7
Middle temporal cortex	L	-60	-55	5	28	4.09	21
Inferior temporal cortex	L	-52	-42	-12	66	3.89	37
Superior occipital gyrus	L	-14	-79	32	23	3.68	19
Fusiform gyrus	L	-36	-70	-6	77	4.45	19
Hippocampus	L	-37	-19	-14	75	4.01	
Parahippocampal gyrus	L	-24	-7	-27	116	5.06	

Peaks of brain activity reported in Talairach coordinates from the contrast between the last 2 min (when participants were highly familiar with the path) and the first 2 min of the familiarization phase (when they were not familiar with it). BA, Brodmann area.

TABLE 2. Neural activity related to bottom-up attentional mechanisms

Anatomical region	Hemisphere	x	y	z	Voxels	t-value	BA
Pre-motor cortex	R	7	8	52	135	3.655	6
Temporo-parietal junction	R	54	-40	20	12	3.044	40/22
Middle temporal gyrus	R	45	-57	7	26	3.652	37/39
Anterior cingulate cortex	R	10	20	29	15	3.565	24/32
Perirhinal cortex	R	25	-36	-14	43	3.909	36
Middle occipital gyrus	R	33	-77	17	17	3.204	19
Thalamus	R	5	-14	5	16	3.38	
Cerebellum	R	16	-32	-13	166	4.034	
Lingual gyrus	L	-6	-79	3	952	4.433	18
Cuneus	L	-9	-86	16	90	3.459	18
Putamen	L	-24	1	8	11	3.279	

Peaks of brain activity reported in Talairach coordinates related to the perceptual detection of unexpected events while following a familiar path (bottom-up attentional mechanisms involved in the detection of stimuli). These peaks resulted from the comparison of the perceptual event with performance of the same part of the path when no unexpected stimuli occurred. BA, Brodmann area.

## Discussion

This report describes the patterns of neural activity observed (i) while subjects moved along a familiar path, (ii) when they detected a sudden unexpected event along the familiar pathway and (iii) when such an event required a modification of planned performance.

When participants reach a target location by following a familiar path, they need to process incoming visual information along the full length of the path and execute a series of motor responses to reach the desired target location. This type of processing resulted in bilateral activity in the frontal, temporal and parietal cortex (Fig. 2; Table 1). The pattern of bilateral activity observed within the frontal and parietal lobes, which involved the dorsal motor/pre-motor cortex and the superior parietal cortex, is consistent with evidence that both frontal

and parietal regions contribute to spatial attention, from lesion studies in humans (Mesulam, 1981; Posner *et al.*, 1984), lesion and single neurone recording studies in the monkey (Petrides & Iversen, 1979; Bushnell *et al.*, 1981; Colby *et al.*, 1996; Nakamura & Colby, 2000), and functional neuroimaging studies (Ungerleider & Haxby, 1994; Kastner *et al.*, 1999; Shulman *et al.*, 1999; Corbetta *et al.*, 2000, 2002; Hopfinger *et al.*, 2000). These previous studies provide converging evidence that pre-motor and motor frontal regions and the posterior parietal cortex, which are closely linked anatomically (Petrides & Pandya, 1984), create a neural circuit that is responsible for higher level control of movement in space (Andersen & Gnadt, 1989; Milner & Goodale, 1995; Petrides & Pandya, 2006). Here, we show that such a neural circuit also subserves the cognitive functions involved when individuals move within the environment, thereby allowing them to attend to relevant information and apply appropriate motor responses (Corbetta *et al.*, 1998; Culham *et al.*, 1998; Nobre *et al.*, 2000) to reach a known location. As frontal and parietal regions show responses related to attention, memory and eye movement (Bruce & Goldberg, 1985; Gnadt & Andersen, 1988; Colby *et al.*, 1996), we suggest that in human locomotion this neural circuit is responsible for selecting, processing and controlling the spatial information that individuals are expected to process while following a familiar path to a target.

Of particular interest for our study is the question of neural activity in response to the sudden appearance of unexpected events while navigating along a familiar path. The detection of unexpected events resulted in increased neural activity within the supplementary motor cortex and the temporo-parietal junction of the right hemisphere (Fig. 3). It has been suggested that a right-sided neural network acts as an alerting mechanism for the detection of changes occurring during performance (Corbetta & Shulman, 2002). Several neuroimaging studies have shown increased activity in the supplementary/pre-motor cortex and the temporo-parietal junction when participants detected unexpected stimuli (Corbetta *et al.*, 2000; Perry & Zeki, 2000), independent of their location (Arrington *et al.*, 2000; Kirino *et al.*, 2000; Marois *et al.*, 2000), sensory modality (Downar *et al.*, 2000) or response demands (Braver *et al.*, 2001). In addition, neuropsychological studies show that damage to this neural network impairs the detection of infrequent stimuli (Wilkins *et al.*, 1987; Knight & Scabini, 1998; Daffner *et al.*, 2000). Our findings are consistent with these studies and suggest that a right fronto-parietal attentional network is involved in detecting unexpected events while individuals move in the environment, a daily life activity that has never been investigated in previous studies. In addition to this right fronto-parietal network, however, we found increased bilateral activity in higher visual areas in the lingual and middle occipital gyri (Table 2). In accordance with previous findings (Kastner *et al.*, 1999; Hopfinger *et al.*, 2000), this increased neural activity may reflect enhanced extra sensory processing of unexpected objects, which will allow subjects to make navigational decisions.

Finally, the present data demonstrate a distinction between the neural responses to unexpected events that do not require any adjustment in planned performance and unexpected events that do require such an adjustment. A selective response in the mid-ventrolateral pre-frontal cortex (areas 45 and 47/12) in the right hemisphere was observed when subjects face an unexpected environmental stimulus that requires a change in the usual performance (Fig. 4), irrespective of the type of change required by the unexpected event, but not when the stimulus did not require a behavioural response. This cortical region has been shown to play a critical role in executive processing during active controlled retrieval of specific aspects of information from both short-term and long-term memory (Petrides, 1996). As supported by functional neuroimaging studies in humans (Owen, 1997; Petrides, 2000) and single neurone recording

TABLE 3. Neural activity related to direct contrasts among action events

Anatomical region	Hemisphere	x	y	z	Voxels	t-value	BA
Event B > Event C							
Middle temporal gyrus	L	24	-48	-36	19	6.43	20
Inferior occipital gyrus	L	18	-43	-71	8	5.5	19
Event B > Event D							
Superior frontal gyrus	R	201	22	61	28	7.04	10
Motor cortex	R	50	57	-22	37	6.21	1
Cingulate gyrus	R	25	10	-50	33	5.74	31/32
Inferior parietal lobe	R	29	55	-51	25	6.36	40
Inferior temporal gyrus	R	78	43	-72	5	5.75	37
Middle occipital gyrus	R	380	24	-86	13	7.47	18
Middle frontal gyrus	L	109	-40	40	24	6.61	9
Pre-central gyrus	L	117	-1	-23	66	6.65	4
Superior parietal lobe	L	146	-20	-63	52	7.47	7
Cuneus	L	121	-12	-86	34	6.72	19
Event C > Event B							
Inferior frontal gyrus	R	24	34	20	1	5.35	47
Middle frontal gyrus	L	35	-27	-1	60	5.9	6
Pre-central gyrus	L	13	-27	-19	64	5.45	4
Middle temporal gyrus	L	54	-59	-35	4	7.56	21
Superior parietal lobe	L	34	-41	-66	44	6.05	7
Inferior parietal lobe	L	158	-49	-55	44	6.12	40
Pre-cuneus	L	22	-6	-62	35	5.64	7
Event C > Event D							
Middle frontal gyrus	R	69	40	37	25	6.06	46/9
Middle temporal gyrus	R	16	61	-52	3	5.15	21
Superior parietal lobe	R	125	42	-52	49	5.61	7
Inferior parietal lobe	R	73	53	-39	43	6.44	40
Middle frontal gyrus	L	44	-26	2	61	5.91	6
Inferior frontal gyrus	L	151	-50	30	5	7.19	45
Superior parietal lobe	L	51	-13	-59	63	6.18	7
Pre-cuneus	L	60	-6	-68	30	6.24	7
Hippocampus	L	23	-28	-15	10	5.78	
Event D > Event B							
Superior frontal gyrus	L	18	-11	20	60	5.34	6
Superior temporal gyrus	L	35	-60	-48	20	6.76	22
Pre-cuneus	L	21	-9	-58	41	6.09	7
Event D > Event C							
Middle frontal gyrus	L	26	-36	34	9	5.93	46/9
Caudate nucleus	R	15	16	-2	26	5.77	

Peaks of brain activity reported in Talairach coordinates from the comparison among action events (B, C and D). See Materials and methods for description of the events. BA, Brodmann area.

studies in monkeys (Owen, 1997; Petrides, 2000), these executive processes are initiated consciously by the subjects and guide their plans and intentions while performing a given task (Petrides, 2005). We suggest that, in the context of navigating through an environment, the detection of unexpected stimuli that require performance adjustments triggers the planning of a new motor response (different from the one usually adopted) and/or the retrieval of specific information. For instance, the occurrence of an unexpected accident blocking the usual pathway to a given target location will require an individual to follow a different pathway in order to reach the same target location. This implies, first, the retrieval of knowledge about the environment and then the programming and execution of a series of motor responses different from the ones usually adopted. All of these new action-planned displacements are arguably triggered by the detection of a single event interfering with a usual performance.

The findings that we have discussed up to this point emphasize the role of cortical circuits in human navigation. However, our data also show activity in other cerebral structures. The activity that we found in the hippocampal complex and striatum, when participants performed the familiarization phase, is consistent with the role of these brain regions in human navigation (Maguire *et al.*, 1998; Epstein *et al.*,

1999; Hartley *et al.*, 2003; Iaria *et al.*, 2003). Previous studies show that the hippocampus is fundamental in the creation and use of a cognitive map of the environment (Iaria *et al.*, 2007), whereas the striatum subserves procedural memory, which allows individuals to move in an automatic manner after they have become familiar with the environment (Hartley *et al.*, 2003; Iaria *et al.*, 2003). Although both the hippocampus and striatum were shown to be involved when individuals performed the task, the paradigm that we adopted in this study does not allow us to assess the degree to which the subjects made use of a cognitive map in order to follow the familiar pathway or adopted a complete procedural approach to follow the same pathway. This makes it difficult to establish separately the role of the hippocampus and striatum in this specific navigational task. However, the evidence that both of these brain structures were engaged in performing the task suggests that presumably both hippocampal and striatal processes were involved during the familiarization phase, when subjects were learning both the cognitive map of the environment and a familiar path through it. Thus, both of these memory functions are suggested to be fundamental for successful navigation through familiar surroundings complementing the attentional systems involved as individuals move in the environment.

TABLE 4. Neural activity related to direct contrasts between action events and the perceptual event

Anatomical region	Hemisphere	x	y	z	Voxels	t-value	BA
Event B > Event A							
Superior frontal gyrus	R	68	21	55	36	6.4	9
Superior frontal gyrus	R	279	7	-11	67	6.94	6
Superior frontal gyrus	R	289	11	63	30	7.76	10
Middle frontal gyrus	R	33	36	60	5	6.09	10
Superior temporal gyrus	R	26	55	1	4	6.38	22
Inferior parietal lobe	R	31	58	-25	27	6.45	40
Superior frontal gyrus	L	128	-6	3	66	7.71	6
Superior frontal gyrus	L	92	-10	63	30	6.46	10
Middle frontal gyrus	L	463	-38	37	28	7.46	8
Inferior parietal lobe	L	39	-57	-27	20	6.73	40
Event C > Event A							
Superior frontal gyrus	R	180	24	-8	63	6.45	6
Inferior parietal lobe	R	27	46	-36	52	5.26	40
Middle frontal gyrus	L	163	-26	0	61	6.26	6
Middle frontal gyrus	L	96	-28	31	46	6.81	8
Middle frontal gyrus	L	61	-27	57	13	7.39	10
Middle frontal gyrus	L	164	-42	37	27	6.6	9
Inferior frontal gyrus	L	123	-53	8	4	7.18	44
Superior parietal lobe	L	52	-5	-63	56	6.27	7
Inferior parietal lobe	L	29	-57	-31	22	6.19	40
Pre-cuneus	L	137	-8	-69	30	6.13	7
Superior frontal gyrus	R	180	24	-8	63	6.45	6
Event D > Event A							
Superior frontal gyrus	L	72	-11	5	63	5.82	6
Middle frontal gyrus	L	163	-36	34	12	7.15	46/9

Peaks of brain activity reported in Talairach coordinates resulting from the independent contrasts between action events (B, C and D) and the perceptual event (A). See Materials and methods for description of the events. BA, Brodmann area.

In summary, the present study demonstrated that a selective right fronto-temporo-parietal network responds when individuals face unexpected events during navigation. These findings are consistent with a recent attentional model (Corbetta & Shulman, 2002) and show how previous findings regarding visual attention in both human and non-human animals are related to real-life situations such as human navigation. Furthermore, activity in the right ventrolateral pre-frontal cortex, which is implicated in active controlled retrieval of task-relevant information, increases when unexpected events require adjustments in performance. These data extend earlier findings from visual attention tasks to the more complex real-life ability of navigation and suggest that similar neural mechanisms subservise bottom-up attentional systems during spatial navigation and are crucial for effective locomotion in real surroundings.

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