Neural signatures of detours, shortcuts and back-tracking during navigation

Abbreviated Title: Neural responses to detours, shortcuts and back-tracking

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Significance Statement

Adaptation to change is important for survival. Although real-world spatial environments are prone to continual change, little is known about how the brain supports navigation in dynamic environments. Here, we used fMRI to examine the brain activity elicited when humans took forced detours, identified shortcuts and spontaneously adjusted their routes by back-tracking along their recent path. Both externally and internally generated changes in the route activated the fronto-parietal attention network, whereas only internally generated changes generated increased activity in the dorsal anterior cingulate cortex and a concomitant disengagement from the default-mode network. The results provide new insights into how the brain plans and re-plans in the face of transformations of space.

Abstract

Central to the concept of the 'cognitive map' is that it confers flexibility in behaviour allowing animals to take efficient detours, exploit shortcuts and realise when they need to back-track rather than continue on a poorly chosen route. Currently the neural underpinnings of such behaviour remains unclear. During fMRI we tested human subjects on their ability to navigate to a set of goal locations in a virtual desert island riven by lava, which occasionally shifted to block selected paths (necessitating detours) or receded to open new paths (affording shortcuts). We found that detours activated a wide network of frontal regions compared to shortcuts. Activity in right dorsolateral prefrontal cortex specifically also increased when participants encountered new paths that appeared to provide a shortcut in the direction of the goal but which added distance to the path (false short-cuts). During spontaneous back-tracking events, activity increased in frontal regions and the dorsal anterior cingulate cortex, while activity in regions associated with the core default-mode network were suppressed. These results help inform current models as to how the brain supports navigation and planning.

Introduction

A challenge all motile animals face is adapting to changes in an environment so that they can efficiently return to safety or find food. Adaptations include spotting newly-created shortcuts and minimizing the lengths of forced detours. Tolman (1948) conceptualized this ability as arising from an internal 'cognitive map' (or, in control theoretic terms, an internal model) of the environment. Indeed, evidence from recordings in rodents and fMRI in humans has supported the view that hippocampus contains a cognitive map (Epstein, Patai, Julian, & Spiers, 2017; O'Keefe & Nadel, 1978; Spiers & Barry, 2015). However, the evidentiary basis in humans and other animals of the navigational functions of the cognitive map in the face of change is incomplete.

Early studies in rodents (Tolman & Honzik, 1930) along with more recent studies, in rats and other mammals, support this view (Alvernhe, Save, & Poucet, 2011; Alvernhe, Van Cauter, Save, & Poucet, 2008; Chapuis, 1987; Chapuis, Durup, & Thinus-Blanc, 1987; Poucet, Thinus-Blanc, & Chapuis, 1983; Winocur, Moscovitch, Rosenbaum, & Sekeres, 2010). However, the evoked neural responses at the moment of encountering changes in the environment have received little investigation in rodent studies.

A number of functional neuroimaging studies in humans have studied the evoked responses to detours (Howard et al., 2014; Iaria, Fox, Chen, Petrides, & Barton, 2008; Maguire et al., 1998; Rauchs et al., 2008; Rosenbaum, Ziegler, Winocur, Grady, & Moscovitch, 2004; Simon & Daw, 2011; Spiers & Maguire, 2006; Xu, Evensmoen, Lehn, Pintzka, & Håberg, 2010). Rather than revealing hippocampal activity these studies have consistently reported increased prefrontal activity. Across studies, there was evidence of: i) increased activity in right lateral prefrontal regions when detecting changes in the environment, ii) activity in frontopolar cortex when re-planning and setting sub-goals, and iii) superior prefrontal cortical activity when processing conflict between route options (Spiers & Gilbert, 2015). Such responses are consistent with the view that the prefrontal cortex (PFC) supports flexible behaviour in response to changing affordances in the environment (Shallice, 1982; Spiers, 2008).

Given the central role of the hippocampus in supporting cognitive maps (Epstein et al., 2017; O'Keefe & Nadel, 1978) it is surprising that activity was not reported in fMRI studies examining detours (Spiers & Gilbert, 2015). However, a study in which people navigated London's Soho region (UK) found that the change in the path distance to the goal caused by detours was correlated with right posterior hippocampal activity: the larger the change in the path the greater the activity (Howard et al., 2014). This result is consistent with the proposal that the hippocampus might simulate the future path to the goal (Javadi et al., 2017a;

Ólafsdóttir, Barry, Saleem, Hassabis, & Spiers, 2015; Ólafsdóttir, Bush, & Barry, 2018; Spiers & Gilbert, 2015), with larger changes in the path leading to greater demands on simulation. In addition, in the study by Howard et al., 2014, activity in the caudate was also found to correlate with the distance to the goal at forced detours, consistent with this region coding a prediction error about future events (O'Doherty et al., 2004) and a role in spatial planning (Simon & Daw, 2011).

While some studies have examined both shortcuts and detours in changing environments (Simon & Daw, 2011; Yoshida & Ishii, 2006) these previous paradigms made it difficult to dissociate the specific effects of detours and shortcuts. Of course, detours and shortcuts both change the path to the goal, and so one might ask whether there a universal response to the change in the path, or whether the typically greater demands of re-planning at detours elicit highly distinct patterns of activity. Furthermore, it is not clear whether these or other regions are involved in avoiding false shortcuts, which seem plausible until long-term knowledge of the environment is considered. In addition to externally caused changes in route, how do different brain regions respond when someone spontaneously realises they have made and error and decide to back-track along a recent route? To explore these questions, we combined fMRI with virtual reality (VR) environment ('LavaWorld') in which participants navigated an island looking for hidden treasure with paths constrained by lava, which had the capacity to shift and open new paths (shortcuts) or close others off (detours).

Methods

Participants

Twenty-two subjects (mean age: 21.8 ±2.3 years, range: 19-27; 14 female). Participants were administered a questionnaire regarding their navigation abilities/strategies (Santa Barbara Sense of Direction Scale; mean score=4.9, range: 3.7-5.7). All participants had normal to corrected vision, reported no medical implant containing metal, no history of neurological or psychiatric condition, color blindness, and did not suffer from claustrophobia. All participants gave written consent to participate to the study in accordance with the Birkbeck-UCL Centre for Neuroimaging ethics committee. Subjects were compensated with a minimum of £70 plus an additional £10 reward for good performance during the scan. One participant was excluded from the final sample because there was severe signal loss from the medial-temporal area in their functional scan.

VR environment: Lavaworld

A virtual island maze environment was created using Vizard virtual reality software (© WorldViz). The maze was a grid network, consisting of 'sand' areas that were walkable, and 'lava' areas, which were unpassable and as such were like walls in a traditional maze. However, the whole maze layout was flat, so there was visibility into the distance over both sand and lava. This allowed participants to stay oriented in the maze throughout the task. Orientation cues were provided by four unique large objects in the distance. Movement was controlled by 4 buttons: left, right, forwards and backwards. Pressing left, right or backwards moved the participant to the grid square to the left, right or behind respectively, and rotated the view accordingly. Similarly, pressing forward moved the participant to the next square along. See Figure 1 for a participant viewpoint at one point in the maze. Participants were tested over two days, on day 1 they were trained on the maze, and on day 2 they were tested in the MRI scanner.

Training

On the first day, participants were trained on the maze (25 x 15 grid) to find goal locations. During this phase, all goal objects (20 in total, distributed across the maze) were visible at all times, and participants navigated from one to the next based on the currently displayed target object (displayed in the top-right corner of the screen). After one hour of training,

subjects were given a test to establish how well they had learnt the object locations. On a blank grid, where only the lava was marked, participants had to place all the objects they remembered. They were given feedback from the experimenter, and if needed, prompts as to the missing objects. This memory-test was repeated twice more during the training, after 1.5 and 2 hours. At completion, for participants to return for the fMRI phase on the second day, they had to score at 100% accuracy in placing the objects.

Training **Test**

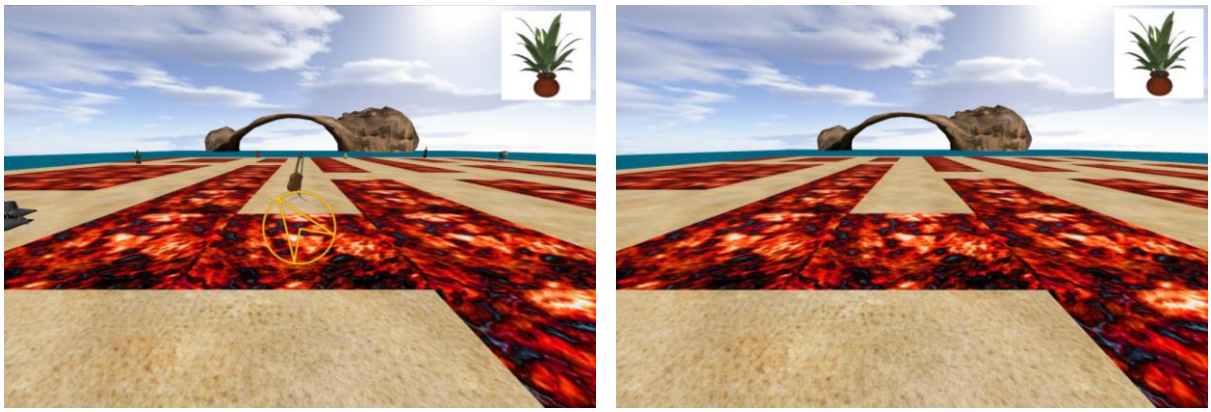

Figure 1: LavaWorld. *Example view of training environment and current goal object (top right corner). A distal cue is visible (arch), and 3 others were located at the other cardinal directions. The sand represents the path that can be moved along, whereas the red 'lava' blocks in the path. During Training, objects were visible across the whole maze, and participants used the controls to move forward, left/right and backward to collect them, with an arrow guiding them towards the object (in the first of three rounds of training). During the Test phase, the objects were not visible and the environment could change, such that the lava shifted around to reveal new paths (Shortcuts or False Shortcuts), or could close an existing path (Detours). See Figure 2 for examples.*

Test & fMRI scan

On the test day, participants were given a brief refresher of the maze with the objects. While in the MRI scanner, participants performed the test phase of the experiment. A single trial in the test phase is defined as being informed which is the new goal object, and then finding the way to, and arriving at, it. During the test phase, two things were different from training: 1) target objects were not visible, so participants had to navigate between them based on their memories of the locations, and 2) the lava could move, blocking some paths and creating new paths. Participants were informed that this was a temporary change and that after reaching the goal the environment would revert to the baseline state. During each journey to an object, a change occurred in the lava layout. At the point of a change, the screen froze for 4 seconds to ensure that participants had an opportunity to detect the change and consider their path options. These changes could either be Detours (when a piece of lava was added to block the current path on the grid, thus forcing the participant to take an new longer route to their goal); Shortcuts (a piece of lava was removed and replaced with sand, allowing the participant to pick a shorter route); False Shortcuts (visually identical to Shortcuts, but choosing a route through them would increase the net distance to the goal because of the layout of the maze; False Shortcuts came in two classes: False Shortcuts Towards and False Shortcuts Away from the goal); and a condition in which the screen froze, but no lava was added/removed). Behavioral data showed that participants were much slower to respond in conditions with no change, which may be because they were unsure if they had missed a subtle change. Thus we focused our analysis on the other conditions. For

Detours and Shortcuts, there were also two levels of change to the (optimal) new path, either 4 or 8 grid steps extra/less, respectively. See Figure 2 for example schematics of these changes. Finally, there were control 'Follow' trials which started with an arrow that indicated the direction to travel. In this case, participants were required to follow the twists and turns of the arrow until a new target object appeared. The comparison of Navigation' vs 'Follow' movements allowed us to relate our results to those of previous experiments (Howard et al., 2014; Javadi et al., 2017a)(Howard et al., 2014; Javadi et al., 2017a; Patai et al., 2017). Before scanning, participants were allowed to familiarize themselves with the scanner button pad, and the changes that would occur. This involved presenting them with a novel environment that had not been experienced on day one, and which had no object, different distal cues and a different maze layout, to avoid any confounds or confusion with training and test mazes. Participants could then practice the task in this new environment, and accustom themselves to the controls (button pad with 4 active buttons: left, right, forward, and turn around) and to the appearance of changes to the lava.

Spatial Parameters

Spatial parameters were calculated in the same manner as in Howard et al (2014) and Javadi et al (2017). In brief, Path Distance (PD), Euclidian Distance (ED), Egocentric Goal Direction (EGD) and the number of optimal upcoming Turns were calculated at each change point. All parameters were highly correlated ($p>0.001$, see Table 1A), except for PD and EGD. Based on our previous work (Howard et al. 2014, Patai et al., 2017), our main analysis involved using PD as an independent parametric regressor (Table 1B). We also considered a control model that included both PD and EGD, as these measures were not correlated. The other parameters were not explored independently. Spatial parameter values were rescaled between 0 and 1, where 1 is the maximum value, e.g. the greatest distance.

Table 1A: Correlation between Spatial Parameters at Change Point / Start (Object onset).

PD: new path distance; PD%: relative change in path distance (compared to pre-change path distance); EGD: egocentric goal direction; ED: Euclidian distance, Turns: number of upcoming turns. Note PD% does not exist at the start of trial, i.e when the target object is presented, as this measure assumes a change from the original path, which is only available at Change Points.**p<0.001; * p<0.05

	PD	PD%	ED	EGD	Turns
PD		0.43**	0.64**/0.07**	-0.03/-0.05*	0.58**/0.56**
PD%			-0.1**	0.09**	0.49**
ED				-0.02/-0.07**	0.11**/-0.11**
EGD					-0.22**/0.04

Table 1B: Details of GLM parameters for the fMRI models

MODEL	CONDITIONS	PARAMETRIC REGRESSORS	DURATION
Terrain change type	Detours (+8/-8), Shortcuts (-8/-4), False Shortcuts (Away/Towards), No Change (Control)	-	4s
New Path at Change	All conditions together	PD & PD+EGD (control)	4s
Back-tracking (step-matched)	Back-tracking vs Non-Back-tracking	-	0s

Figure 2: Examples of a changes that occurred during routes to the goal. *Participants start their path from the last object they found and goes towards the current (new) goal location along the shortest path available. For Detours, at some point along the route, the participant's path is blocked and they are forced to take a detour around it to reach their goal. In the case of a shortcut, a grid point would be unblocked, thus revealing a novel, shorter route to the goal (originally optimal path shown in grey if no shortcut had been presented). In the case of False Shortcuts, taking this opening would be detrimental as it would lead to a longer path to the goal, despite the path seeming to head towards (or away) from it. The full grid was 25x15 squares, and is shown from above in these examples. +/- 4 or 8 refers to the amount added or subtracted in steps.*

fMRI Scanning & Preprocessing

Scanning was conducted at the Birkbeck-UCL Centre for Neuroimaging (BUCNI) using a 1.5 Tesla Siemens Avanto MRI scanner (Siemens Medical System, Erlangen, Germany) with a 12 channel head coil. Each experimental session lasted around 60 minutes and was separated in three parts (each of approximately 15-20 minutes). Approximately 980 functional scans were acquired per session (depending on routes taken), using a gradient-echo incremental EPI sequence (TR=3400ms, TE=50ms, TA=3.315s, flip angle= 90°). The slice thickness was 2mm with a gap of 1mm, TR=85ms, TE=50ms, slice tilt = 30°. The field of view was 192 mm, and the matrix size was 64 x 64. The scan was a whole brain acquisition, with 40 slices and a repetition time of 3.4 s. A T1-weighted high-resolution structural scan was acquired after the functional scans (TR=12ms, TE=5,6ms, 1x1x1mm resolution). Ear plugs were used for noise reduction, foam padding was used to secure the head in the scanner and minimize head movements. Stimuli were projected to the back screen, a mirror was attached to the head coil and adjusted for the subjects to see full screen. All fMRI preprocessing and analysis was performed using SPM12. To achieve T1 equilibrium, the first six dummy volumes were discarded. During preprocessing, we used the new Segment (with 6 tissue classes) to optimize normalization. Otherwise, we used all default settings, and we performed slice timing correction. No participants had any abrupt motion changes over 4mm.

Experimental Design and Statistical Analysis

We used a 2 x 2 within subjects design, with two levels of change type (detour or shortcut) and two levels of magnitude (long or short). Participants performed a total of 120 routes, with one change occurring in each route. Each route started from a previous goal and ended at the new goal object for that trial. We used repeated-measures ANOVAs to test for behavioural differences (accuracy, extra steps, back-tracking trials) between conditions. We also calculated d-prime and criterion (signal detection theory measures) to quantify the bias to take a False Shortcuts Towards instead of Away from a goal (both false alarms calculated relative to correct Shortcuts, which are hits). We recorded the response time to make the first choice after the 4 seconds elapsed, but due to the 4 second delay we do not interpret this as a traditional decision-making reaction time.

To analyse the fMRI data, we constructed multiple models, based on a priori predictions from previous work (Howard et al, 2014). Please see that Table 1B for a description of the models, events included and regression parameters. We used a standard preprocessing pipeline in SPM and report all results uncorrected at p=0.005, minimum 5 contiguous voxels (Howard et al., 2014). A priori regions of interest were small volume corrected using anatomical masks (WFU Pick atlas [Maldjian, Laurienti, Kraft, & Burdette, 2003; Tzourio-Mazoyer et al., 2002]) and a functional mask for the dorsomedial PFC (Kaplan et al., 2017) was employed in one follow-up exploratory analysis.

A ‘Back-tracking’ event was defined by when participants pressed the backwards button and returned to a step along the route they had just come down. Non-back-tracking events were picked from the particpants’ other paths and were matched to these in the relative number of steps taken before the back-tracking happened (for example: halfway through the route). We did not use the absolute number of steps, because trials that contained a back-tracking event were often much longer, and thus the step number at which a back-tracking event occurred could have already been at (or past) a goal point in a non-back-tracking trial. We used step matching rather than elapsed time matching because participants’ speed was not controlled and we wanted to match the events based on actual navigation steps and not potential time differences due to stationary behavior.

Results

Behaviour

Our primary measure of navigation in this study is the accuracy of the whole route, in other words whether participants took the optimal path to the target. We ran a repeated measures ANOVA to test for effects of terrain change type on participants' accuracy in finding the correct path. We found that there was a significant effect of terrain change type ($F(1,120)=17.7, p<0.001$), such that Detours (+8) and False Shortcuts Towards the goal resulted in less optimal path taking (both $t(1,20)<-3.6, p<0.002$) compared to all other conditions (see Table 2, and Extended Data Table 1 for comprehensive t-tests).

To follow up the errors in which participants did not take the optimal path, we looked at the number of extra steps taken on a route. We found a significant effect of terrain change type ($F(1,120)=8.3, p<0.001$), with overall more steps off-route in the Detours (+8) and False Shortcuts Towards conditions. When quantifying the number of extra steps as a proportion of the total (new) number of optimal steps from the terrain change point onward for a given route, in fact Shortcuts resulted in the largest proportion off-route (see Table 2). Some of these extra steps were due to participants turning around, i.e., "Back-tracking"; these were again more common especially in the Detours (+8) condition ($F(1,120)=8.5, p<0.001$, compared to all $t(1,20)>2.1$, $p<0.051$, see Extended Data Table S4 for details). Overall, only 19% of the extra steps were such back-tracking events (and this ratio was not significantly different between conditions, $F(1,65)=2.17$, $p=0.068$). Moreover, we calculated the ratio of correct, compared to incorrect, back-tracking trials ("correct" is defined as a trials in which back-tracking would actually bring the participant closer to the goal), and found that overall 85% (±2% s.e.m, range: 50-100%) of back-tracking events were correct or optimal, and occurred equally frequently across all conditions ($F(1,5)=2.2, p=0.066$). Thus, in the majority of Back-tracking events participants became aware that they were heading away from the goal and spontaneously decided to turn around.

Table 2: Behavioural Results Summary [mean (±s.e.m)]

	Detour (+8)	**Detour (+4)**	**Shortcut (-8)**	**Shortcut (-4)**	**False Shortcuts Towards**	**False Shortcuts Away**
Accuracy [%]	64.1(±3.9)	80(±2.3)	84.6(±2.6)	84.6(±2.8)	65.8(±3.1)	81.3(±1.9)
Extra Steps	1.9(±0.26)	0.99(±0.14)	1.5(±0.37)	1.2(±0.3)	2(±0.31)	0.97(±0.17)
Extra Steps [proportion]	1.2(±0.11)	1.4(±0.6)	2.1(±1.07)	1.7(±0.37)	1.3(±0.18)	1.4(±0.32)
Back-tracking [#]	7.1(±1.3)	3.7(±0.7)	2.2(±0.6)	2.6 (±0.6)	4.3(±0.6)	3.5(±0.4)
Back-tracking [% of extra]	22(±5.5)	19(±2.4)	19(±4.4)	22(±6)	14(±2.6)	29(±3.8)
Correct Backtracking [%]	85(±3.1)	83(±3.7	78(±5.5)	70(±7.8)	80(±4.5)	71(±7.7)

fMRI Results

fMRI analyses revealed that bilateral hippocampus, posterior cingulate and retrosplenial cortex, as well as frontal areas were more active when participants were actively navigating than when they merely followed an arrow on the screen (Extended Data Table 3). Both the left and the right hippocampus were significantly more active in the navigate than the follow condition (small-volume correction, FWE $p<0.05$), in line with previous findings (Howard et al., 2014; Patai et al., 2017, for an overview see Spiers & Gilbert 2015).

Caudate, but not hippocampal, activity responds to changes in the path to the goal at Detours

We predicted that hippocampal activity would track the change in the path distance to the goal when the structure of the environment changed. We found no evidence to support this argument, both with specific ROIs and at a low uncorrected threshold ($p < 0.005$). This was also true when purely large Detours (+8) were compared with small Detours (+4). By contrast we found that activity in the caudate nucleus bilaterally tracked the change in the path distance across the events (Table 3), complementing past evidence that this region tracked the magnitude of change at Detours (Howard et al., 2014).

Superior and right lateral prefrontal cortex respond to preferentially to Detours

We then investigated the brain areas that have been found in previous studies when comparing Detours to non-Detours, including the superior frontal gyrus (SFG), the right lateral prefrontal (rlPFC) and frontopolar cortex (Spiers & Gilbert, 2015), using a combined mask of these areas. A linear contrast of terrain change type: Detours (+8) > Detour (+4) > Shortcuts (-4) > Shortcuts (-8), revealed a significant effect, with specifically the SFG and rlPFC activity scaling with the deviation from the optimal path prior to the change (Figure 3A and Table 3). False Shortcuts Towards the goal also significantly activated the rlPFC compared to Shortcuts (Figure 3B, and Table 3). By contrast False Shortcuts Away from the goal did not drive activity in rlPFC (Table 3). Frontopolar cortex was not found to be modulated by Detours, Shortcuts, or False Shortcuts.

Prefrontal responses evoked during spontaneous internally generated Back-tracking events

Next, we were interested in the brain areas that were activated by spontaneous, internally generated route changes, i.e. Back-tracking events. To investigate their neural correlates, we compared moments in routes where a back-tracking event occured (defined as a return to a previous grid point along a single journey towards a target), to equivalent events where no back-tracking happened (equalized according to relative steps along a journey). When comparing Back-tracking to non-Back-tracking events, we again found significant SFG and rlPFC activations (Figure 4A, and Table 3). These results suggest that the prefrontal regions previously found to be involved in detour processing are also active when route changes occur due to spontaneous, internally generated events. We did not find evidence that the frontopolar cortex was responsive to Back-tracking.

Outside our ROIs drawn from Spiers and Gilbert (2015), we found that during Back-tracking, activity in a region of medial prefrontal cortex survived whole-brain FWE correction (Figure 4). This activation overlapped with the dorsal anterior cingulate area (dACC) reported by a recent study when difficult navigational decisions were required (Kaplan et al., 2017). We used a functional ROI (includes the dACC and Supplementary motor area (SMA)) from Kaplan et al. (2017) to investigate whether this area was also active during terrain change points, and found that for both the linear contrast above (Detours (+8) > Detour (+4) > Shortcuts (-4) > Shortcuts (-8)) and False Shortcuts Towards > Shortcuts contrast this area was significantly active (Table 3). However when plotting the peak activation, we found that Backtracking events resulted in a significantly larger activation of the dACC than the other contrasts (both $t>5.4, p<0.001$; Figure 4, bottom right), pointing to a potentially unique role during the processing of internally generated route changes, which presumably occurs when participants become aware their current route plan is not effective.

Table 3: Results of small-volume correction in ROIs during Terrain Changes and Back-tracking

	Combined Frontal Mask	SFG	Frontopolar	rlPFC	dACC	Caudate	Left HC	Right HC
D+8 > D+4 > S-4 > S-8	**p=0.001 Z=4.97**	**p=0.001 Z=4.97**	n.s.	**p=0.001 Z=4.26**	**p=0.002 Z=4.73**	**p=0.02 Z=3.93**	n.s.	p=0.077 Z=3.23
False Shortcut Towards > Shortcuts	**p=0.001 Z=5.28**	n.s.	p=0.075, Z=3.34	**p=0.001 Z=5.28**	**p=0.023 Z=4.20**	n.s.	n.s.	n.s.
Back-tracking > Non-back-tracking	**p<0.001 Z=5.63**	**p<0.001 Z=5.63**	n.s.	**p=0.015 Z=4.07**	**p<0.001 Z=5.91**	n.s.	n.s.	n.s.
Back-tracking > Turns	**p<0.001 Z=5.21**	**p<0.001 Z=5.21**	n.s.	**p=0.02 Z=4.0**	**p<0.001 Z=5.65**	n.s.	n.s.	n.s.

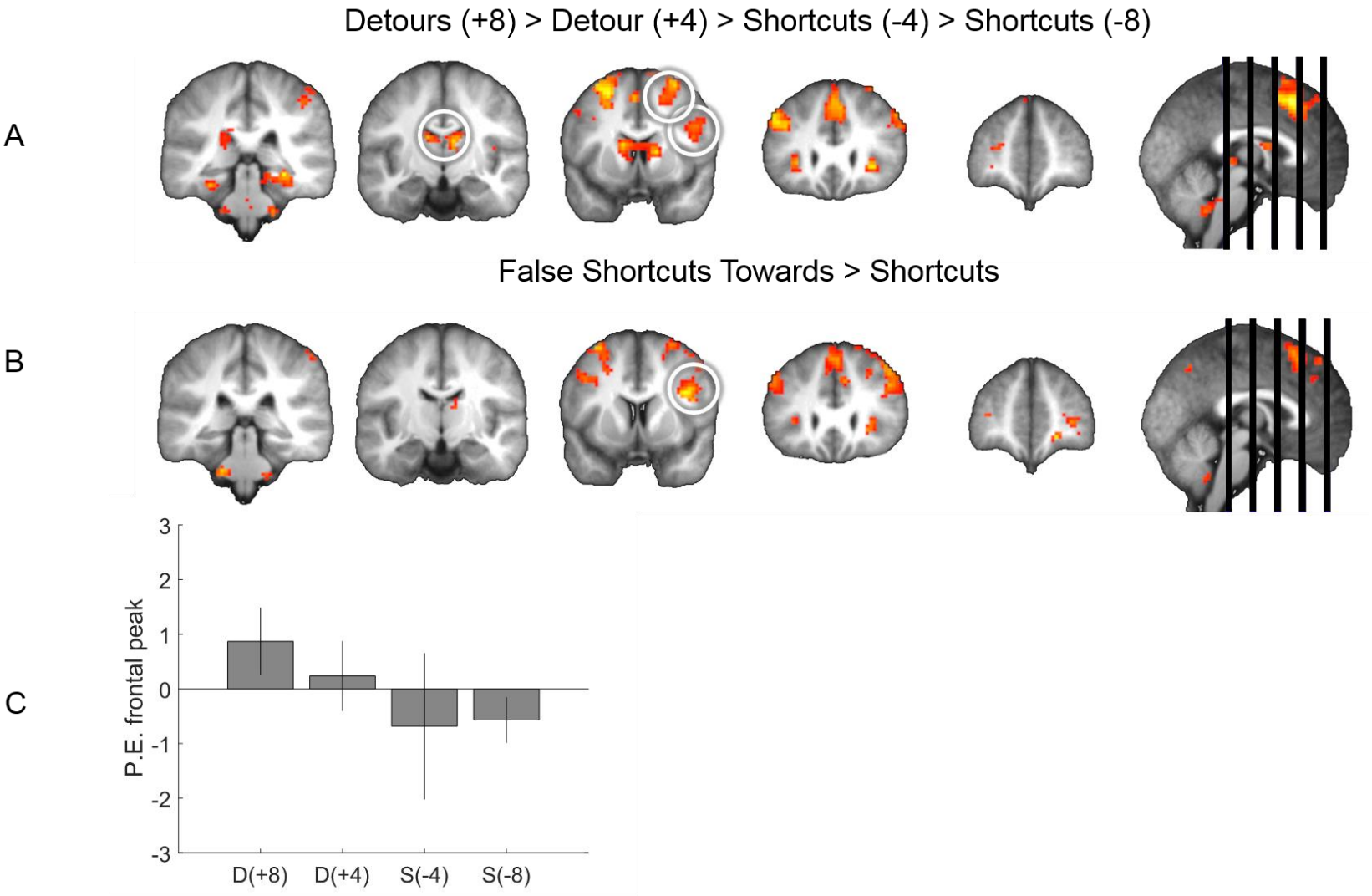

Figure 3: Prefrontal Areas involved during processing of Terrain Changes. *A) Superior frontal gyrus and right lateral PFC were engaged in the linear contrast of Detours and Shortcuts [Detours (+8) > Detour (+4) > Shortcuts (-4) > Shortcuts (-8)] and B) right lateral PFC when comparing False Shortcuts Towards the goal to Shortcuts. Figures are thresholded at p=0.005 uncorrected. C) Parameter estimates from the peak frontal voxel in the linear contrast from A, to illustrate the effect.*

Back-tracking events disengage from the putative Default-Mode Network

Because Back-tracking involved a visual change in view (180°) compared to Non-back-tracking events we explored whether similar regions would be active when participants turned left or right compared to when they did not turn. We found a significant response in the functional dACC mask when comparing Turns to Non-turns, however the peak was located in the SMA. When Back-tracking was compared to turns the dACC was significantly more active in Back-tracking events, in which an equivalent amount of visual change is contrasted (90° difference in change of viewpoint). Conversely, Turns compared to Back-tracking resulted in significant responses in the hippocampus, anterior medial PFC and posterior cingulate cortex. These regions are overlapping with those implicated in the default-mode network (DMN) (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010). To explore whether the results match the default-mode network more explicitly we created an aggregate ROI including the medial PFC, the precuneus/posterior cingulate cortex, bilateral parahippocampal cortex and angular gyrus. We found that Back-tracking significantly suppressed this putative DMN compared with Turns, and this was also the case when comparing Back-tracking to Non-back-tracking and Detour events, highlighting disengagement from this network when participants spontaneously instigated a route change (Figure 5).

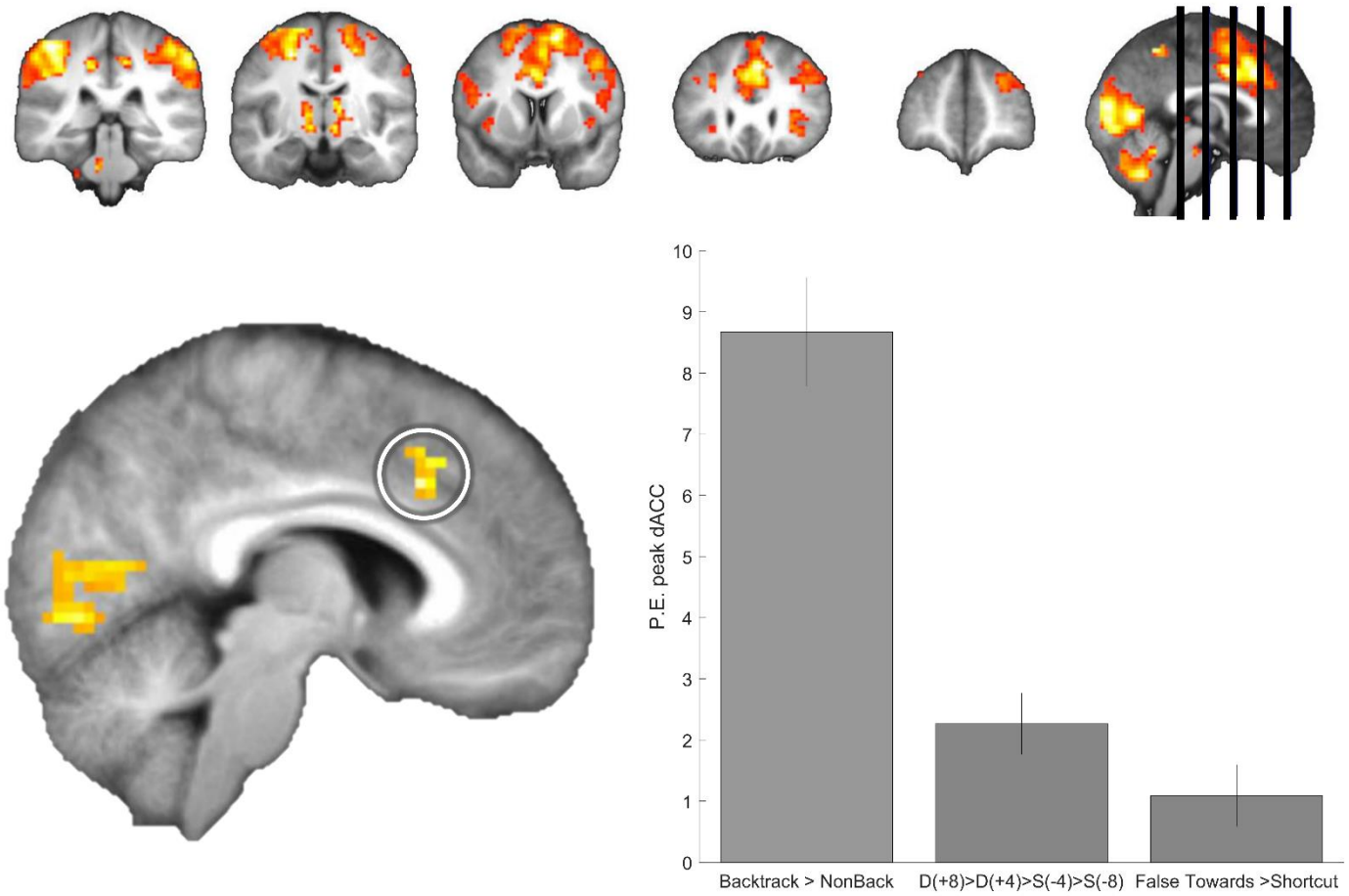

Figure 4: Back-tracking activates a range of frontal areas, as well as the dorsal anterior cingulate cortex. *Top: Similarly to Detours, the superior frontal gyrus and right lateral PFC are activated during Back-tracking compared to Non-back-tracking events. Figures are thresholded at p=0.005 uncorrected. Bottom: Whole-brain results (FWE p<0.05) revealed a significant activation in the dorsal anterior cingulate cortex. Extracting parameter estimates from the peak voxel in dACC [MNI: x:6 y:20 z:35, note Kaplan et al. (2017) = x:6 y:23 z:37] show that Back-tracking and Detours activate this region significantly, however Back-tracking activates it significantly more than Detours and False Shortcuts Towards the goal.*

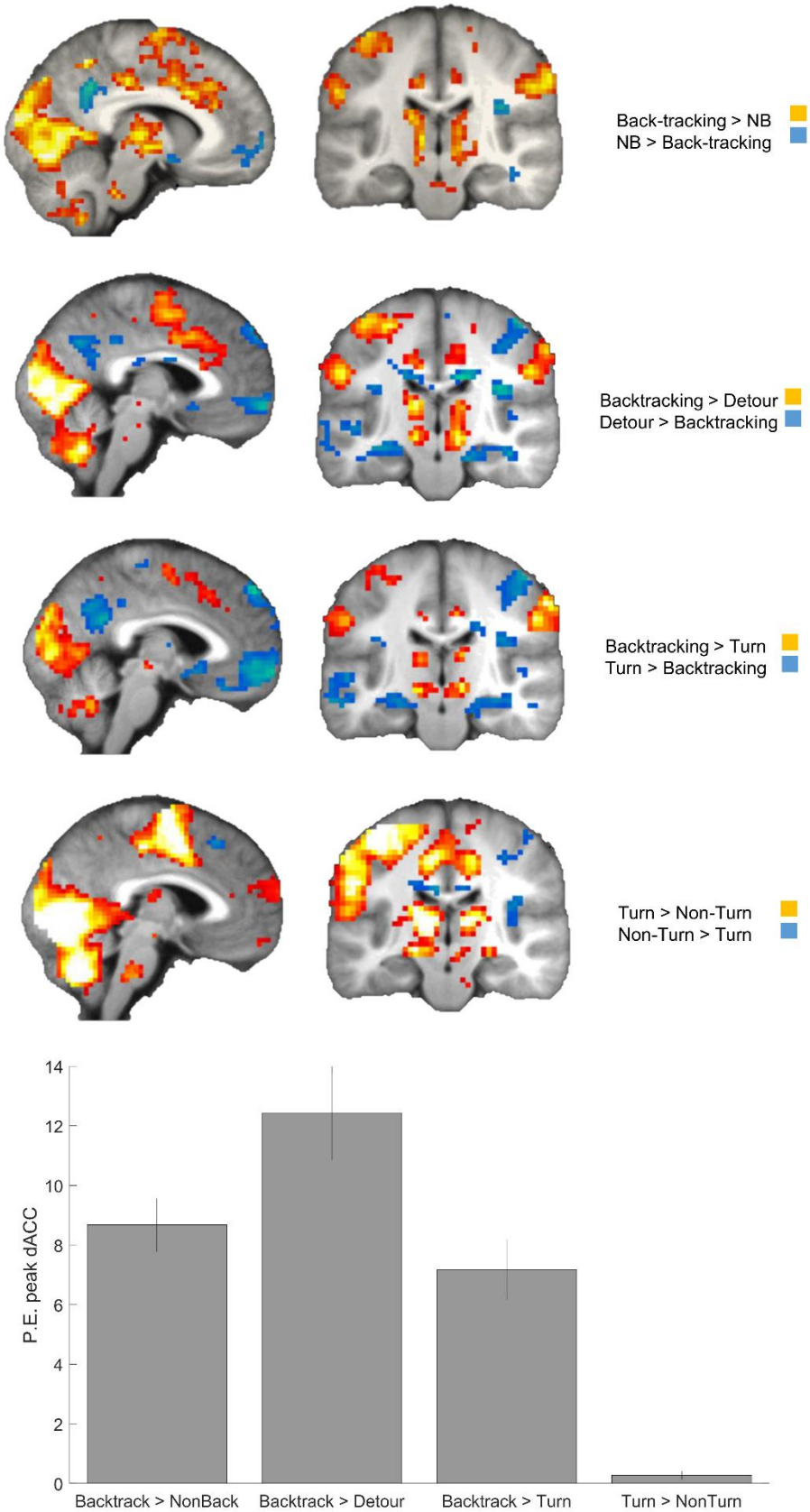

Figure 5: Back-tracking events disengage regions in the putative Default-mode network when compared to other events. *Results are shown at p=0.005 uncorrected. Significant results in the combined DMN mask: Backtracking compared to Non-backtracking (p=0.038,Z=4.21), Turns (p=0.006,Z=4.62) and Detours (p=0.008,Z=4.55).*

Discussion

A core tenet of the cognitive map theory is that it supports flexible navigation by enabling an animal to make use of shortcuts and take efficient detours (O'Keefe & Nadel, 1978; Tolman, 1948). Despite the wide acclaim for this idea, rather little research, especially in humans, has been directed at the neural mechanisms of such adaptative behaviour (Spiers and Gilbert, 2015; Epstein et al., 2017). Using fMRI and a VR task involving navigation through a landscape that changed its layout sporadically we ewere able to examine the neural responses to forced detours, novel shortcuts, false shortcuts and spontaneously generated path changes (Back-tracking). We find: i) superior and lateral PFC and caudate activity respond to Detours, maximally when there is a large change in the path, i) rlPFC responds when false shortcuts to the goal need to be avoided and iii) a sub-region of anterior cingulate that increases its activity during spontaneous Back-tracking in the context of de-activation of the regions associated with the default-mode network. We find no evidence to support the suggestion that hippocampal activity tracks the increase in distance to the goal at detours (Spiers and Glibert, 2015).

The role of prefrontal cortex, hippocampus and caudate in responding to detours and shortcuts

Based primarily on evidence from nine fMRI studies, Spiers & Gilbert (2015) made a number of preliminary predictions about how PFC and the hippocampus might respond to forced detours and changes in the layout. Lateral PFC was suggested to provide a prediction error signal in response to changes in the path options (responding whenever an unpredicted change in the possible paths occurs). The superior and anterior PFC were thought to support re-formulation of the route plan (responding at all events that require reconsidering the change in route plan). The hippocampus was postulated to simulate the future path the goal (responding the greater the increase in the path to the goal), drawing on rodent place cell studies (Ólafsdóttir et al., 2015; Pfeiffer & Foster, 2013). Here we failed to find evidence that the hippocampus specifically encodes the change in the path distance to the future goal. One possibility is that the hippocampus simulates future possible scenes (Hassabis & Maguire, 2007), re-constructing the different locations that lie between the current location and the future goal (Javadi et al., 2017b; Spiers & Barry, 2015). However, in the case of the current study the environment was sparse with few features to distinguish different parts of the island, which could conceivably lead to a lower demand for scene-construction during navigation. Consistent with this argument, previous studies reporting hippocampal activity correlated with the future path to the goal used real-world stimuli with numerous nameable landmarks located along the paths (Howard et al., 2014; Javadi et al., 2017b; Patai et al., 2017).

By contrast to the hippocampus we found that activity in lateral and superior PFC, as well as the caudate, responded the larger the increase change in the path to the goal. The caudate response is consistent with a prior result from Howard et al. (2014) which found that the larger the Detour the more activity was elicited in the caudate nucleus. The caudate has traditionally been associated with 'response-leaning' and stimuli-action associations (Dahmani & Bohbot, 2015; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Packard & McGaugh, 1996; West et al., 2015). Thus, speculatively the caudate responses may relate to a signal linked to updating the transition structure in the environment at that particular location where the change occurs. An alternative is that the caudate plays an important role in updating its representations in relation a model of the environment. A previous fMRI study in which the participants had to navigate to goal locations in a continually changing environment found that caudate responses were more consistent with the application of a model-based representation of the environment (Simon & Daw, 2011).

The PFC responses we observed are consistent with the predicted roles of the superior PFC supporting resolving path conflict and the rlPFC processing a prediction error

signal between the predicted state of the world and the encountered layout (Spiers & Gilbert, 2015). Two types of prediction error could be processed in the current paradigm. One is the signed prediction error signal linked to the difference in the path before and after the change in the layout (+ve for detours, -ve for shortcuts). The other is an unsigned prediction error where the amount of change is coded rather than the direction of change (+ve for both detours and shortcuts). Our results show a wide network of regions including our PFC and caudate ROIs were driven in a manner consistent with the signed prediction error (maximal for +8 Detours and less for the shortcuts). Our results are thus more consistent with the PFC and caudate coding the increase in path rather than an unsigned prediction error, and rather than being driven in a clear linear manner by the unsigned prediction error, the data suggest these regions might be driven in a threshold manner by large detours over the other conditions. Future research carefully varying the amount of path change at different detours will be required to explore these possibilities.

It is possible the PFC responses to Detours are driven by the presence of the physical barrier appearing to block the route. This is certainly a possibility in several past studies (Iaria et al., 2008; Maguire et al., 1998), though not all (see Howard et al., 2014) However, we found increased rlPFC for events in which the path opened but choosing it was an error (False Shortcuts) compared to a path opening and it being useful (Shortcuts). Thus, the response of rlPFC in the current study cannot purely be ascribed to a role in detecting a prediction error in the path. Rather, its response is consistent with it playing a role in behavioural control: suppressing the pre-potent response to move towards the goal drawing on the observation that there is a now a barrier or that there is a new path opening that is not helpful.

Our current data do not provide a statistical dissociation between the roles of the rlPFC and the superior PFC, both were active at Detours and maximally at large Detours and both show similar activity profiles when participants choose to Back-track. Indeed, our study was not designed to separate these responses. Future studies that separate prediction errors from route conflict would be a useful way to dissociate these regions and perhaps compare their responses with the lateral PFC, which has been shown to express activity consistent with a breadth-first-search of future street options when a detour occurs (Javadi et al., 2017).

Spontaneous Internally Driven Changes in Route - Backtracking

Across both externally (Detours, False Shortcuts) and internally (Backtracking) driven changes we found increased activation in the dorso-medial PFC, an area that has been implicated in various contexts including hierarchical planning (Balaguer, Spiers, Hassabis, & Summerfield, 2016), times when demanding choices need to be made at a future point in a maze (Kaplan et al., 2017), and also model updating, irrespective of difficulty or simple error-related signalling (Kolling et al., 2016; O'Reilly et al., 2013). However, we found activation in the dorsal anterior cingulate cortex was much more pronounced during Back-tracking, possibly reflecting stronger engagement of planning and error signals when participants spontaneously realized that they were on a sub-optimal path. This is further supported by the result that nearly 80% of Back-tracking events were correct, resulting in a shorter path to the goal. One previous study also found medial PFC to be correlated with a model-based estimate of behaviour relating to putative events of back-tracking in a simple maze (Yoshida & Ishii, 2006), and our peak activation for the dACC is highly proximal to the one previously reported. This highlights the role of the medial PFC/dorsal anterior cingulate in situations in which re-evaluation and updating from internal monitoring are required. It remains to be tested where the underlying error signal comes from, whether it is the medial PFC/dACC itself or whether this area is involved in orchestrating the reorienting of attentional and memory systems based on incoming uncertainty signals.

Additionally, when comparing Back-tracking to Non-back-tracking, Detours or Turn events, we found a disengagement from the putative default-mode network (including the medial PFC, hippocampi, posterior cingulate cortex), further underscoring the notion that internally generated route changes resulted in a global resetting of attention from internal to external sources. Consistent with this interpretation in a parallel study using the same task and magnetoencephalography we find a suppression of alpha oscillations during spontaneous Back-tracking events, which has previously been links to switches in attention (Javadi et al., 2018). While our results provide potentially interesting insights to spontaneously switching the route during navigation it is important to note that Back-tracking did not occur equally frequently among participants and that the novelty of the motor command to press a rarely-used response button may have contributed to the responses in various brain regions in this analysis. A potential solution will be to develop a task in which there are forced, but infrequent, back-tracking events (to control for the response novelty) and a requirement for spontaneous button presses that are unrelated to the task, in order to reveal the neural correlates of internally generated events specific to changing a route plan.

Overall, our results help evaluate putative models of how the brain responds during shortcuts and detours and extend them to situations in which the change in plan is driven by an internal monitoring process. Future studies separating conflict between route options from prediction errors, search processes and updating representations will be needed to better understand how the brain adapts to changing environments. Ultimately integrating research with humans and other animals across methods will be important to help advance current theory in this domain.

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Extended Data

Table S1: **Paired Samples T-Test comparing all terrain change types: Accuracy**

		t	df	p
Detour (+8)	**-** Detour (+4)	**-4.210**	**20**	**< .001**
Detour (+8)	**-** Shortcut (-8)	**-5.659**	**20**	**< .001**
Detour (+8)	**-** Shortcut (-4)	**-5.858**	**20**	**< .001**
Detour (+8)	**-** False Shortcut away	**-4.507**	**20**	**< .001**
Detour (+8)	- False Shortcut towards	-0.442	20	0.663
Detour (+4)	- Shortcut (-8)	-1.468	20	0.158
Detour (+4)	- Shortcut (-4)	-1.375	20	0.184
Detour (+4)	- False Shortcut away	-0.487	20	0.632
Detour (+4)	**- False Shortcut towards**	**3.655**	**20**	**0.002**
Shortcut (-8)	- Shortcut (-4)	-0.012	20	0.990
Shortcut (-8)	- False Shortcut away	1.047	20	0.307
Shortcut (-8)	**- False Shortcut towards**	**5.059**	**20**	**< .001**
Shortcut (-4)	- False Shortcut away	1.068	20	0.298
Shortcut (-4)	**- False Shortcut towards**	**6.197**	**20**	**< .001**
False Shortcut away	**- False Shortcut towards**	**5.515**	**20**	**< .001**

Note. Student's T-Test.

Table S2: **Paired Samples T-Test comparing all terrain change types: Extra steps**

Paired Samples T-Test

		t	df	p
Detour (+8)	- Detour (+4)	3.159	20	0.005
Detour (+8)	- Shortcut (-8)	1.406	20	0.175
Detour (+8)	- Shortcut (-4)	2.293	20	0.033
Detour (+8)	- False Shortcut away	3.427	20	0.003
Detour (+8)	- False Shortcut towards	-0.286	20	0.778
Detour (+4)	- Shortcut (-8)	-1.293	20	0.211
Detour (+4)	- Shortcut (-4)	-0.442	20	0.663
Detour (+4)	- False Shortcut away	0.083	20	0.935
Detour (+4)	- **False Shortcut towards**	-2.844	20	0.010
Shortcut (-8)	- Shortcut (-4)	0.861	20	0.399
Shortcut (-8)	- False Shortcut away	1.499	20	0.149
Shortcut (-8)	- False Shortcut towards	-1.329	20	0.199
Shortcut (-4)	- False Shortcut away	0.503	20	0.620
Shortcut (-4)	- **False Shortcut towards**	-3.115	20	0.005
False Shortcut away	- **False Shortcut towards**	-3.852	20	< .001

Note. Student's T-Test.

Table S3: **Paired Samples T-Test comparing all terrain change types: Extra steps proportions**

		t	df	p
Detour (+8)	- Detour (+4)	-1.359	18	0.191
Detour (+8)	**- Shortcut (-8)**	**-3.384**	**17**	**0.004**
Detour (+8)	**- Shortcut (-4)**	**-4.244**	**16**	**< .001**
Detour (+8)	- False Shortcut away	-1.933	18	0.069
Detour (+8)	- False Shortcut towards	-1.895	19	0.073
Detour (+4)	**- Shortcut (-8)**	**-3.471**	**16**	**0.003**
Detour (+4)	**- Shortcut (-4)**	**-4.095**	**15**	**< .001**
Detour (+4)	- False Shortcut away	0.272	18	0.789
Detour (+4)	- False Shortcut towards	-0.654	18	0.522
Shortcut (-8)	**-** Shortcut (-4)	**2.239**	**15**	**0.041**
Shortcut (-8)	**-** False Shortcut away	**2.954**	**16**	**0.009**
Shortcut (-8)	**-** False Shortcut towards	**3.175**	**17**	**0.006**
Shortcut (-4)	- False Shortcut away	1.885	15	0.079
Shortcut (-4)	**-** False Shortcut towards	**3.710**	**16**	**0.002**
False Shortcut away	- False Shortcut towards	0.827	18	0.419

Note. Student's T-Test.

Table S4: **Paired Samples T-Test comparing all terrain change types: Back-tracking occurrences**

		t	df	p
Detour (+8)	**-** Detour (+4)	2.548	20	0.019
Detour (+8)	**-** Shortcut (-8)	4.458	20	< .001
Detour (+8)	**-** Shortcut (-4)	3.696	20	0.001
Detour (+8)	**-** False Shortcut away	2.759	20	0.012
Detour (+8)	- False Shortcut towards	2.073	20	0.051
Detour (+4)	- Shortcut (-8)	1.786	20	0.089
Detour (+4)	- Shortcut (-4)	1.884	20	0.074
Detour (+4)	- False Shortcut away	0.386	20	0.704
Detour (+4)	**-** False Shortcut towards	-0.669	20	0.511
Shortcut (-8)	- Shortcut (-4)	-0.559	20	0.583
Shortcut (-8)	- False Shortcut away	-1.989	20	0.061
Shortcut (-8)	**- False Shortcut towards**	-2.350	20	0.029
Shortcut (-4)	- False Shortcut away	-1.579	20	0.130
Shortcut (-4)	**-** False Shortcut towards	-2.024	20	0.056
False Shortcut away	**-** False Shortcut towards	-1.116	20	0.278

Note. Student's T-Test.

Table S5: **Paired Samples T-Test comparing all terrain change types: Back-tracking in relation to overall extra steps**

		t	df	p
Detour (+8)	- Detour (+4)	0.824	18	0.421
Detour (+8)	- Shortcut (-8)	1.475	15	0.161
Detour (+8)	- Shortcut (-4)	0.155	16	0.879
Detour (+8)	- False Shortcut away	-1.057	18	0.305
Detour (+8)	- False Shortcut towards	1.448	18	0.165
Detour (+4)	- Shortcut (-8)	0.066	16	0.948
Detour (+4)	- Shortcut (-4)	-0.509	17	0.618
Detour (+4)	- **False Shortcut away**	-2.398	18	0.028
Detour (+4)	- False Shortcut towards	1.319	19	0.203
Shortcut (-8)	- Shortcut (-4)	-0.295	15	0.772
Shortcut (-8)	- False Shortcut away	-1.565	15	0.138
Shortcut (-8)	- False Shortcut towards	1.125	16	0.277
Shortcut (-4)	- False Shortcut away	-0.657	16	0.520
Shortcut (-4)	- False Shortcut towards	1.573	17	0.134
False Shortcut away	- False Shortcut towards	4.005	18	< .001

Note. Student's T-Test.

Table S6: **Paired Samples T-Test comparing all terrain change types: Percentage of 'Correct' Back-tracking Events**

		t	df	p
Detour (+8)	- Detour (+4)	1.503	21	0.148
Detour (+8)	- Shortcut (-8)	0.941	17	0.360
Detour (+8)	- Shortcut (-4)	2.343	21	0.029
Detour (+8)	- False Shortcut away	1.592	17	0.130
Detour (+8)	- False Shortcut towards	1.724	21	0.099
Detour (+4)	- Shortcut (-8)	0.362	17	0.722
Detour (+4)	- Shortcut (-4)	2.020	21	0.056
Detour (+4)	- False Shortcut away	1.259	17	0.225
Detour (+4)	- False Shortcut towards	1.073	21	0.296
Shortcut (-8)	- Shortcut (-4)	1.902	17	0.074
Shortcut (-8)	- False Shortcut away	-1.394	17	0.181
Shortcut (-8)	- False Shortcut towards	-0.638	17	0.532
Shortcut (-4)	- False Shortcut away	-1.983	21	0.061
Shortcut (-4)	- False Shortcut towards	-1.279	17	0.218

Note. Student's T-Test.