

# *An fMRI study of parietal cortex involvement in the visual guidance of locomotion*

Article

Accepted Version

Billington, J., Field, D. T. ORCID: <https://orcid.org/0000-0003-4041-8404>, Wilkie, R. M. and Wann, J. P. (2010) An fMRI study of parietal cortex involvement in the visual guidance of locomotion. *Journal of Experimental Psychology. Human Perception and Performance*, 36 (6). pp. 1495-1507. ISSN 0096-1523 doi: <https://doi.org/10.1037/a0018728> Available at <https://centaur.reading.ac.uk/15521/>

It is advisable to refer to the publisher's version if you intend to cite from the work. See [Guidance on citing](#).

To link to this article DOI: <http://dx.doi.org/10.1037/a0018728>

Publisher: American Psychological Association

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the [End User Agreement](#).

[www.reading.ac.uk/centaur](http://www.reading.ac.uk/centaur)

**CentAUR**

Central Archive at the University of Reading

Reading's research outputs online

## **An fMRI study of parietal cortex involvement in the visual guidance of locomotion**

**Jac Billington<sup>1</sup>, David T. Field<sup>2</sup>, Richard M. Wilkie<sup>3</sup>, and John P. Wann<sup>1</sup>**

<sup>1</sup> Department of Psychology, Royal Holloway, University of London, Egham, Surrey, TW20 0EX, UK.

<sup>2</sup> Department of Psychology, University of Reading, Reading, RG6 6AL, UK.

<sup>3</sup> Institute of Psychological Sciences, University of Leeds, Leeds LS2 9JT, UK.

Corresponding Author: J. Billington; Department of Psychology, Royal Holloway, University of London, Egham, Surrey, TW20 0EX, UK; Tel: 01784 414368; Email: [Jaclyn.billington@rhul.ac.uk](mailto:Jaclyn.billington@rhul.ac.uk).

### **Abstract**

Navigating through the environment typically involves anticipating impending changes in heading trajectory in addition to maintaining the current direction of travel. We explored the neural systems involved in the “far road” and “near road” mechanisms proposed by Land and Horwood (1995) using simulated forwards or backwards travel. During forwards egomotion the distant road edges provided future heading information, which participants used to improve their heading judgments. During backwards egomotion the road edges did not enhance performance because they no longer provided prospective information. This behavioural dissociation was reflected at the neural level, where only simulated forwards travel increased activation in a region of the superior parietal lobe and the medial intraparietal sulcus. Providing only near road information during a forwards heading judgment task resulted in activation in the motion complex (MT+). We propose a complementary role for the posterior parietal cortex and MT+ in detecting future path information and maintaining current lane positioning respectively.

Keywords: Heading, SPL, IPS, MT+, and road features.

## Introduction

The ability of an animal to perform goal directed movements through complex environments whilst avoiding obstacles is crucial to that animal's survival. Setting aside the possible presence of confounding eye or head movements, one of the main cues for detecting locomotor direction is optic flow (Warren & Hannon, 1988). There is a strong body of research investigating how direction of travel can be extracted from flow, see Lappe, Bremmer, & van den Berg (1999) for a review. Whilst much of this work has concentrated on detecting instantaneous heading, more recent studies have modelled the way in which information from flow might be used to enable the negotiation of scene features such as obstacles or road boundaries (Fajen & Warren, 2003; Wilkie & Wann, 2002; Wilkie, Wann, & Allison, 2008). Successfully avoiding boundaries at high-speeds requires a level of prospective control that goes beyond the immediate information supplied by instantaneous heading. Here we build on previous work that has identified the cortical regions implicated in detecting heading, with a view to improving our understanding of how the brain integrates the perception of self-motion from flow with the 3D spatial features that shape future path.

### *Detecting Heading from Flow*

There is increasing evidence that both the middle superior temporal (MST) cortex and ventral intraparietal (VIP) cortex perform crucial roles in detecting direction of heading from studies with primate and, more recently, human populations. MST is an area which, alongside area MT, composes the human motion complex (MT+), thought to be the functional equivalent of MST and MT in primates. Whilst area MT is thought to be tuned to cues associated with motion in the visual field (Lagae, Maes, Raiguel, Xiao, & Orban, 1994), it seems that MST in particular responds to optic flow cues which are concordant with egomotion (expansion/ contraction and rotation) in both primates (Duffy & Wurtz, 1995; Page & Duffy, 2008) and humans (Dukelow et al., 2001; Huk, Dougherty, & Heeger, 2002; Morrone et al., 2000; Smith & Wall, 2007). Area VIP is located in the dorsal stream and receives input from both MT and MST (Andersen, Asanuma, Essick, & Siegel, 1990). In macaques, area VIP has been found to respond to components of optic flow (Schaafsma & Duysens, 1996) and, furthermore, representation of heading in VIP is in head centred coordinates (rather than retinal coordinates), suggesting that this region may compensate for eye-movements when encoding instantaneous heading cues (Zhang, Heuer, & Britten, 2004). More recently, Wall and Smith (2008) have found that whilst both MST and VIP neurons respond strongly to a single optic flow stimulus, consistent with egomotion, MST also responds to local optic flow patches which are surrounded by other optic flow patches, which is inconsistent with egomotion.

Studies which have required human participants to make active heading judgments have found additional activation in several dorsal regions of the parietal lobe. Peuskens, Sunaert, Dupont, Van Hecke, and Orban (2001) found that heading judgments in response to global flow patterns activated a region of the intraparietal sulcus (IPS), which the authors claim may be the human homologue of area 7a in primates. Receiving inputs from both MST and VIP, area 7a responds to optic flow signals as well as retinotopic stimulus position and eye position, implicating this region as the neural basis of spatial representation for the purpose of motion through space (Read & Siegel, 1997).

### *Integrating heading with forward obstacles or paths*

In natural environments navigating through space does not simply involve the detection of instantaneous heading via optic flow. Egomotion necessitates a continual response to adjust heading, the segregation of ground features to enable the detection of obstacles, and the selection of viable pathways. A recent study observed the neural correlates of making heading judgments using ground flow patterns with and without overlaid road markings (Field, Wilkie, & Wann, 2007). It was found that the presence of continuous road features which provided information about both current trajectory and future path specifically activated areas of bilateral superior parietal lobe (SPL), medial to the focus of activation in the Peuskens et al. (2001) study. A region anterior to the SPL peak of activation responded to error signals when heading was not maintained within road markings. Together, this suggests a dorsal network of regions which not only detect basic cues to egomotion, but also integrate information regarding current and future path boundaries within the visual scene.

Convergent with work on heading detection and steering, research in related fields supports the idea of a parietal contribution to egomotion. Wolbers, Hegarty, Buchel, and Loomis (2008) explored the regions involved in updating the spatial locations of discrete ground features when an observer moves forward (as indicated by optic flow). During the basic task of updating spatial estimates Wolbers and colleagues found bilateral activation of superior parietal cortex; this highlights the role of the SPL in spatial encoding and updating of future targets, obstacles or paths during forwards locomotion. This finding is concordant with research which suggests that the SPL plays a role in visual marking; that is, encoding and subsequent inhibition of old spatial features during visual search (Pollmann et al., 2003). Such inhibitory processes could undoubtedly play a part in maintaining information regarding future path online whilst simultaneously maintaining current heading. The notion of a parietal involvement in egomotion is strengthened by studies which have implicated a role for the inferior parietal lobe in computing egocentric and body centric aspects of wayfinding tasks (Maguire et al., 2008). In addition to this, Seubert, Humphreys, Müller and Gramann (2008) have found that patients with parietal (inferior and superior) lesions have difficulties reporting vector translations and drawing heading paths after a simulated tunnel journey shown from an egocentric viewpoint.

Within the stimuli used by Field et al. (2007) there were at least two highly salient features provided by the road; near road edges, which were informative about instantaneous lane position and whether a heading/steering error has occurred; and distal road edges, which provided information regarding future path or, more specifically, the direction of travel which needed to be attained/maintained in 1-2sec time. It can be argued that perceiving future path is an essential requirement for smoothly adjusting current path for tasks such as steering a bend (Wilkie & Wann, 2003; Wilkie & Wann, 2006). The alternative is to attempt to iteratively correct the direction of travel, moment by moment, with respect to near road edges, which is not a robust strategy as speed of travel increases. Land and Horwood (1995) investigated the behavioural responses to near and far road edge information, using occlusion of road features at varying vertical extents. Presentation of near road edges only allowed for accurate control of lane positioning; however, cues to distant road edges were required to allow smooth steering around simulated bends. The authors interpreted their results as suggesting a near road mechanism for accurate lane positioning and a far road mechanism for timely steering anticipation respectively. Thus, the case for the brain activation identified by Field et al. (2007) being caused by processing of specific future path information would be strengthened by a clear behavioural effect if far road features were presented in isolation. The use of such preparatory heading information in order to improve lane positioning at a later point in time would suggest that this region is not only involved in representing egocentric coordinates but also in storage and inhibition of such coordinates until they should be appropriately utilised. Field et al. (2007) did not test the far road in isolation, but here we address this by presenting far and near road features independently. We required participants to “passively” steer using a joystick. This means participants attempted to indicate the path that they perceive themselves to be on, but their heading remained computer controlled and there are no visual consequences of them making a mistake (or error feedback from mistakes). We predicted that presenting far road features would improve accuracy and timing of their passive steering responses and also reproduce the SPL activation found by Field et al. (2007), but this area would not be activated by near road edges. There is the possibility, however, that the far road edges just provide a salient environmental feature, and as such their motion within the scene aids the detection of heading (Li & Warren, 2000). We addressed this in two ways; firstly we included a condition where the projected view was opposite to the direction of travel (i.e. travelling backwards). The logic behind the inclusion of the backwards condition was that road edges provide equivalent local motion cues during backward and forward travel, but they only indicate future path during forward travel. In addition to this we calculated the local motion of the roads edges in the scene and correlated these with steering adjustments to assess whether participants were using these as a cue to steering.

## Materials and Methods

### *Participants*

14 neurotypical, paid volunteers (7 males and 7 females) aged between 20 and 35 (mean = 27.21, sd = 4.79) took part in this study. 13/14 participants were right handed, one participant was left handed. The study was approved by a local ethical committee; all participants were screened according to standard fMRI scanning guidelines and gave their written consent to take part in the study.

### *Stimulus Presentation*

Stimuli were projected on to a screen at the end of the scanner bore via a projector in the scanner control room. Participants viewed the screen whilst lying in the bore of the scanner via a mirror positioned ~15 cm from their eyes. The screen refresh rate was 60 Hz and the resolution was 1024\*768 pixels. The horizontal and vertical extent of the screen was 34° and 30° respectively.

### *Experimental Paradigms*

This study comprised of four separate experiments. Two of these experiments were localisers for regions known to be active during saccadic eye movement (localiser 1) and during the detection of optic flow components consistent with egomotion (localiser 2). Whilst we were not specifically interested in the main results of these two localisers we used activation from these experiments to create regions of interest (ROIs) for the purpose of either exclusively masking activation in the two main experiments, or for the purpose of comparing signal change in these ROIs across conditions in the two main experiments. Details of these procedures are given below.

Due to restrictions on the amount of time a participant was allowed to spend in the scanner in a 24 hour period (<90 mins), two separate scanning sessions were carried out on two separate days. Session 1 consisted of experiment 1 and localiser 1, and session 2 consisted of experiment 2 and localiser 2. The order in which participants received these sessions was alternated to control for practice effects in the two main experiments. A subset of participants came in for a third session in which eye movement data were recorded in the scanner environment. In total 12 of the 14 participants returned for two scanning sessions and completed all experiments. One participant did not complete localiser 2 and one participant did not complete experiment 2.

*Localiser 1, parietal eye field localiser.* We used a saccadic eye movement task to locate the parietal eye fields (PEF), a parietal region thought to be the putative human homologue of the lateral intraparietal area (LIP) in monkeys. The PEFs are commonly activated when making saccadic eye movements (Kan, Misaki, Koike, & Miyauchi, 2008) as well as suppressing them (Schraa-Tam et al., 2008). The PEFs are also linked with the perception of retinal motion (Erickson & Thier, 1991) and are known to have strong connections to the frontal eye fields (Corbetta et al., 1998; Perry & Zeki, 2000). The functional localisation of PEF in the saccadic eye movement task allowed us to use exclusive masking procedures in order to remove activation from contrasts in experiments 1 and 2 which may have been directly related to planning eye movements or spatial shifts of attention in response to the road edges, rather than integrating future path information per se; this procedure was effective in our previous study (Field et al., 2007). The saccade localiser task was used in two further instances; first, to determine whether eye movement or attentional effects resulted in higher activation in the region found to be involved in detecting future path and, second to see whether the PEFs were activated to a different extent across each of the heading conditions.

Participants were presented with alternating fixation (Fix) or saccade (Sacc) conditions. During the Fix condition only one fixation dot was present in the centre of the screen and participants were asked to remain fixated on that dot. During the Sacc condition a dot jumped randomly round the screen, changing position every 500ms. The maximum horizontal eccentricity of the dot was 12.5 degrees from the centre of the screen and the maximum vertical eccentricity was 6.25 degrees from the centre of the screen. Participants were asked to track this dot in the visual scene as accurately as possible. In total there were 8 blocks of the Sacc condition, which were 20 seconds each in duration. Each Sacc block was interspersed with a Fix block with 16 second duration; the total epi scanning time was 4 minutes and 52.5 seconds.

*Localiser 2, human motion complex localiser.* The purpose of this experiment was to localize the MT and MST components of MT+ in order to assess whether different simulated egomotion conditions resulted in differential BOLD response in a region known to respond to egomotion cues. The experimental paradigm used was based on experimental procedures outlined by several researchers (Dukelow et al., 2001; Huk et al., 2002; Smith & Wall, 2007). The MST component of MT+ has been found to respond to ipsilateral and contralateral optic flow patterns, whilst the MT component had been found to respond primarily to contralateral stimuli (Dukelow et al., 2001; Huk et al., 2002; Smith & Wall, 2007; Wall & Smith, 2008). To differentiate between contralateral and ipsilateral activation we presented patches of alternately expanding and contracting dots in either the left or right visual hemisphere. The patches subtended a visual angle of 5°, and comprised of uniformly distributed moving dots (0.15 dots/ degree<sup>2</sup>) which each subtended the visual angle at 0.3° and had a dot life of 150ms. The eccentricity of the centre of these patches (left or right) was 13.5° from the centre of the screen. Participants were told to focus on a central fixation cross throughout the duration of the experiment. 16 second blocks of alternately expanding and contracting dots were interleaved with 16 second blocks of static dot patches. This experiment consisted of 2 runs, each of 4 minutes and 25 seconds, presenting a total of 8 blocks of each of the left and right optic flow patterns and 8 blocks each of the left and right static patterns.

*Experiment 1, forward/ backward heading task.* Participants were presented with simulated self motion along a sum-of-sines path, but with no active control over their direction of motion. All scenes contained a flat ground plane with a gravel type texture. Motion across such a textured ground plane provides sufficient information to make judgments of heading that are accurate to ~4° (Wilkie & Wann, 2003). In some conditions there were additional road features which either offered information about future path, or acted as a low level visual control. In order to replicate more natural viewing conditions, no constraints were placed on eye movements during the presentation of these stimuli, though eye movements were recorded as outlined in the data collection section.

Participants were told that they would move through the simulated environments either forwards or in reverse along a curving trajectory. In both forwards and backwards travel conditions participants indicated their current heading direction relative to their midline, using the amplitude of the joystick response to indicate the heading angle, equivalent to passive steering. A 15 minute practice session prior to the first scanning session ensured participants were familiar with the stimuli from all five experiments. Importantly, this allowed participants the opportunity to not only practice making heading judgments under different conditions in experiments 1 and 2, but also to actively steer through comparable self motion scenes with the same road features. This practice session allowed them to become accustomed to both the sensitivity of the joystick and to the requirement of the forwards and backward condition responses. In all conditions participants travelled at a constant speed of 8 m/s. Whilst the winding trajectory of the roadway was the same in all conditions, and optically identical for forwards and backwards travel, the initial start position was varied between sessions.

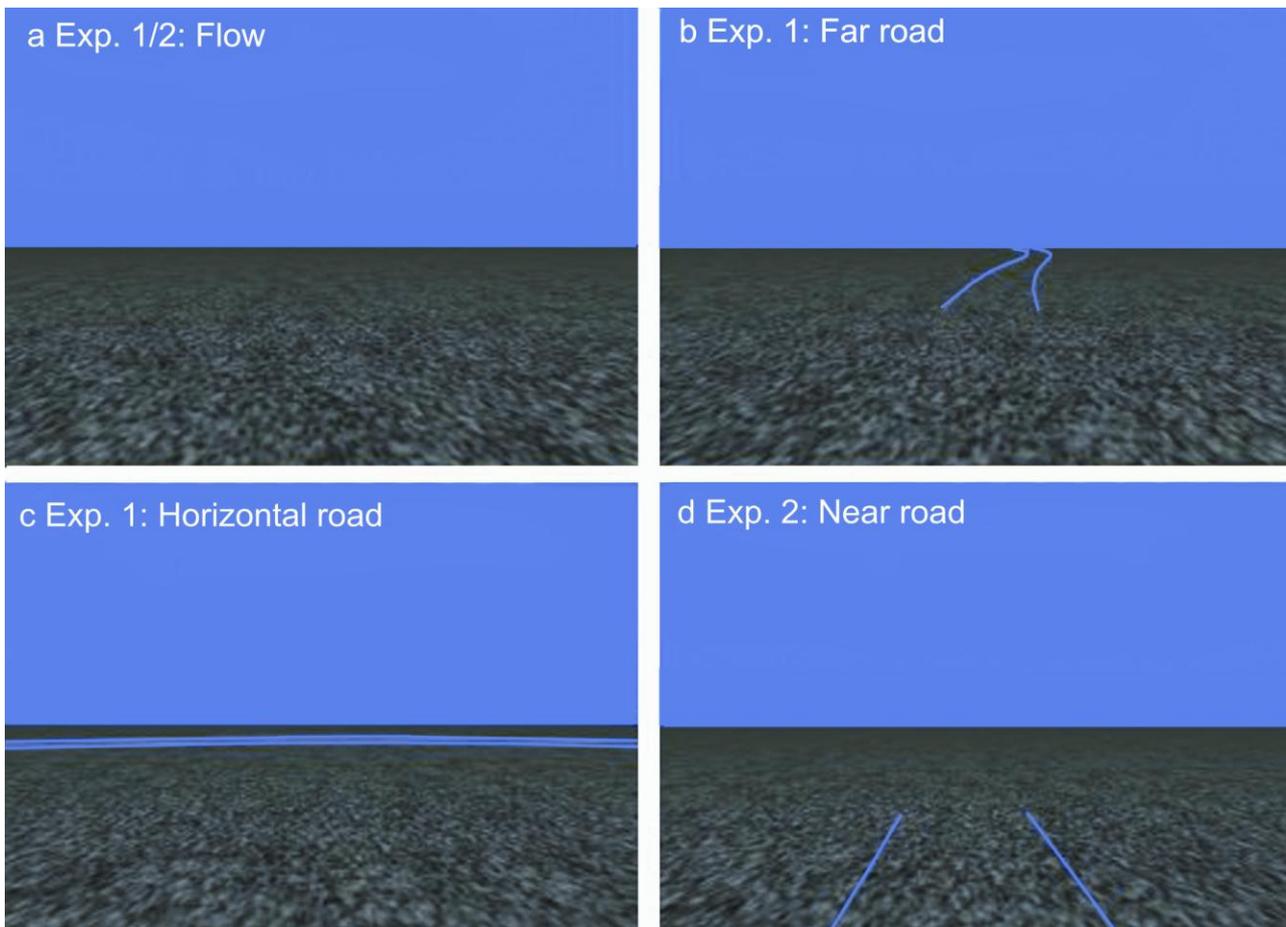


Figure 1: Examples of rendered single frames taken from the moving stimuli presented in experiments 1 and 2. Frames a, b and c represent forward and backward stimuli from experiment 1. Frame a shows the ground flow in conditions 1 and 2; the optic flow would be moving towards the viewer in condition 1 (forward flow) and away from the viewer in condition 2 (backward flow). This same principle was followed for conditions 3 and 4 (b, forward / backward far road) and conditions 5 and 6 (c, forward / backward horizontal road). Frame d represents stimulus from experiment 2, in which ground flow moved towards the viewer in order to simulate forward motion only with near road features. The baseline contrast for this condition was the forward flow stimuli from experiment 1, condition one (frame a).

There were six conditions in total, two of which (conditions 1 and 5) were used in the previous study by Field et al. (2007). The first two conditions (figure 1a, flow) consisted of a textured gravel ground plane on the lower half of the screen with a horizon and sky in the upper half of the screen. Simulated self motion gave the impression of either following a winding course (condition 1, forward flow [Flow<sub>f</sub>]) or reversing along a winding course (condition 2, backward flow [Flow<sub>b</sub>]); in both of these conditions current heading direction could, in principle, be discerned from global optic flow patterns. Conditions 3 and 4 both consisted of the same textured gravel plane and trajectory as in the flow conditions but with the addition of a far road feature which was clipped at 12m (1.5s) ahead of the instantaneous position (figure 1b, far road). In condition 3 (forward far road [FarRd<sub>f</sub>]) this gave the participant additional information about future path so that they could anticipate what their trajectory would be in 1.5s, alongside the task of judging their current heading from ground flow patterns. The low level road features provided in condition 4 (backward far road [FarRd<sub>b</sub>]) were identical; however, this did not allow the participant to anticipate future heading judgement as the road only provided information about where they had travelled 1.5s earlier. Comparison of conditions 3 to 4 allows us to identify activation specific to integrating current heading with information about future path and separate this from responding to current heading and viewing low level visual properties of the road.

Direct comparison of conditions 3 and 4 (FarRd<sub>b</sub> > FarRd<sub>f</sub>), however, would result in activation in regions which may respond more to contracting as opposed to expanding flow patterns, or regions which may be sensitive to task difficulty. Therefore two further conditions were added which could be used to control for

the possibility that viewing backward optic flow would result in more activation than viewing forward optic flow. These conditions contained an irrelevant road feature which was drawn horizontally 32m (3s) ahead ( $\sim 2.8$  degrees under the horizon line: figure 1c). Condition 5, overlaid this horizontal road for forward motion [HorRd<sub>f</sub>] and condition 6, backward motion with a horizontal road [HorRd<sub>b</sub>]. This road feature was made to wind in the same manner as the relevant road feature which allowed us to present stimuli with all the low level properties of the road but without providing any information about future path. Using both these conditions as comparative baseline to the respective FarRd<sub>f</sub> and FarRd<sub>b</sub> conditions will allow us to rule out activation which as a result of differences in task difficulty or in low level visual properties of expanding/ contracting flow patterns.

Each condition was presented 8 times in the scanner, and each presentation consisted of a 16 second block. Trial blocks were interspersed with 16 second rest blocks consisting of a black rectangle instead of the texture ground plane with the same horizon and sky. Data were collected across two epi runs of 11 minutes 25 seconds each.

*Experiment 2, near road heading task.* In this experiment we wished to determine the activation associated with gleaned information from near road edges as opposed to the far road edges. Two conditions were randomly interleaved that both required participants to indicate their heading direction during forward motion. We repeated Condition 1, forward flow, from experiment 1, and also ran Condition 2 (Near road [NrRd<sub>f</sub>]) in which we added near road markings which projected 6m (0.75s) forward although near clipping by the rendered window meant that only 4m of these were visible. The near road edges were weakly informative about current path curvature, in that they tilted a small amount in the direction of travel, but did not supply information about future path curvature. Each condition was presented eight times each, with a trial block length of 16 seconds. The condition blocks were interspersed with rest blocks identical to those in experiment 1. The total epi scan acquisition time was 7 minutes and 8 seconds.

#### *Behavioural Data Collection and Analysis*

*Heading responses.* Behavioural data for experiments 1 and 2 was collected using an MRI compatible joystick (fORP; Current Designs, Inc., Philadelphia, PA) with a sampling rate of 50Hz. The x coordinate range of the joystick was  $\pm 32768$ . The extent to which participants were indicating left heading (+ve coordinates) and right heading (-ve coordinates) was recorded alongside time since trial onset and simulated distance. Prior to analysis half the road coordinates and responses were flipped, so that trials in which participants started out with a leftwards heading could be directly compared to trials where participants started out with a rightwards heading. The minimum and maximum x coordinates of the actual road over time were -6.25m (rightmost extent) and +4.16m (leftmost extent) with a mean of -0.72.

In order to scale the joystick responses to be concordant with the road coordinates, average joystick x coordinates were collapsed across trials to ascertain mean values at each time point. The range of these average responses was then scaled to match the range of the mean road x coordinates. The new minimum and maximum values of the scaled individual joystick responses fell within the range -23.08 to +21.08 with a mean of -0.41. Several cross correlations were carried out between joystick response and the fluctuation in heading as indicated by ground flow. To address the issue of whether the participants were just using the motion of the distant road (12m ahead) to signal instantaneous heading we calculated equivalent correlations the instantaneous position of the road on the screen and also its velocity on the screen. Both the instantaneous heading and the position of the distant road on the screen are all derived from the same sum-of-sines road trajectory, but have different phase with respect to instantaneous road position. If we treat these variables as samples of an on-going time series, then a strong correlation can always be achieved if the cross-correlation with the joystick is calculated across all possible phase differences (e.g. -10sec to +10sec), but these would not be plausible lag/leads for the participant response. To constrain this, cross-correlations were calculated within a lag window of 4sec to -0.5s. This means that we accept that the participants' response might lead instantaneous heading or road motion by 0.5s or lag by up to 4s, but outside that range we are considering correlations to be spurious. The output of the cross-correlation procedure is the optimal value of the correlation and the phase (lag) at which that occurred.

*Eye tracking.* Eye movement data were collected using a View Point Eye Tracker (Arrington Research, 2002) which was set up to collect data via an eye camera attached to the fMRI head coil in the scanner bore. This data were collected for a subset of 6 of the participants in a separate session to the fMRI data collection session because of restrictions placed on the amount of time a participant can spend in the exam room during a 24 hour period. The View Point Eye Tracker collected data with a spatial accuracy of approximately 0.15 degree visual arc and a temporal sampling of 30 Hz. Participants were asked to watch a total of three presentations of each condition from Experiments 1 and 2 whilst indicating their current heading in the same manner as they did in the main experiments.

#### *fMRI data collection and analysis*

*Scan acquisition and pre-processing.* fMRI data were collected using a Siemens Trio 3 Tesla scanner with an 8 channel head array coil. Functional images were collected using 46 slices covering the whole brain (slice thickness 3 mm, inter-slice distance 0 mm, in-plane resolution 3mm×3mm) with an echo planar imaging sequence (TR = 2.5 s, TE = 30 ms, flip angle = 90 degree). Prospective motion correction (PACE) was used to correct for small head movements between volumes (Lee et al., 1996). All experiments in this study employed a block design and all fMRI data analysis was carried out using SPM5 software (Wellcome Trust Centre for Neuroimaging, London). Prior to analysis, all images were corrected for slice timing using the middle slice as a reference slice. Images were realigned to the first image in the first session. Distortions in the epi sequences were corrected using field maps and the custom Fieldmap toolbox (Hutton et al., 2002; Jezzard & Balaban, 1995). All images were normalized using affine and smooth non-linear transformations to an EPI template in Montreal Neurological Institute (MNI) space. Finally, all images were smoothed with a full width half maximum Gaussian kernel of 6 mm.

*1<sup>st</sup> and 2<sup>nd</sup> level analysis.* Individual statistical contrasts were set up using the general linear model to fit each voxel with a combination of functions derived by convolving the standard haemodynamic response with the time series of the events and removing low-frequency noise with a high pass filter with a frequency cut off of 128s. An additional session regressor was added to experiments with more than one run. Contrast maps were created at the individual level and carried forward to group analysis using 2<sup>nd</sup> level one-sample t-tests in SPM5. At the group level, voxel height thresholds were set at  $p = 0.001$  (uncorrected) and then an additional extent threshold ( $k$ ) was set in order to correct for multiple comparisons (Friston, Holmes, Poline, Price, & Frith, 1996). Thus, reported activation passed a cluster level extent threshold of  $p = 0.05$  (FWE corrected); individual  $k$  values set for each contrast will be reported in the results section. All results are reported in Talairach space (Talairach & Tournoux, 1988)

*ROI analysis.* Where appropriate, regions of interest (ROIs) were created and percent signal change extracted using the Marsbar toolbox for SPM (Brett, Anton, Valabregue, & Poline, 2002). Regions of interest were created for MT+ (MST/MT), PEFs, and the parietal region we believed to be involved in detecting future path (Field et al., 2007). Clearly distinguishable MT and MST regions within MT+ were found in 9 of the 14 participants. In accordance with (Huk et al., 2002), area MT fell posterior to area MST within MT+, and area MT was larger than area MST (Average MT = 2296 mm<sup>3</sup>, Average MST = 378mm<sup>3</sup>). In order to compare the level of activation in MT/ MST elicited for each of the road conditions percent signal change was extracted for the forward far road, forward flow, forward horizontal road and forward near road conditions in comparison to baseline in each individual. Overall, BOLD response in MST was marginally greater than in MT; however, this result was non-significant. This non-significance probably reflects the fact that, whilst MST neurons are responding to global optic flow components, MT neurons are still responding to local motion vectors in our stimuli. Accordingly, results will be discussed in terms on MT+ only.

In order to establish whether the eye movement results were reflected at the neural level in areas involved in shifting spatial attention and saccadic eye movement, ROIs for the PEFs were created for each of the 14 participants and % signal change was extracted for each of the road conditions vs. baseline. A PEF ROI in this case was classed as activation above  $p = 0.001$  uncorrected in the Sacc > Fix contrast from localiser 1 and located within the parietal lobes.

## Results

### *The Impact of Road Features*

*Behavioural results.* The response pattern for the forward heading conditions in a typical participant is displayed in figure 2a. A series of cross correlations between individual participant joystick response and heading from flow revealed strong average correlations for all forward conditions, indicating that during all forward egomotion trials participants were able to steer in response to current heading (Table 1). Non-parametric analysis, however, revealed that there were significant condition related differences in response lag between the joystick steering response and instantaneous heading ( $\chi^2 = 9.92$ ,  $p < 0.05$ ). One sample T-tests showed that whilst average lag values for Flow<sub>f</sub>, HorRd<sub>f</sub> and NrRd<sub>f</sub> (ranging from -0.652 to -0.819 secs) were significantly different from 0 ( $p < 0.001$ ), the lag value for FarRd<sub>f</sub> (-0.155 secs) was not. Thus, although participants were able to reproduce the general pattern of the road in all conditions, in most conditions this was with a response lag of more than 0.65 seconds. The presence of a far road feature, truncated some 12m (1.5s travel time) from the observer enabled them to eliminate that lag. This adjustment was not evident for the same feature when participants were travelling backwards.

| Condition | Heading |         | Distant Road Position on Screen |         | Road Velocity on Screen |         |
|-----------|---------|---------|---------------------------------|---------|-------------------------|---------|
|           | r       | Lag (s) | r                               | Lag (s) | r                       | Lag (s) |
| Flowf     | 0.786*  | -0.652  |                                 |         |                         |         |
| Flowb     | 0.842*  | -0.715  |                                 |         |                         |         |
| FarRdf    | 0.860*  | -0.155  | 0.460*                          | -0.558  | 0.827*                  | -1.153  |
| FarRdb    | 0.794*  | -0.817  | -0.063                          | -0.687  | 0.531*                  | -0.558  |
| HorRdf    | 0.829*  | -0.819  |                                 |         |                         |         |
| HorRdb    | 0.854*  | -0.833  |                                 |         |                         |         |
| NrRdf     | 0.842*  | -0.771  |                                 |         |                         |         |

Table 1: Cross correlation results; participant response lag in respect to heading, road position on screen and road velocity on screen. \* = Significantly different from zero,  $p < 0.001$ .

It is possible that the advantage gained from seeing a roadway 12m (1.5 sec) ahead was that the position or motion of this feature directly cued heading judgments. If the road is to the right of the screen or moves rightward, participants could assume that they are heading to the left of the screen. In fact the cue is misleading because the road curvature 12m ahead also changes its projection on the screen in addition to the observed position. The cross correlations between joystick response and the position of the road on the screen revealed lower r values than for the correlation with heading (Table 1). The correlation of the joystick with road motion on the screen was comparable to that of heading, but only when the joystick was aligned with very long lag. We suggest that it is implausible that the participant notes the motion of the distant road feature, waits 1.1s, and then responds to it, by which time it is moving in a different direction. The lags encountered in the simple flow conditions (~0.8s) are because it takes some time to identify and integrate flow field changes, the same is not true of discrete lateral motion. Overall, this suggests that the reduction in response lag in the FarRd<sub>f</sub> was not due to participants responding to the distant road as a heuristic cue but rather due to the use of the path information the road supplied to synchronize their passive steering with the flow field information.

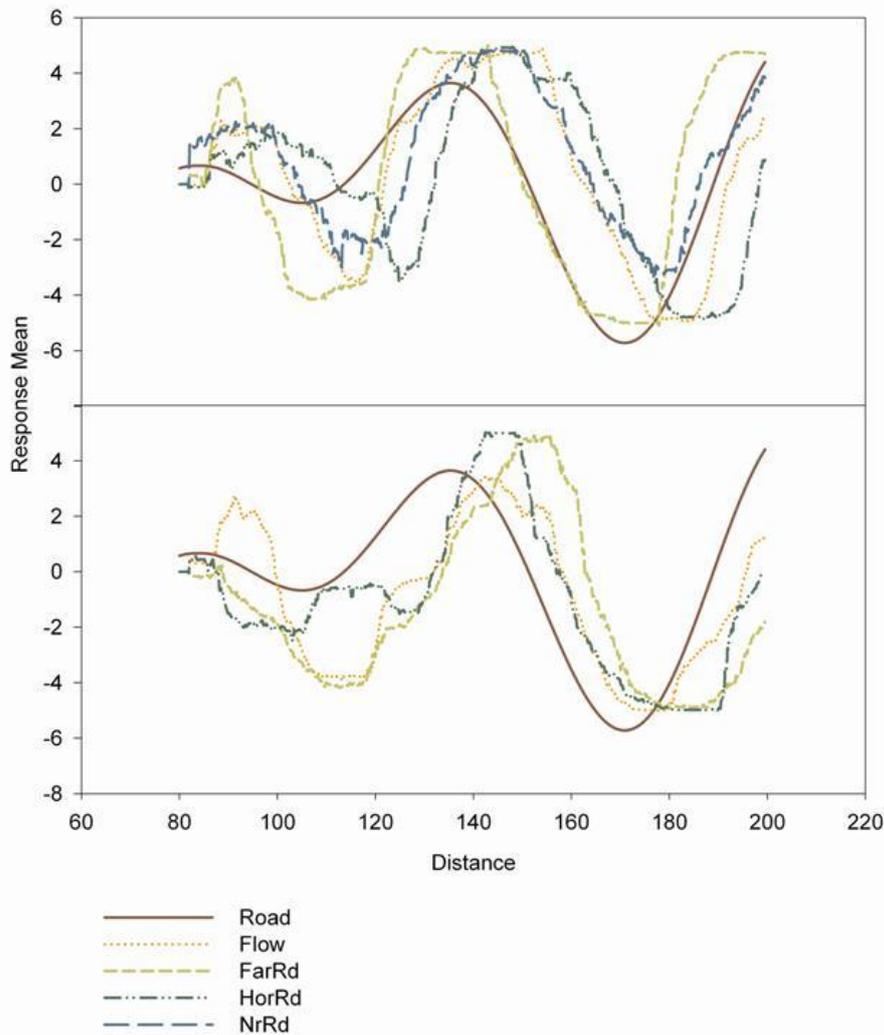


Figure 2: Joystick responses in an individual participant as overlaid on the actual road trajectory in the forwards (2a) and backwards (2b) heading conditions. Temporal lag values and statistics are reported in the results section and table 1.

*Neural results.* In order to see which brain regions respond to the presence of a relevant distant road feature a whole brain second level analysis was conducted on the  $\text{FarRd}_f > \text{Flow}_f$  contrast from experiment 1 ( $p = 0.05$  FWE, cluster level  $k = 75$ ), see table 2 and figure 3. The primary peak of activation was in the right middle temporal gyrus, with a further peak of activation in the left middle temporal gyrus. These regions correspond to what is thought to be the human motion complex (MT+) (Dukelow et al., 2001; Smith & Wall, 2007; Wall & Smith, 2008). Activation was also evident in the left and right SPL extending into the left and right precuneus. Peaks of activation were also found in the left middle occipital gyrus and the right inferior temporal gyrus when viewing a far road feature.

Our behavioural analysis also indicated that a near section of road acted to improve, albeit non-significantly, the temporal lag in heading response. We explored these behavioural results at the neural level in order to see whether BOLD response in the previous contrast was specific to detecting a far road feature, as opposed to simply detecting a meaningful road feature. A whole brain second level analysis was conducted on the  $\text{NrRd}_f > \text{Flow}_f$  contrast from experiment 2 ( $p = 0.05$  FWE, cluster level  $k = 60$ ), see table 2.

The activation revealed in this contrast was focused in left and right MT+. Figure 3 shows the main areas of activation in both the  $\text{FarRd}_f > \text{Flow}_f$  (blue) and  $\text{NrRd}_f > \text{Flow}_f$  (red) contrasts, the overlap in activation is shown in purple in figure 3. MT+ activation is common to both contrasts and the percent signal change in this region for both  $\text{FarRd}_f$  (mean % SC = 1.41, sd = 0.50) and  $\text{NrRd}_f$  (mean % SC = 1.58, sd = 1.64) was not significantly different. However, only the far road paradigm produced activation in cortical regions beyond MT+ in the parietal and temporal cortices, as shown by the contrast  $\text{FarRd}_f > \text{Flow}_f$  ( $p = 0.05$ , FWE corrected) masked by  $\text{NrRd}_f > \text{Flow}_f$  ( $p = 0.01$ , uncorrected); see inset in figure 3.

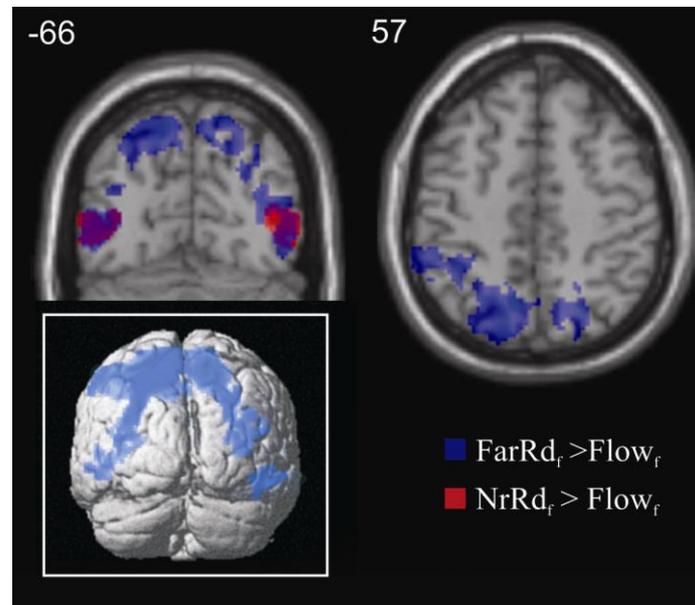


Figure 3: Activation in superior parietal lobe, inferior parietal sulcus and middle temporal region (MT+) when attending to far road and near road stimuli during forward egomotion. Areas in blue reflect  $\text{FarRd}_f > \text{Flow}_f$ , whilst areas in red reflect  $\text{NrRd}_f > \text{Flow}_f$ . Areas of overlap between these two conditions are show in purple. Activation is shown at the cluster level,  $p = 0.05$  (FWE corrected). Inset box represents  $\text{FarRd}_f > \text{Flow}_f$  (cluster level,  $p = 0.05$ ; FWE corrected) masked by  $\text{NrRd}_f > \text{Flow}_f$  ( $p = 0.01$ , uncorrected) rendered on a 3-D structural image.

TABLE 2 – See end

It was thought that the comparison of the  $\text{FarRd}_f$  condition to  $\text{Flow}_f$  would result in activation in areas involved in the detection of future path, but it would also elicit activation in areas which are associated with detecting the low level features of the road and the execution/suppression of eye movements in response to moving visual stimuli. These neural processes are not specific to detecting and integrating future path information but may be located anatomically adjacent to regions involved in the detection of future path. To segregate activation which was related to detecting future path information, first, a whole brain group analysis of the contrast  $\text{FarRd}_f > \text{HorRd}_f$  was performed ( $p = 0.05$  FWE, cluster level  $k = 75$ ) with the intention of removing activation which was associated with the detection of low level visual road features. Second, an exclusive mask of the contrast  $\text{Sacc} > \text{Fix}$  from localiser 1 ( $p = 0.01$ , uncorrected) was used to remove activation in PEF which arose as a result of eye movements and shifts in spatial attention, see table 1 and figure 4. We acknowledge that some of the  $\text{Sacc} > \text{Fix}$  contrast activations were in regions of white matter; however, this is believed to be a consequence of using a lenient threshold in order to create a conservative exclusive mask.

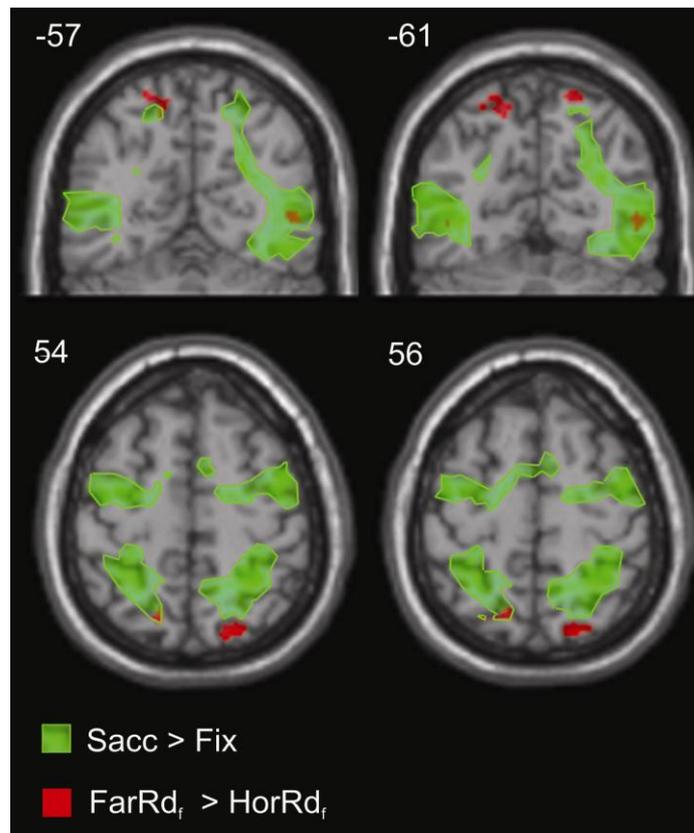


Figure 4: Activation associated with the detection of future path, activation shown in red which represents surviving BOLD response after  $\text{FarRd}_f > \text{HorRd}_f$  (cluster level,  $p = 0.05$ ; FWE corrected) was masked exclusively by  $\text{Sacc} > \text{Fix}$  ( $p = 0.01$ ; uncorrected, shown in green). Activation shown in orange within the green boundary represents BOLD response for the contrast  $\text{FarRd}_f > \text{HorRd}_f$  (cluster level,  $p = 0.05$ ; FWE corrected) which was removed by the mask.

In the  $\text{FarRd}_f > \text{HorRd}_f$  contrast, activation (shown in orange and red in figure 4) was less extensive than the parietal lobe activation elicited in  $\text{FarRd}_f > \text{Flow}_f$  but remained in bilateral SPL extending into the medial wall of the IPS; activation in regions corresponding to MT+ also remained. Applying an exclusive mask of  $\text{Sacc} > \text{Fix}$  (shown green in figure 4), set at a liberal threshold to exclude all voxels associated with planned eye movement or spatial shifts of attention, removed MT+ activation, whilst the cluster in the right SPL extending into the mIPS remained (shown in red outside the green mask outline, in figure 4). In the context of forward egomotion, this area may be said to be a candidate area for detecting and responding to future path information over and above other general task related processes.

### *Backwards Compared to Forwards Motion*

*Behavioural results.* The scaled heading response from a typical participant during backwards heading is displayed in figure 2b. A series of cross correlations between participant joystick response and heading from flow revealed strong (see table 1) correlations for all backward conditions, indicating during all backward egomotion trials participants were able to steer in response to heading cues in a way which was comparable to that of forward egomotion. Non-parametric analysis revealed that there were no significant condition related differences between the three backward egomotion conditions. One sample T-tests showed that the average lag values for  $\text{FarRd}_b$ ,  $\text{Flow}_b$  and  $\text{HorRd}_b$  were all significantly different from 0 ( $p < 0.001$ ). Thus, although participants were able to follow the pattern of the road, they were unable to make anticipatory judgements in order to reduce their response lag below 0.715 secs. Joystick responses were not significantly correlated with road position on screen, and the correlation between joystick response and road velocity on screen was lower than the aforementioned heading correlations and associated with a 0.558 sec lag. Thus, participants were not using distal road features as heuristic cues but,

rather, making joystick responses based on heading cues. Unlike FarRd<sub>f</sub> trials participants were not able to make anticipatory judgments about future changes in heading in FarRd<sub>b</sub> trials.

*Neural results* . The behavioural data suggest that accuracy of participants' judgments when travelling backwards were equivalent to those when they were travelling forwards. However, the data also indicated that whilst a far road feature could reduce lag when travelling forwards it did not reduce lag when travelling backwards. This would suggest that the superior parietal lobe region involved in detecting future path information activated during forward far road should not be strongly activated during backward far road. The contrast FarRd<sub>b</sub> > Flow<sub>b</sub> ( $p = 0.05$  FWE, cluster level  $k = 75$ , table 3) revealed activation in the left SPL, extending into the left precentral gyrus. Peak activation in the right hemisphere was in the middle occipital gyrus. Activation was also present in right MT+, and the average signal change in bilateral MT+ for FarRd<sub>b</sub> was not significantly different from that of FarRd<sub>f</sub> at 1.35 %. The activation clusters in the parietal lobe were lateral to those observed in the FarRd<sub>f</sub> > Flow<sub>f</sub> contrast and the extent of activation is much reduced. A second contrast was carried out on FarRd<sub>b</sub> > HorRd<sub>b</sub> to look at activation in the presence of backward far road whilst removing any activation which may have been due to low level visual properties of the road feature. No activation remained at the group cluster level ( $p = 0.05$  FWE,  $k = 75$ ) in this contrast.

TABLE 3 – See end

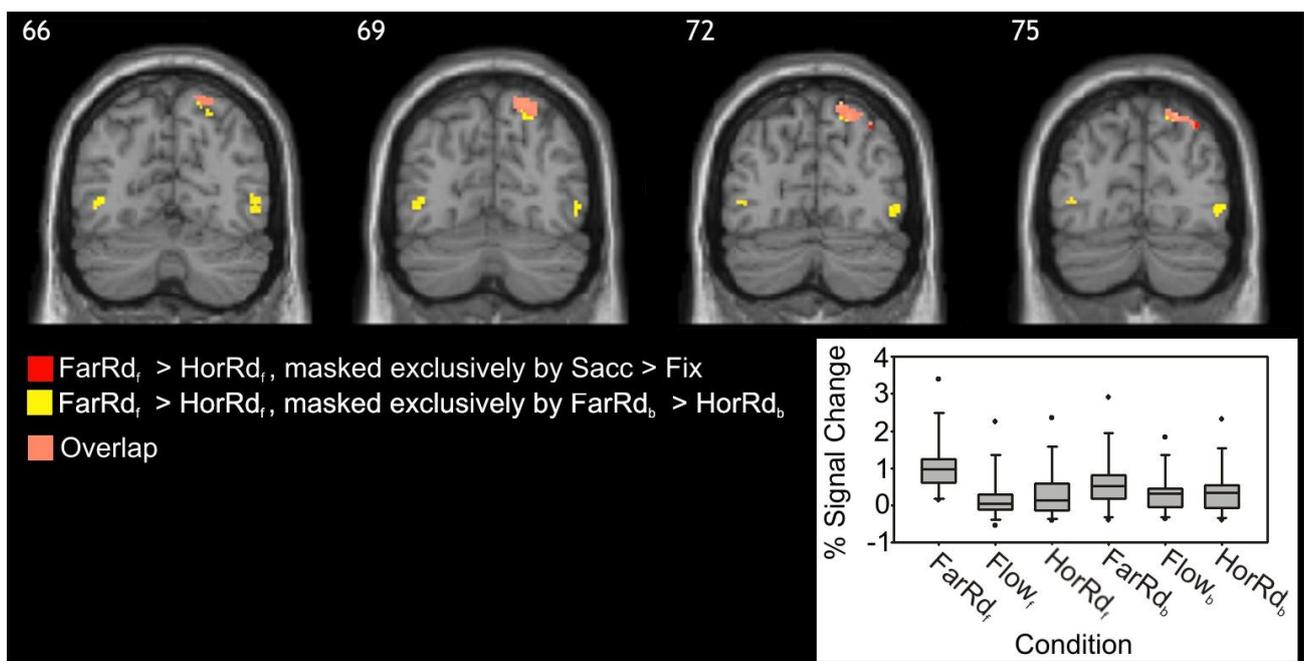


Figure 5: Activation associated with the detection of future path. Activation in red and pink represents BOLD response during contrast 1; FarRd<sub>f</sub> > HorRd<sub>f</sub> (cluster level,  $p = 0.05$ ; FWE corrected) masked exclusively by Sacc > Fix  $p = 0.01$  ( $p = 0.01$ ; uncorrected). Activation shown in yellow and pink represents BOLD response during contrast 2; FarRd<sub>f</sub> > HorRd<sub>f</sub> (cluster level,  $p = 0.05$ ; FWE corrected) when masked by FarRd<sub>b</sub> > HorRd<sub>b</sub> ( $p = 0.01$ ; uncorrected). In right SPL contrast 1 consisted of 157 active voxels whilst contrast 2 consists of 152 active voxels. The overlap between these two volumes is shown in pink. The graph (inset) shows percent signal change in all conditions vs. baseline in the ROI defined by FarRd<sub>f</sub> > HorRd<sub>f</sub> masked exclusively by Sacc > Fix  $p = 0.01$  (pink and red).

In order to locate activation in the presence of forward far road which was not present in backward far road, the contrast FarRd<sub>f</sub> > HorRd<sub>f</sub> ( $p = 0.05$  FWE, cluster level  $k = 75$ ) was exclusively masked by FarRd<sub>b</sub> > HorRd<sub>b</sub>, see table 3. The mask was reduced to a  $p = 0.01$  (uncorrected) level in order to maximise the voxels in the mask and thereby give the most conservative map of activation specific to forward far road. Activation remained in the right SPL and mIPS, as well as in left and right MT+ (shown in yellow in figure 5). This activation is comparable to the first method we used to isolate activations specific to forwards motion, by exclusively masking the FarRd<sub>f</sub> > HorRd<sub>f</sub> contrast with activation in the PEF localiser (figure 5, shown in

red). There was a large degree of overlap (figure 5, shown in pink) in the SPL/ mIPS activation for these two methods of isolating future path activation, with only 5 less voxels present when using activation in the PEF localiser as a mask in comparison to the backward far road mask.

### Eye movements & spatial attention

The averaged gaze locations are shown in figure 6. This analysis used a binning procedure to compare the horizontal and vertical trends for gaze clustered to the left, centre and right, for each condition. As expected, participants gaze was  $\sim 2\text{deg}$  higher during the forward far road condition (blue circles) as compared to flow-only (black circles) or horizontal road (green circles). When a near road was present (red circles) gaze position was lower. On average, participants looked lower during the presentation of backward stimuli, around  $5^\circ$  below the horizon.

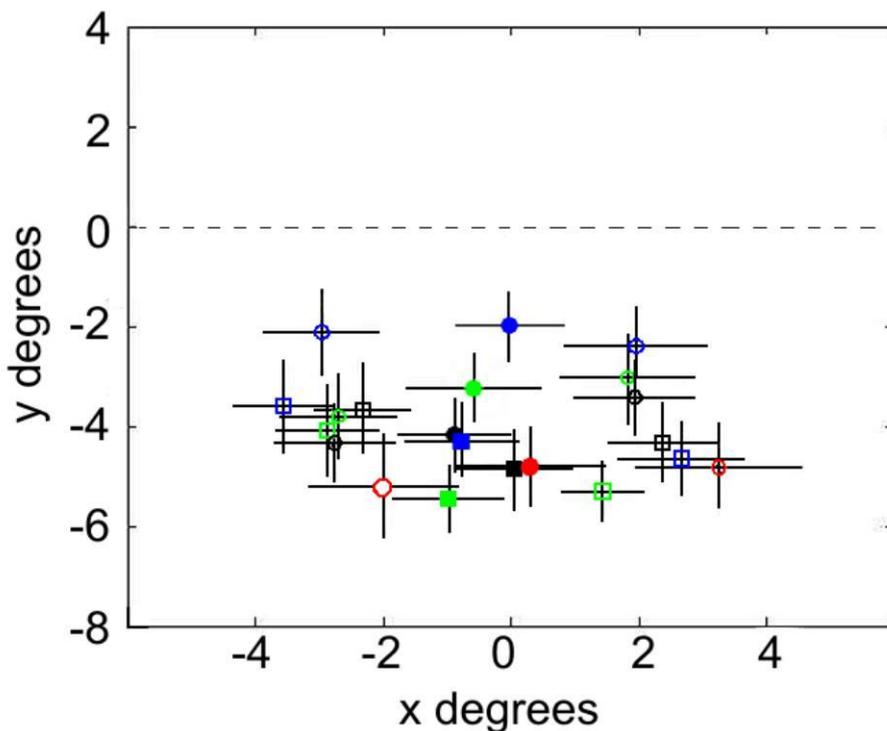


Figure 6: Eye movement data for all conditions showing average x, y position with 95% confidence intervals. The dotted line shows the position of the horizon. Only 12deg vertically are horizontally are shown as this captures the mean data. Forward conditions are shown as circles, whilst backward conditions are shown as squares. Black represents flow-only, green represents horizontal road and blue represents far road. Red circles are for the near road which was only present for forward motion. Data were sorted into 3 bins (left, centre, right) for each condition on the basis that the allocation of records to any one bin should minimize the sum of the standard errors across bins. This yields a mean for left gaze and right gaze within each condition, with the central gaze position presented as a filled symbol.

The average number of saccades per 16 second trial was calculated for each condition. The near road elicited the most saccades (144.2), followed by the backward flow condition (117.7) and the backward horizontal road (110.2). The remainder of the conditions elicited the least number of saccades (forward flow; 99.6: forward horizontal; 102.6: backward far road; 101.4, and forward far road; 103.9). Overall, there was also no clear relationship between the amount of saccades and either forward/ backward ground flow or road feature.

In order to look at whether there was an effect of the conditions in the heading task on activation in the PEFs, percent signal change was extracted for each of the conditions in this area, results can be seen in figure 7. The FarRd<sub>f</sub> condition was associated with significantly higher activation in the PEFs and both Flow<sub>f</sub>

and Flow<sub>b</sub> conditions were associated with significantly lower activation in PEF. It was apparent, however, that there was no significant relationship between number of saccades or focus of gaze and strength of activation in PEF. This proposal is further supported by the fact that one of our earlier whole brain contrasts comparing the condition with the most saccades (NrRd<sub>f</sub>) with the condition with the least saccades (Flow<sub>f</sub>) did not result in PEF activation, or any other parietal activation.

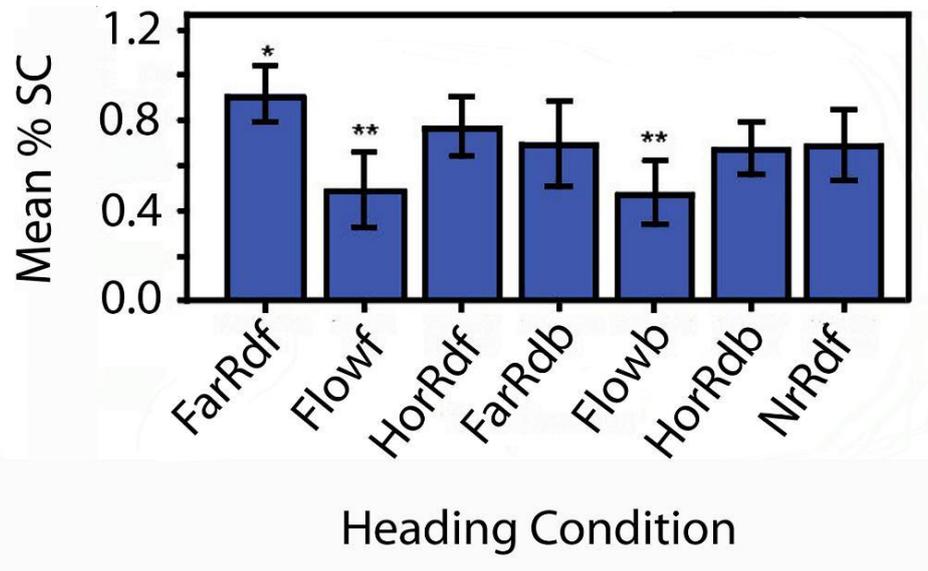


Figure 7: Average signal change (%) in PEF across each of the road conditions. \* = Significantly higher than all other conditions,  $p < 0.01$ . \*\* = Significantly lower than all other conditions,  $p < 0.05$ .

In order to test whether the region we propose is involved in processing future path was simply responding to either planned or executed eye movements, a future path area ROI was created separately for each individual using the same contrast as the group level analysis: FarRd<sub>f</sub> > HorRd<sub>f</sub> ( $p = 0.001$ , FWE corrected), masked exclusively with FarRd<sub>b</sub> > Flow<sub>b</sub> ( $p = 0.05$ , uncorrected). Average % signal change in this region indicated modest deactivation in comparison to baseline during Fix (mean = -0.40, sd = 0.66) and Sacc (mean = -0.16, sd = -0.83) in our PEF localiser experiments. These near zero signal change values demonstrate that the BOLD response in this region is not simply a function of differences in shifts of attention or eye movements.

## Discussion

This study has confirmed that the ability to respond to current path curvature during locomotion is enhanced by adding information about the future path (~1.5s ahead), which agrees with Land and Horwood (1995). The change in behavioural performance produced by the future path information is linked to the presence of a specific superior parietal activation. The link between the behavioural effect and the specific BOLD response suggest that activation in this region is produced by the processing of future path information.

The presence of a far road feature during forwards egomotion reduced the temporal lag between actual heading and the joystick steering response from ~0.8s to 0.15s. This effect was not present during backwards egomotion where the same road features were displayed, but they did not carry the same informational value. We also demonstrated that it was not a consequence of using local motion of road edges as simple reference cues to steering. Together, these results suggest that participants were using future path information to enhance steering judgments some 1.5s later, a strategy which could not be used when travelling backwards. As a result participants looked on average higher in the visual scene during the forward far road condition, towards an area in which the far road features were located, and looked on average lower in the visual scene in conditions which required backward heading judgments, effectively ignoring far road information. These findings are in concordance with a far road/near road mechanism proposed by Land and Horwood (1995), in which anticipation of future road curvature, along with information regarding current road positioning, affords greater steering accuracy.

The neural results of this investigation complimented the present behavioural findings and were comparable with activation patterns in both Field et al. (2007) and Peuskens et al. (2001). A focal point of neural activity in the SPL extending into the mIPS was evident in the presence of a far road feature, but not a near road feature. Moreover, this region responded only to far road features during forward egomotion and was unresponsive during backward egomotion, suggesting that this activation was specific to making anticipatory judgments about road curvature in order to enhance performance during forwards egomotion. On the other hand, only MT+ showed a significant activation to near road stimulus. This finding is concordant with previous studies that have found MT+ responds to optic flow patterns (Dukelow et al., 2001; Huk et al., 2002; Morrone et al., 2000; Smith & Wall, 2007) and suggests that that, in part, Land and Horwood's (1995) near road mechanism might be identified with processing in MT+; however, we acknowledge that this conclusion must be tentative because in the present study the actual function of the near road mechanism was not engaged as lane positioning during the heading task was always exactly central and so there was no error signal. In Field et al.'s (2007) previous paper cortical activity related to road position errors and error correction was highlighted, although the interaction interactions with MT+ were not confirmed. Further studies of both active steering and passive heading judgments in a near and far road task would be needed to clarify error correction mechanisms. But within the present study the overall pattern of activation in the SPL/ mIPS and MT+ regions clearly identifies with Land and Horwood's (1995) far road and near road mechanisms respectively.

Before we expand on the role of the SPL and mIPS in the detection of future path, alternative explanations for activation in this region must be discounted. Both SPL and IPS have previously been associated with shifts of attention (Corbetta et al., 1998; Hopfinger, Buonocore, & Mangun, 2000) and planning and executing eye movements (Kan, Misaki, Iwata, Koike, & Miyauchi, 2007; Schraa-Tam et al., 2008). We argue, however, that activation in this region when processing future path information does not simply reflect a heightened reliance on either of these processes. Not only was activation associated with these processes segregated using an independent functional localiser of PEF, we also used a post-hoc percent-signal-change analysis to reveal that execution of saccadic eye movements did not result in any change in BOLD response in our future path related SPL/mIPS region. Given that all conditions were also matched in terms of motor response, activation in this region relating to motor planning or intention (Snyder, Batista, & Andersen, 2000) can also be discounted.

Wolbers et al. (2008) highlighted areas of parietal cortex that were involved in spatial updating of target coordinates over a delay of 4.25 – 5.75s. Such a role is also in concordance with the premise that the SPL is involved in spatial encoding and inhibition (Pollmann et al., 2008). To produce the observed reduction in steering lag the participants need to continuously encode directional changes that will be required in 1.5s time. Studies on way finding and navigation (Maguire et al., 1998; Seubert et al., 2008) have already implicated the parietal lobe in egocentric aspects of such tasks and activation in our task may be consequence of a similar function in relation to changes in heading. Furthermore, studies on visual-motor coordination suggest that neurons in the parietal cortex may be specialised in a way which could facilitate detection and response to future path changes. In macaques, the medial intraparietal cortex (MIP) is thought to be part of the parietal reach region (PPR), which is associated with goal directed motor planning and execution (Cohen & Andersen, 2002; Eskandar & Assad, 1999). Recent research has implicated the mIPS as the putative human homologue of MIP (Grefkes & Fink, 2005) and activation in mIPS and SPL has been found in response to visually guided hand movements towards a target using fMRI (Grefkes, Ritzl, Zilles, & Fink, 2004), suggesting this region may have similar functionality in humans. Cohen and Andersen (2002) claim that MIP is just one component part of the PPR and is involved in the transformation of information in different modalities (visual, auditory, motor) into a common frame of reference. Such transformations facilitate communication between regions, allowing for easy coordination of movement as a response to sensory input. More importantly for the task of responding to future path information the neurons in the posterior parietal cortex, including IPS, have been found to show sustained activation during the delay of pointing responses and are said to be capable of storing representations of intended, but not executed, movements in humans (Fernandez-Ruiz, Goltz, DeSouza, Vilis, & Crawford, 2007). It is possible that the temporal response properties of neurons in the posterior parietal cortex may be ideally suited to encoding both transient and impending motor responses. Whilst the aforementioned studies have been primarily focused on reaching movements, or movements in near space, the specialisation of the neurons in posterior parietal cortex may also be well suited to controlling locomotion and generating planned movements in response to visual information such as impending changes to heading direction. Activations in our study could reflect the storage of information about future road curvature and/ or the transformation of far road information into a common egocentric reference frame for motor execution.

This combination of behavioural results that confirmed improved synchronization of participants' steering responses and fMRI methods suggest that the SPL/ mIPS is responding to impending changes in heading imposed by path constraints. The results also lead us to hypothesise that MT+ may be associated with near road edge-detection system that contributes towards the maintenance of current lane position. These mechanisms unpin the common skill exhibited by humans who travel at speed and follow designated paths. Every driver recognises that it is essential to see the path a few seconds ahead to steer effectively. There are some specific examples; such as following another vehicle on an unknown dimly lit road, that highlight how useful it can be to encode future directional changes. This study highlights the cortical areas which may handle that class of information.

### **Funding**

This work was supported by and award from the UK Engineering and Physical Sciences Research Council [EP/D055342/1] to JPW, DTF & RMW.

## References

- Andersen, R. A., Asanuma, C., Essick, G., & Siegel, R. M. (1990). Corticocortical connections of anatomically and physiologically defined subdivisions within the inferior parietal lobule. *Journal of Comparative Neurology*, *296*, 65-113.
- Brett, M., Anton, J., Valabregue, R., & Poline, J. (2002, June 2nd-6th). *Region of interest analysis using an SPM toolbox*. Paper presented at the The 8th International Conference on Functional Mapping of the Human Brain, Sendai, Japan.
- Cohen, Y. E., & Andersen, R. A. (2002). A common reference frame for movement plans in the posterior parietal cortex. *Nature Reviews Neuroscience*, *3*, 553-562.
- Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., et al. (1998). A common network of functional areas for attention and eye movements. *Neuron*, *21*, 761-773.
- Desmurget, M., Epstein, C. M., Turner, R. S., Prablanc, C., Alexander, G. E., & Grafton, S. T. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nature Neuroscience*, *2*, 563-567.
- Duffy, C. J., & Wurtz, R. H. (1995). Response of monkey MST neurons to optic flow stimuli with shifted centers of motion. *Journal of Neuroscience*, *15*(7), 5192-5208.
- Dukelow, S. P., DeSouza, J. F. X., Culham, J. C., van den Berg, A. V., Menon, R. S., & Vilis, T. (2001). Distinguishing subregions of the human MT plus complex using visual fields and pursuit eye movements. *Journal of Neurophysiology*, *86*, 1991-2000.
- Erickson, R. G., & Thier, P. (1991). A neuronal correlate of spatial stability during periods of self-induced visual-motion. *Experimental Brain Research*, *86*, 608-616.
- Eskandar, E. N., & Assad, J. A. (1999). Dissociation of visual, motor and predictive signals in parietal cortex during visual guidance. *Nature Neuroscience*, *2*, 88-93.
- Fajen, B. R., & Warren, W. H. (2003). Behavioral dynamics of steering, obstacle avoidance, and route selection. *Journal of Experimental Psychology-Human Perception and Performance*, *29*, 343-362.
- Fernandez-Ruiz, J., Goltz, H. C., DeSouza, J. F. X., Vilis, T., & Crawford, J. D. (2007). Human parietal "reach region" primarily encodes intrinsic visual direction, not extrinsic movement direction, in a visual-motor dissociation task. *Cerebral Cortex*, *17*, 2283-2292.
- Field, D. T., Wilkie, R. M., & Wann, J. P. (2007). Neural systems in the visual control of steering. *Journal of Neuroscience*, *27*, 8002-8010.
- Friston, K. J., Holmes, A., Poline, J. B., Price, C. J., & Frith, C. D. (1996). Detecting activations in PET and fMRI: Levels of inference and power. *Neuroimage*, *4*, 223-235.
- Grefkes, C., & Fink, G. R. (2005). The functional organization of the intraparietal sulcus in humans and monkeys. *Journal of Anatomy*, *207*, 3-17.
- Grefkes, C., Ritzl, A., Zilles, K., & Fink, G. R. (2004). Human medial intraparietal cortex subserves visuomotor coordinate transformation. *Neuroimage*, *23*, 1494-1506.
- Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuroscience*, *3*, 284-291.
- Huk, A. C., Dougherty, R. F., & Heeger, D. J. (2002). Retinotopy and functional subdivision of human areas MT and MST. *Journal of Neuroscience*, *22*, 7195-7205.
- Hutton, C., Bork, A., Josephs, O., Deichmann, R., Ashburner, J., & Turner, R. (2002). Image distortion correction in fMRI: A quantitative evaluation. *Neuroimage*, *16*, 217-240.
- Jezzard, P., & Balaban, R. S. (1995). Correction for geometric distortion in echo-planar images from B-0 field variations. *Magnetic Resonance in Medicine*, *34*, 65-73.
- Kan, S., Misaki, M., Iwata, K., Koike, T., & Miyauchi, S. (2007). An active role of MST in maintaining visual stability during saccades in the natural environment. *Neuroscience Research*, *58*, S94-S94.
- Kan, S., Misaki, M., Koike, T., & Miyauchi, S. (2008). Different modulation of medial superior temporal activity across saccades: a functional magnetic resonance imaging study. *Neuroreport*, *19*, 133-137.
- Lagae, L., Maes, H., Raignuel, S., Xiao, D. K., & Orban, G. A. (1994). Responses of macaque STS neurons to optic flow components - A comparison of areas MT and MST. *Journal of Neurophysiology*, *71*, 1597-1626.
- Land, M., & Horwood, J. (1995). Which parts of the road guide steering? *Nature*, *377*, 339-340.

- Lappe, M., Bremmer, F., & van den Berg, A. V. (1999). Perception of self-motion from visual flow. *Trends in Cognitive Sciences*, 3, 329-336.
- Lee, C. C., Jack, C. R., Grimm, R. C., Rossman, P. J., Felmlee, J. P., Ehman, R. L., et al. (1996). Real-time adaptive motion correction in functional MRI. *Magnetic Resonance in Medicine*, 36, 436-444.
- Li, L., & Warren, W. H. (2000). Perception of heading during rotation: sufficiency of dense motion parallax and reference objects. *Vision Research*, 40, 3873-3894.
- Maguire, E. A., Burgess, N., Donnett, J. G., Frackowiak, R. S. J., Frith, C. D., & O'Keefe, J. (1998). Knowing where and getting there: A human navigation network. *Science*, 280, 921-924.
- Morrone, M. C., Tosetti, M., Montanaro, D., Fiorentini, A., Cioni, G., & Burr, D. C. (2000). A cortical area that responds specifically to optic flow, revealed by fMRI. *Nature Neuroscience*, 3, 1322-1328.
- Page, W. K., & Duffy, C. J. (2008). Cortical neuronal responses to optic flow are shaped by visual strategies for steering. *Cerebral Cortex*, 18, 727-739.
- Perry, R. J., & Zeki, S. (2000). The neurology of saccades and covert shifts in spatial attention - An event-related fMRI study. *Brain*, 123, 2273-2288.
- Peuskens, H., Sunaert, S., Dupont, P., Van Hecke, P., & Orban, G. A. (2001). Human brain regions involved in heading estimation. *Journal of Neuroscience*, 21, 2451-2461.
- Pollmann, S., Weidner, R., Humphreys, G. W., Olivers, C. N. L., Muller, K., Lohmann, G., et al. (2003). Separating distractor rejection and target detection in posterior parietal cortex - An event-related fMRI study of visual marking. *Neuroimage*, 18, 310-323.
- Read, H. L., & Siegel, R. M. (1997). Modulation of responses to optic flow in area 7a by retinotopic and oculomotor cues in monkey. *Cerebral Cortex*, 7, 647-661.
- Schaafsma, S. J., & Duysens, J. (1996). Neurons in the ventral intraparietal area of awake macaque monkey closely resemble neurons in the dorsal part of the medial superior temporal area in their responses to optic flow patterns. *Journal of Neurophysiology*, 76, 4056-4068.
- Schraa-Tam, C. K. L., van der Lugt, A., Frens, M. A., Smits, M., van Broekhoven, P. C. A., & van der Geest, J. N. (2008). An fMRI study on smooth pursuit and fixation suppression of the optokinetic reflex using similar visual stimulation. *Experimental Brain Research*, 185, 535-544.
- Seubert, J., Humphreys, G. W., Muller, H. J., & Gramann, K. (2008). Straight after the turn: The role of the parietal lobes in egocentric space processing. *Neurocase*, 14, 204-219.
- Smith, A., & Wall, M. B. (2007). Sensitivity to the stereoscopic depth of a moving surface in the human MT complex measured with fMRI adaptation. *Perception*, 36, 179-180.
- Snyder, L. H., Batista, A. P., & Andersen, R. A. (2000). Intention-related activity in the posterior parietal cortex: a review. *Vision Research*, 40, 1433-1441.
- Talairach, J., & Tournoux, P. (1988). *Coplanar stereotaxic atlas of the human brain*. New York: Thieme Medical Publishers.
- Wall, M. B., & Smith, A. T. (2008). The representation of egomotion in the human brain. *Current Biology*, 18, 191-194.
- Warren, W. H., & Hannon, D. J. (1988). Direction of self-motion is perceived from optical flow. *Nature*, 336, 162-163.
- Wilkie, R., & Wann, J. (2003). Controlling steering and judging heading: Retinal flow, visual direction, and extraretinal information. *Journal of Experimental Psychology-Human Perception and Performance*, 29, 363-378.
- Wilkie, R. M., & Wann, J. P. (2002). Driving as night falls: The contribution of retinal flow and visual direction to the control of steering. *Current Biology*, 12, 2014-2017.
- Wilkie, R. M., & Wann, J. P. (2003). Eye-movements aid the control of locomotion. *Journal of Vision*, 3, 677-684.
- Wilkie, R. M., & Wann, J. P. (2006). Judgments of path, not heading, guide locomotion. *Journal of Experimental Psychology-Human Perception and Performance*, 32, 88-96.
- Wilkie, R. M., Wann, J. P., & Allison, R. S. (2008). Active gaze, visual look-ahead, and locomotor control. *Journal of Experimental Psychology-Human Perception and Performance*, 34, 1150-1164.
- Wolbers T, Hegarty M, Buchel C, Loomis JM (2008) Spatial updating: how the brain keeps track of changing object locations during observer motion. *Nature Neuroscience*, 11, 1223-1230.

Zhang, T., Heuer, H. W., & Britten, K. H. (2004). Parietal area VIP neuronal responses to heading stimuli are encoded in head-centered coordinates. *Neuron*, *42*, 993-1001.

Table 2: Activation in forward motion contrasts. Locations are presented in Talairach space at a FWE cluster level threshold,  $p = 0.05$ ,  $k = 75$ .

\*  $k = 60$

\*\* Mask threshold is set at  $p = 0.01$  uncorrected.

| Contrast  | T     | x   | y   | z  | Voxel Volume |
|---|-------|-----|-----|----|--------------|
| <b>Forward far road &gt; forward flow</b>   |       |     |     |    |              |
| Right Middle Temporal Gyrus   | 10.07 | 50  | -70 | 3  | 6677         |
| Left Middle Occipital Gyrus   | 9.29  | -38 | -81 | 21 |              |
| Right Inferior Temporal Gyrus   | 9.08  | 53  | -49 | -9 |              |
| Left Precuneus  | 8.83  | -10 | -60 | 47 |              |
| Left Superior Parietal Lobule   | 8.65  | -24 | -58 | 51 |              |
| Right Precuneus   | 8.13  | 12  | -71 | 53 |              |
| Left Middle Temporal Gyrus  | 8.03  | -46 | -64 | 5  |              |
| Right Superior Parietal Lobule  | 7.11  | 18  | -67 | 57 |              |
| <b>Forward far road &gt; forward horizontal road</b>  |       |     |     |    |              |
| Right Superior Parietal Lobule  | 6.64  | 20  | -67 | 59 | 168          |
| Left Middle Occipital Gyrus   | 6.25  | -46 | -70 | 2  | 142          |
| Right Middle Temporal Gyrus   | 7.92  | 48  | -62 | 9  | 97           |
| Left Superior Parietal Lobule   | 4.84  | -20 | -59 | 62 | 75           |
| <b>Forward near road &gt; forward flow*</b>   |       |     |     |    |              |
| Right Middle Occipital Gyrus  | 9.76  | 42  | -69 | 15 | 606          |
| Left Middle Occipital Gyrus   | 7.05  | -40 | -70 | 7  | 398          |
| <b>Forward far road &gt; forward horizontal road masked exclusively by suppressed saccade &gt; fixation**</b> |       |     |     |    |              |
| Right Superior parietal lobe  | 6.64  | 20  | -67 | 59 | 152          |

Table 3: Activation during backward and forward motion contrasts

| Contrast  | T    | x   | y   | z  | Voxel Volume |
|---|------|-----|-----|----|--------------|
| <b>Backward road &gt; backward flow</b>   |      |     |     |    |              |
| Right Middle Occipital Gyrus  | 7.21 | 42  | -69 | 27 | 364          |
| Left Superior Parietal Lobule   | 7.14 | -28 | -61 | 58 | 149          |
| Left Precentral Gyrus   | 4.82 | -50 | 12  | 42 | 79           |
| Right Middle Temporal Gyrus   | 5.91 | 46  | -68 | 2  | 149          |
| <b>Forward road &gt; forward horizontal exclusively masked by backward road &gt; backward horizontal*</b> |      |     |     |    |              |
| Right Superior Parietal Lobule  | 6.64 | 20  | -67 | 59 | 157          |
| Left Middle Occipital Gyrus   | 6.25 | -46 | -70 | 2  | 93           |
| Right Middle Temporal Gyrus   | 7.92 | 48  | -62 | 9  | 87           |

Locations are presented in Talairach space at a FWE cluster level threshold,  $p = 0.05$ ,  $k = 75$ .

\* Mask threshold is set at  $p = 0.01$  uncorrected.