Navigation representations during active navigation are predominantly goal-directed

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Abstract

Previous experiments revealed that the human brain represents many different navigational features. However, because most fMRI experiments study individual representations in isolation, the relative importance of these many different features to navigation remains unclear. To compare these representations, we recorded BOLD activity while subjects performed a taxi driver task in a large, realistic virtual world. Voxelwise modeling was performed with 21,283 stimulus- and task-related features that encompass 33 different types of information that might be represented during naturalistic navigation. The fit models show that navigational information is represented broadly across the cortex, including in many areas outside known navigation-related ROIs. Among navigational models, goal-directed representations account the most variance, while passive perceptual representations account for much less variance. These data suggest that representations during active naturalistic navigation are predominantly goal-directed.

Keywords: naturalistic tasks; navigation; modelling

Introduction

Previous experiments have revealed that the brain represents many different types of navigationally-relevant information. Anterior visual regions represent scene identity in PPA (Epstein and Kanwisher 1998), scene geometry in RSC (Marchette et al. 2014) and OPA (Lescroart and Gallant 2019), affordances in OPA (Bonner and Epstein 2017) and head direction in RSC (Vass and Epstein 2013). Medial temporal structures provide a representation of an abstract cognitive map in the hippocampus (O'Keefe and Dostrovsky 1971) and distance in the entorhinal cortex (Fyhn et al. 2004). The prefrontal cortex likely represents navigational goals (Brown et al. 2016) and planed routes(Javadi et al. 2017). The parietal cortex represents information for visually-guided navigation (Gourtzelidis et al. 2005) and tracks progress towards a goal (Alexander and Nitz 2015).

Previous studies have examined these representations in isolation and in simplified, constrained tasks. Doing so creates two unresolved issues. First, the brain is nonlinear and behaves differently under simplified conditions than under naturalistic conditions (Wu, David, and Gallant 2006; Matusz et al. 2019). Thus, it is still unclear how the brain represents navigational information during more naturalistic navigation tasks. Second, it is difficult to compare results from experiments that used different tasks and stimuli. Thus, it is unclear whether all navigation information are equally represented in brain activity, or if some representations account for more variance than others.

Methods

To determine now the brain represents navigational information during active navigation, and to determine the variance in brain activity that can be accounted by different navigational representations, we developed an experiment in which subjects drove in a virtual world while brain activity was recorded with fMRI.

Experiment We used Unreal Engine 4 and Carla (Dosovitskiy et al. 2017) to build a 2×3 km virtual city populated by dynamic AI pedestrians and vehicles. Subjects drove a virtual car using a set of MR-compatible steering wheel and pedals. Prior to scanning, subjects learned the layout of the world. In the scanner, three subjects performed a taxi-driver task. Each trial began with a cue that prompted the subject to navigate to a destination. The subject then drove to the destination, following all traffic rules. Once the subject arrived, a new trial began with a new destination. We used the game engine and OBS Studio to produce a ground-truth record of all events in the experiment.

MRI data were acquired on a 3T Siemens Trio with a 32-channel head coil. BOLD data were acquired using a T2*-weighted gradient-echo EPI sequence. Personalized headcases (caseforge, Power et al. 2019) were used to stabilize the head. Data were collected in 11-min-

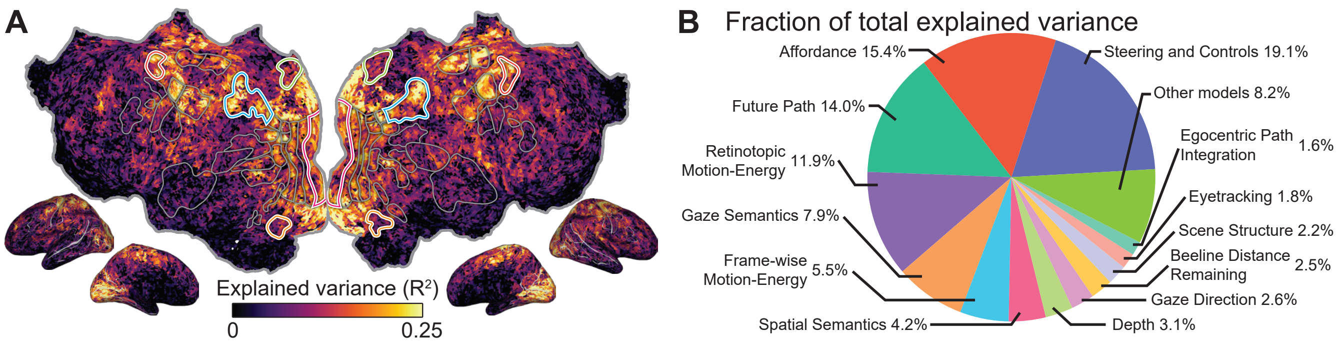

Figure 1: To examine the relative contributions of different navigational representations to brain activity, we simultaneously fit 33 visual, motor and navigational models to data from subjects performing a taxi-driver task in a naturalistic virtual world. A) Models explain significant amounts of brain activity in 40.3% ± 7.8% of cortical voxels (mean ± std across subjects, $p < 0.01$). Significant predictions are found within and beyond known navigation-related ROIs, suggesting that active navigation is supported by broadly distributed networks. B) To understand the relative importance of different representations, we partitioned the total variance explained among the 33 individual models. Models for visual and motor information account for over half the total explained variance. Among models for navigation-related information, goal-directed representations account for the greatest amount of variance. On the other hand, passive perceptual representations account for only a small fraction of response variance. These results suggest that during active navigation, navigational representations in the brain are primarily goal-directed.

ute runs (110 mins total for S1, 180 mins for S2 and S3). Eyetracking data were collected at 60 Hz. Anatomical images and functional localizers were collected separately to reconstruct the cortical surface and define ROIs.

Modelling From the game recordings, we extracted 21,283 features across 33 feature spaces. These feature spaces included low-level visual features such as motion-energy, motor outputs such as the steering wheel and accelerator values, passive perceptual navigational features such as head direction and affordances, and goal-directed navigational features such as route progression and a vector to the destination. Banded ridge regression (Nunez-Elizalde, Huth, and Gallant 2019) was used to simultaneously fit voxelwise encoding models with all feature spaces to the brain data. Model prediction accuracy was evaluated by predicting brain activity in a held-out dataset not used in model fitting.

Results

To understand how the brain represents navigational information in an active task and to determine how different navigational features account for variance in brain activity, we applied voxelwise modeling (VM) to data from subjects performing a taxi-driver task. We jointly fit 33 models with feature spaces that encompassed a variety of visual, motor, and navigation features (see Methods). In this active navigation task, the voxelwise models explain significant amounts of activity variance in 40.3% ± 7.8% of cortical voxels (mean ± std across subjects) voxels ($p < 0.01$) in each subject. (Fig. 1A). Significant model predictions are found in many regions within and beyond known navigation-related ROIs, suggesting that active navigation is supported by broadly distributed networks in the brain.

To determine the relative importance of different representations, we determined the amount of variance explained by each of the 33 models (Fig. 1B). We find that visual and motor models account for over half the total explained variance (51.4%). In the navigational models, goal-directed representations account for the most variance. For example, the “future path” model accounts for 14.3 ± 6.0% (mean ± std across subjects) of the total explained variance. On the other hand, passive perceptual navigational representations explain vanishingly small amounts of the variance in voxel activity. For example, the “head direction” model accounts for 0.3% ± 0.6% of total explained variance. These results show that while many different navigation-related features are represented simultaneously in navigational cortical networks, goal-directed features account for the most variance in these networks.

Discussion

To determine the relative importance of different navigational features to brain activity during active navigation, we developed an immersive and interactive navigation experiment for fMRI, and simultaneously fit 33 visual, motor, and navigational models to the data. Voxelwise models fit to multiple navigation-related feature spaces enabled us to directly compare many navigational representations in the same setting. We find that when subjects navigate actively, most navigational variance can be accounted for by goal-directed models. These models capture representations such planned future paths, distance remaining to the destination, path integration, and progression along the planned route. On the other hand, models for passive perceptual navigation representations, such as the direction that the subject is facing or a grid cell representation of space, account for much less variance in brain activity. These results suggest that during active navigation, navigational representations in the brain are primarily goal-directed.

We note that in these results, the affordance model accounts for a large portion of variance (15.4%) even though affordances are not a goal-driven representation. However, affordances are a very salient feature when driving, as subjects must stay on the road and avoid obstacles. Thus, the importance of affordances during naturalistic navigation may explain the large contribution of this feature space. It is likely that the 33 feature spaces used here do not encompass all possible features, and more models will reveal more fine-grained distinctions in their relative importance. Nevertheless, this study provides the most comprehensive description available currently of navigational representations in the human brain during active navigation. Because the VM framework provides a principled method for post-hoc hypothesis testing, these data can be used to evaluate other potential navigation-related representations.

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