The Role of Landmarks and Travel Pauses in the Generation of Hexadirectional fMRI Signals during Spatial Navigation

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Abstract

As humans navigate in physical, conceptual, or even social domains, functional magnetic resonance imaging (fMRI) signals from the hippocampal formation vary with movement directions, fluctuating in strength with a periodicity of 60 degrees. While grid cells are believed to underlie these hexadirectional fMRI signals, the exact mechanism linking the two is unclear. Three hypotheses have been proposed: conjunctive grid-by-head-direction cells, repetition suppression, and nonlinear transformations of grid-cell activity into BOLD signals. We aim to combine theoretical analysis and fMRI experiments and identify key design parameters for distinguishing among the three hypotheses. Two critical factors emerge from our analysis: the presence of landmarks as a precondition, and pauses between linear path segments as a way to distinguish among the hypotheses. First, we modeled the trajectories represented by grid-cell activity using an extended Kalman filter fitted to behavioral data. Under all three hypotheses, hexadirectional signals emerge when landmarks are present, reflecting the landmarks' role in providing correct directional information. With correct directions, the theoretical analysis further predicts that the pauses measurably increase the hexadirectional strength under the repetition suppression hypothesis, diminish it under the nonlinearity hypothesis, and have no effect under the conjunctive grid-by-head-direction cell hypothesis. We are conducting experiments to examine the predictions.

Keywords: grid cell; hexadirectional fMRI signal; navigation

Introduction

Grid cells are crucial for navigation, displaying a hexagonal periodic firing pattern in their ratemaps (Figure 1A) (Dong & Fiete, 2024). This observation led Doeller, Barry, and Burgess (2010) to hypothesize that grid cells generate hexadirectional functional magnetic resonance imaging (fMRI) signals, which vary with moving directions and exhibit a periodicity of 60 degrees (Figure 1B). These signals have been extensively utilized to investigate human navigation across physical, conceptual, and social domains (Doeller et al., 2010; Constantinescu, O'Reilly, & Behrens, 2016; Liang et al., 2024). However, the origin of these hexadirectional signals remains elusive, as, on average, grid-cell activity should be approximately uniform across movement directions (Figure 1B).

Three hypotheses address this discrepancy. The grid-by-head-direction cell hypothesis (Figure 1C) suggests that some grid cells are also tuned to one of the six directions aligned with grid axes, generating hexadirectional signals (Doeller et al., 2010; Bin Khalid, Reifenstein, Auer, Kunz, & Kempter, 2024).

The repetition suppression hypothesis proposes that a grid cell's activity is suppressed based on the time spent in its firing field (Doeller et al., 2010; Bin Khalid et al., 2024). Participants encounter the same grid cell more frequently in perfectly aligned (0°) directions, leading to stronger suppression (Figure 1D). We define the frequency of encountering the same grid cell as $f = E_t[\max(1, \frac{G(t)}{E_t[G(t)]})]$, where $G(t)$ represents the original activity and E_t denotes time average. These frequencies are similar for intermediate directions (10° or 20°). However, the higher local f in relatively aligned (10°) directions leads to greater suppression. This hypothesis produces hexadirectional signals with reduced activity in aligned directions (Figure 1E).

The nonlinearity hypothesis (Figure 1F) assumes that during linear movements, a grid cell's activity, convolved with a function (here a box function for simplicity) and subject to a nonlinear transformation, produces fMRI signals. (Almog, Galwa-Stokkan, Doan, & Schröder, 2024). While the mean convolved activity is the same across directions, the variance exhibits hexadirectional modulation, which results in hexadirectional average activity after nonlinear transformation.

Role of Landmarks

To model the trajectories encoded by grid-cell activity, we designed an experiment in which participants navigated along piecewise linear trajectories and, at each turning point, reported the direction of a target, either with or without landmarks. We fitted an extended Kalman filter (Kessler, Frankenstein, & Rothkopf, 2024) to each participant's responses and actual trajectory, deriving a distribution of possible encoded trajectories. Based on these inferred trajectories and the three hypotheses, we simulated grid-cell activity and fMRI signals. The results show that hexadirectional signals emerge in the presence of landmarks (Figure 1G), whose role in correcting the encoded directions is crucial.

Discriminating the Three Hypotheses

When participants navigate piecewise linear trajectories in the presence of landmarks, with angles between consecutive linear segments equal multiples of 60°, our theoretical analysis predicts distinct outcomes of pauses under different hypotheses: the pauses between linear segments enhance hexadirectional signals under the repetition suppression hypothesis (Figure 1H), reduce them under the nonlinearity hypothesis (Figure 1I), and have no effect under the conjunctive grid-by-head-direction cell hypothesis. For experimental tests, we recommend a segment length of 1.5 grid scales and a velocity higher than 1.5 grid scales per second

In conclusion, we demonstrate that precise directional knowledge, as provided by landmarks, is necessary for the hexadirectional signals to emerge, and show how to empirically discriminate among three potential mechanisms underlying these signals.

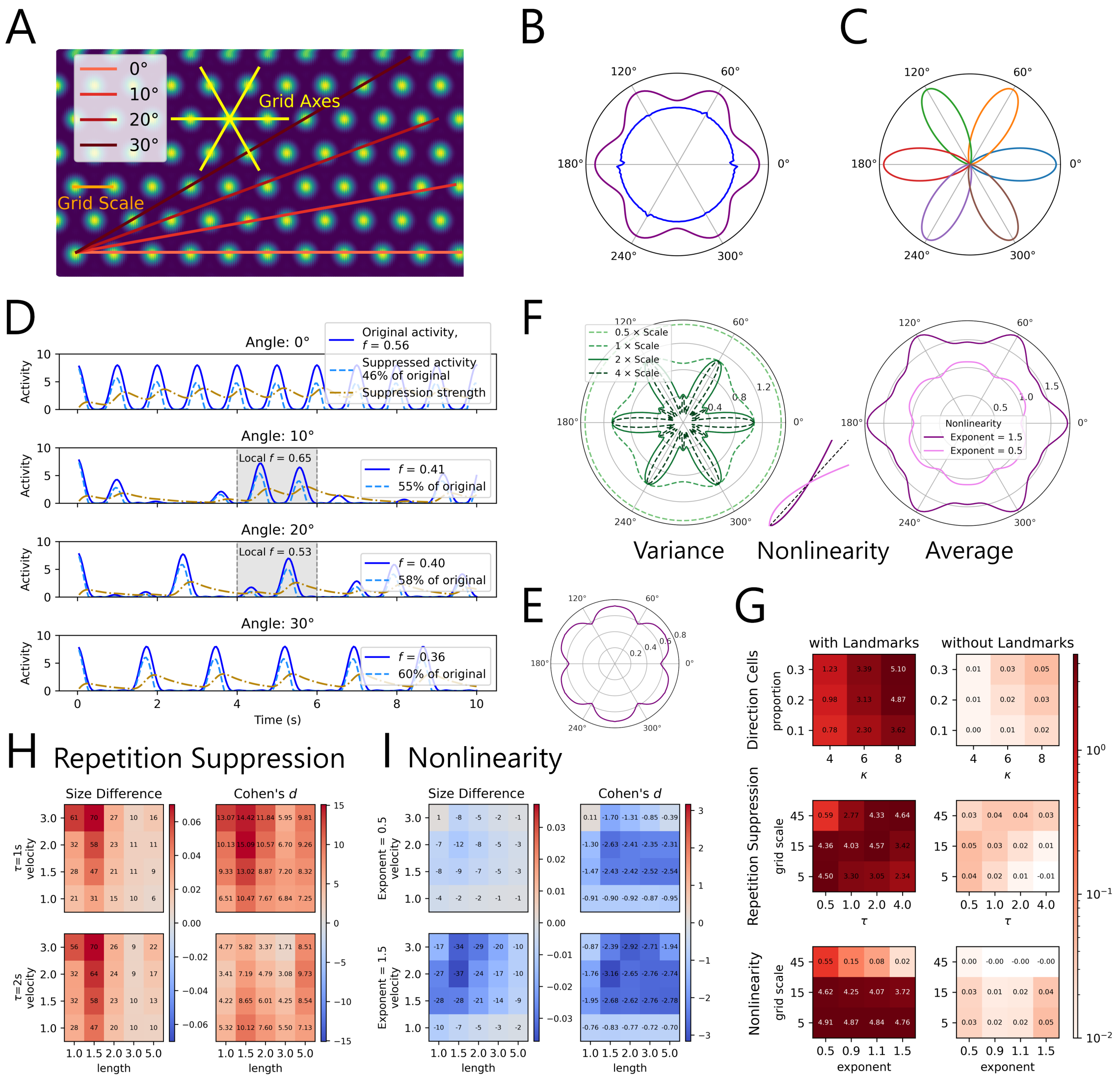

Figure 1: **A**. Grid axes and scale. **B**. Purple: a prototypical hexadirectional signal. Blue: The average activity of grid cells is approximately uniform across directions. **C**. Grid-by-head-direction cells are tuned to one of the six directions aligned with the grid axes. **D**. Activity of grid cells under repetition suppression, along the trajectories shown in (A). $f = E_t[\max(1, \frac{G(t)}{E_t[G(t)]})]$. Values in the boxes are averages from 0-10s. Local f is an average from 4-6s. **E**. Hexadirectional signals produced by repetition suppression exhibit reduced activity in the aligned directions. **F**. Left: when traversing straight paths of varying lengths, the grid-cell activity convolved with a box function shows hexadirectional variance. Middle: sketch of the nonlinearity. Right: nonlinearity ($x^{0.5}$ or $x^{1.5}$) transforms it into hexadirectional modulation of average activity. **G**. Hexadirectional signals emerge in the presence of landmarks. (Proportion: proportion of directionally tuned grid cells. κ: concentration parameter of the von Mises distribution for directional tuning.). **H**, **I**. Difference in hexadirectional strength between trajectories with and without pauses: **H**. Under the repetition suppression hypothesis (τ: repetition time constant, in seconds). **I**. Under the nonlinearity hypothesis (Numbers in the square grids of the size difference columns are in units of 10^{-3}). **Note**. Unit of length: grid scale. Unit of velocity: grid scale per second. The hexadirectional strength is computed as the average difference between aligned (within 15° of grid axes) and misaligned activity. For repetition suppression hypothesis and nonlinearity hypothesis with exponents < 1, the sign of the difference was inverted.

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