



Hippocampal LFP During Rodent Head-Scanning Behavior: Theta and Sharp-Wave Ripples

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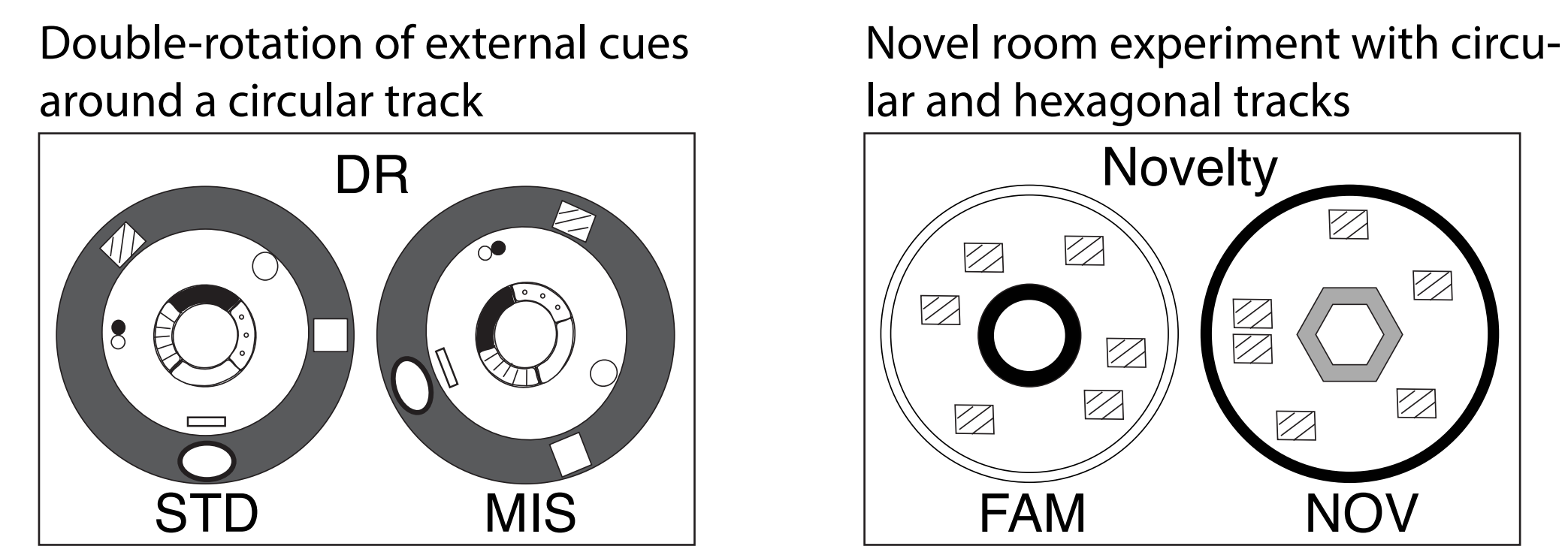
Joe Monaco, Geeta Rao, and James J. Knierim

Zanvyl Krieger Mind/Brain Institute, Johns Hopkins University, Baltimore, MD, 21218

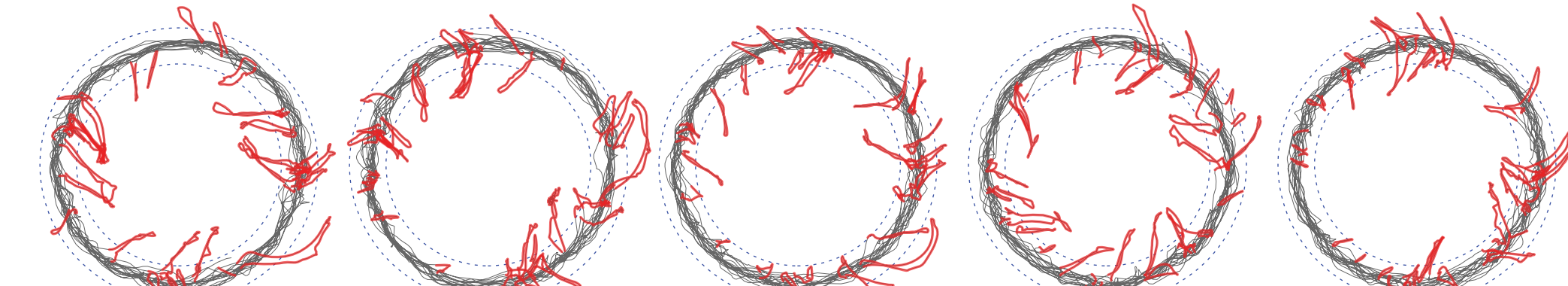
Introduction

The hippocampal spatial map integrates information about the environment as the animal explores, but the mechanisms by which salient information about external sensory cues alters place-cell activity is unclear. We hypothesized that head scanning, a prominent behavior in rats during pauses in locomotion, provides an opportunity for the animal to attend to external cues. We previously [1] showed that place-cell activity during head scans is predictive of subsequent onset or potentiation of place fields during cue rotation and novelty experiments performed on circular and/or hexagonal tracks. Here, to assess possible mechanisms behind this predictive association, we analyzed the hippocampal local field potential (LFP) recordings taken during these experiments for signs of temporal coordination and synchronization that may promote plasticity. First, the dominant hippocampal theta (5–12 Hz) rhythm has been extensively associated with voluntary exploratory motor activity including active locomotion. Early studies have reported that lateral head movements evoke runs of theta activity [2], and head movements have been categorized as exploratory behavior more recently [e.g., 3], but there has not been a clear characterization of theta during head scanning. Second, sharp-wave ripple oscillations (100–250 Hz), prominent in CA1 during non-theta periods and typically associated with non-exploratory or consummatory behaviors, have been shown to support the encoding of spatial memory [e.g., 4]. We investigate both theta and ripples in relation to head scanning behavior and the distinct phases of movement during scanning.

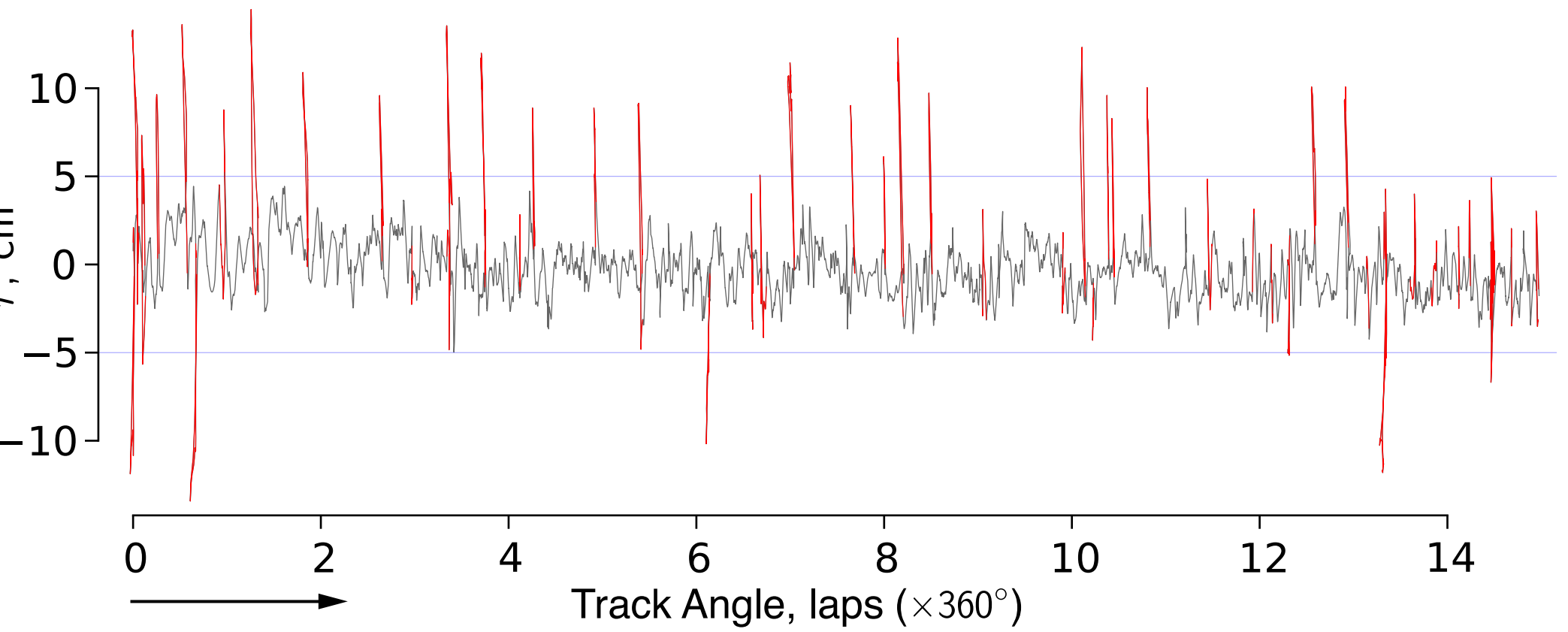
Scanning Behavior



Example trajectories from a DR dataset with head-scan events



An example trajectory, unwrapped, to show scans across the session



Head-scanning behavior is partitioned into distinct phases

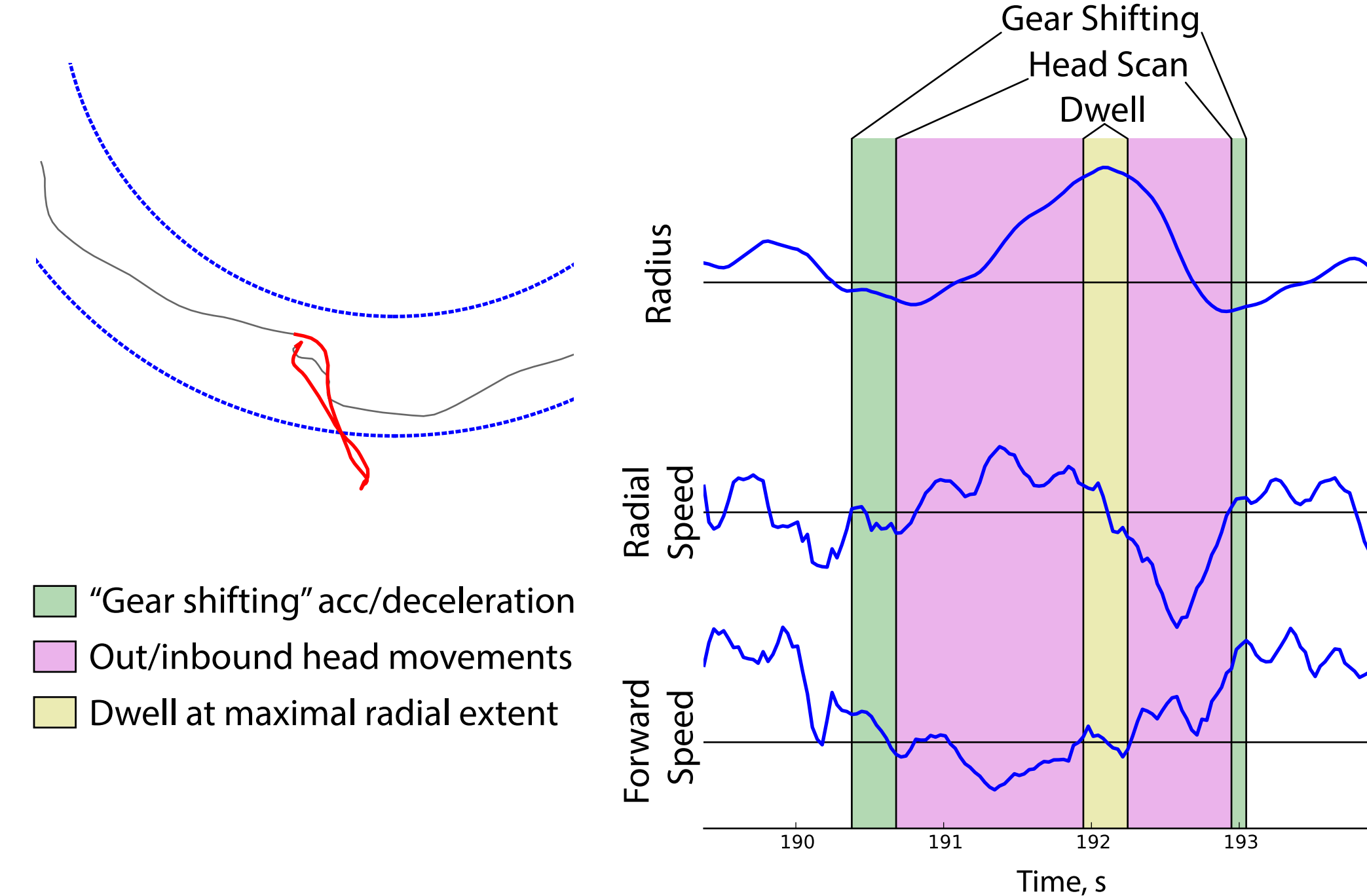


Fig. 1. (top) Schematic representations of the cue double-rotation (DR, left) and novel room (Novelty, right) experiments which provided the behavioral and hippocampal LFP recordings. Circular and hexagonal tracks are ~76 cm outer diameter. (middle) An example 5-session DR dataset is shown with detected head-scan events in red, followed by a single session unwrapped by track angle across the laps. (bottom) An example scan illustrates the phases of scanning movements.

Scans and Place Fields

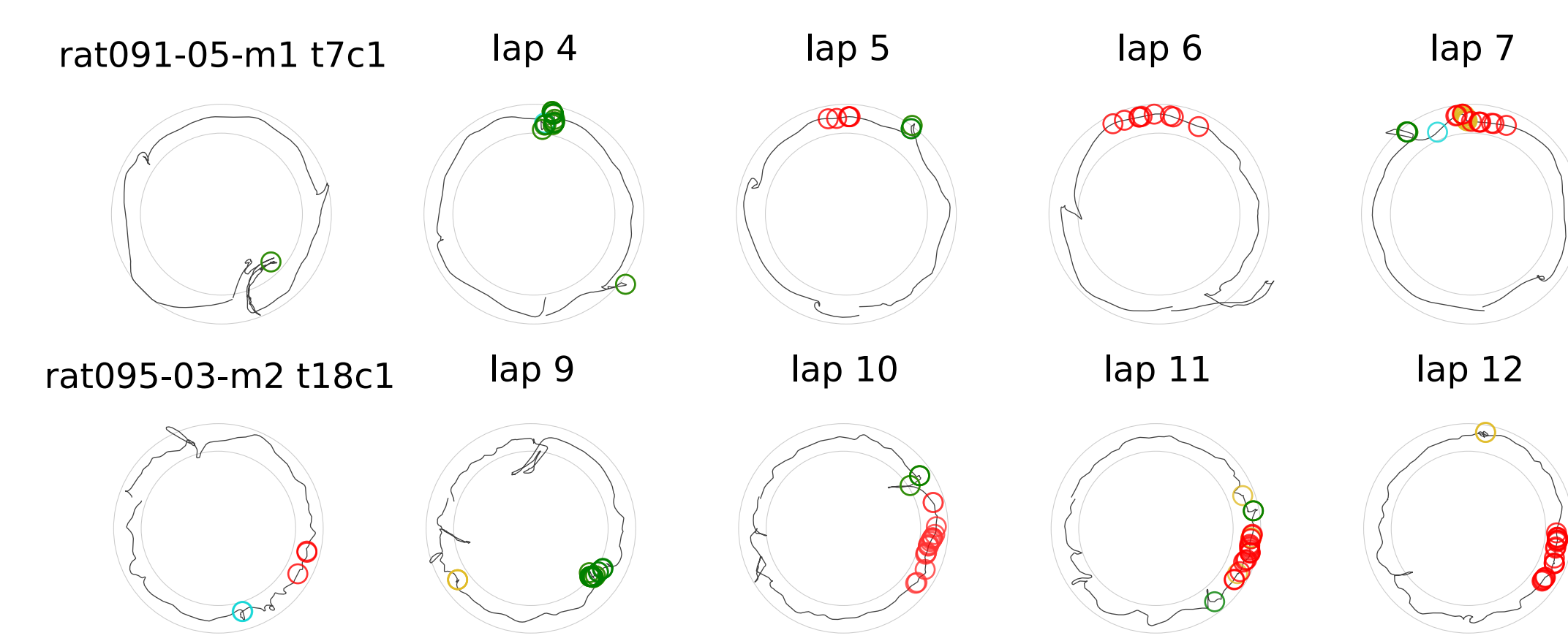
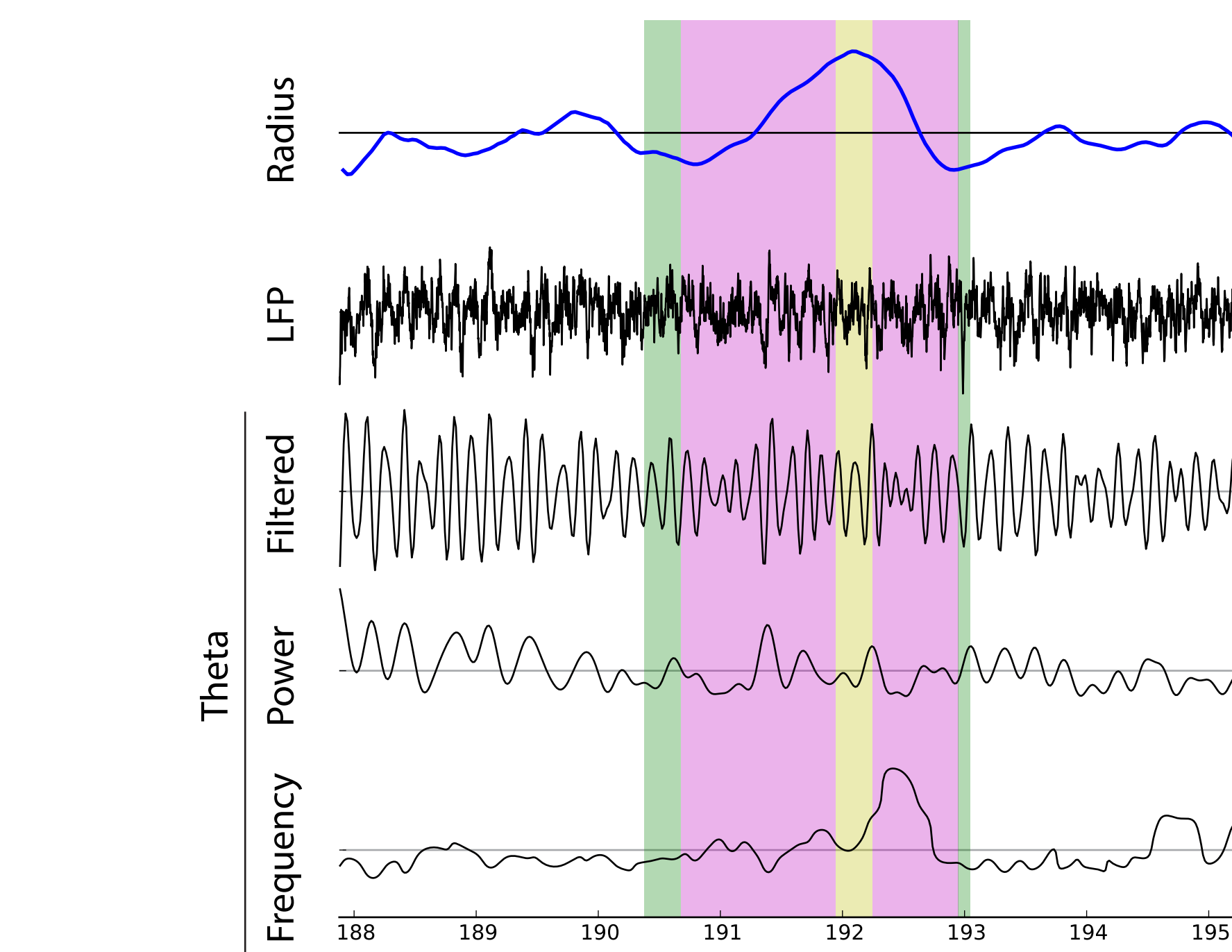


Fig. 2. We previously showed [1] that place-cell activity during head-scanning behavior is predictive of subsequent place-field activation or potentiation. Five laps centered on a potentiation event (lap 5, top; lap 10, bottom) are shown for two example place fields to illustrate the observed effect. Spikes are coded by color: scan (green), gear-shifting (cyan), non-scan pause (yellow), and place field (red).

Theta Power during Scanning

Example head-scan event with ongoing LFP and theta rhythms



Theta rhythm is present during scanning, though reduced compared to forward running

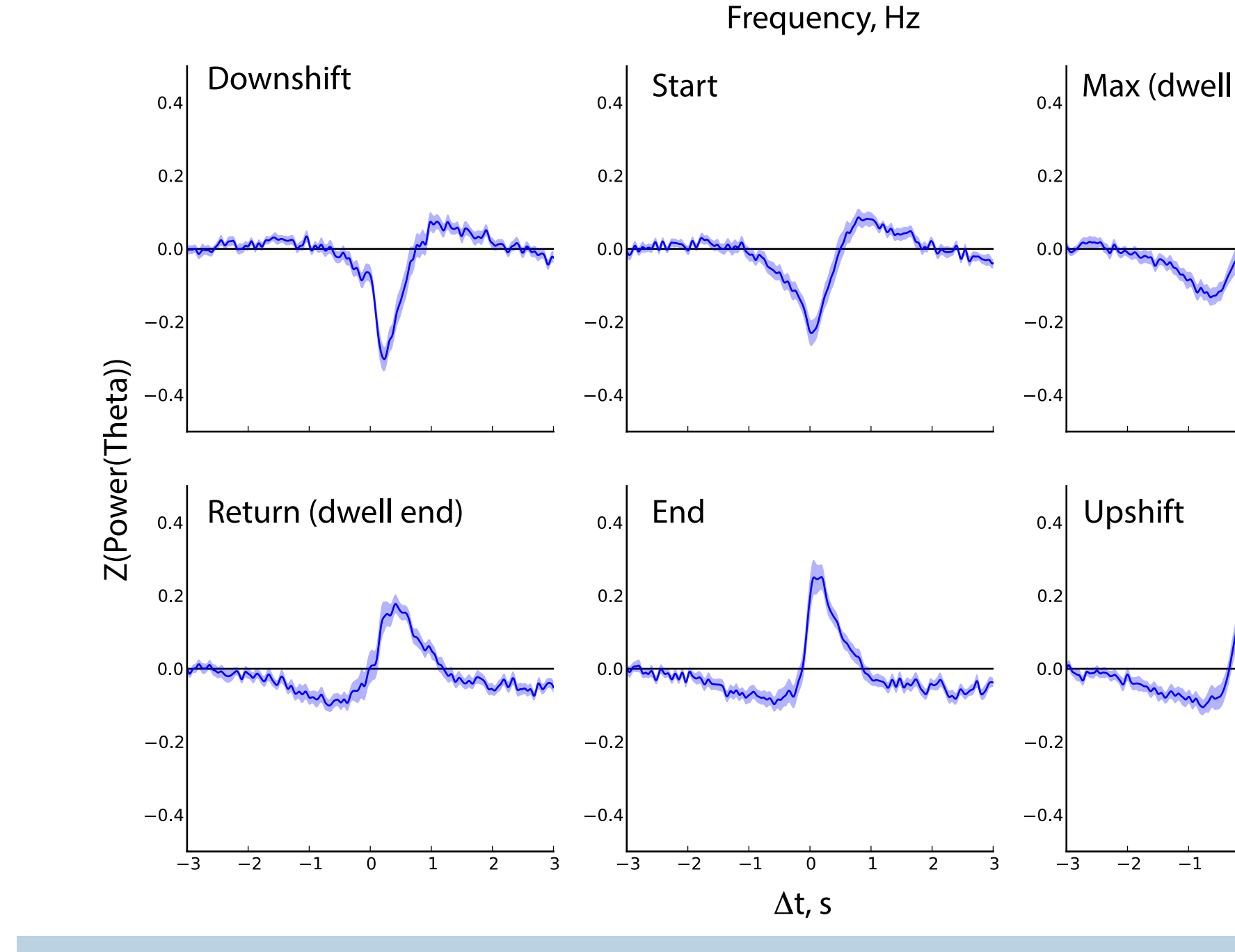
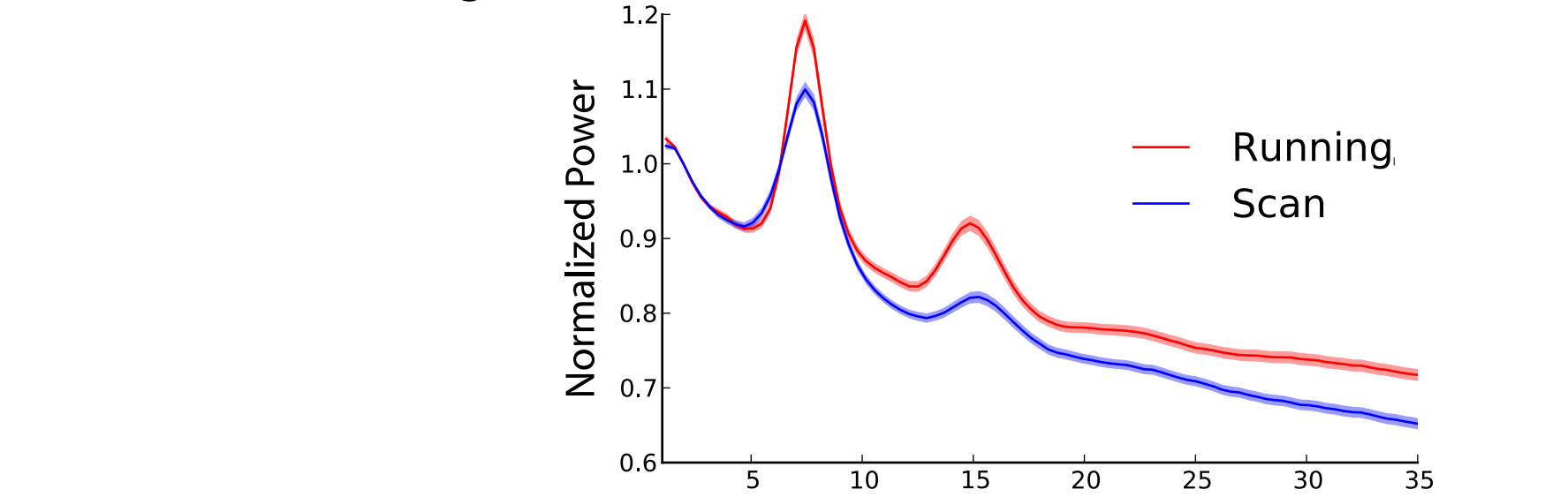


Fig. 3. (top) Example head scan event with concurrent LFP, theta (5–12 Hz) band-pass, Z-scored theta power, and instantaneous theta frequency computed by the analytic signal. (middle) Normalized power spectra for the highest theta-power tetrodes in each dataset (mean and 95% confidence intervals across rats). (bottom) Cross-correlations of theta power time-locked to scans at different points of the behavior. Curves show means and s.e.m. across rats. (right) Power during non-scan pauses is shown for comparison.

Theta Frequency during Scans

Theta frequency during scans is faster overall than non-scanning pauses

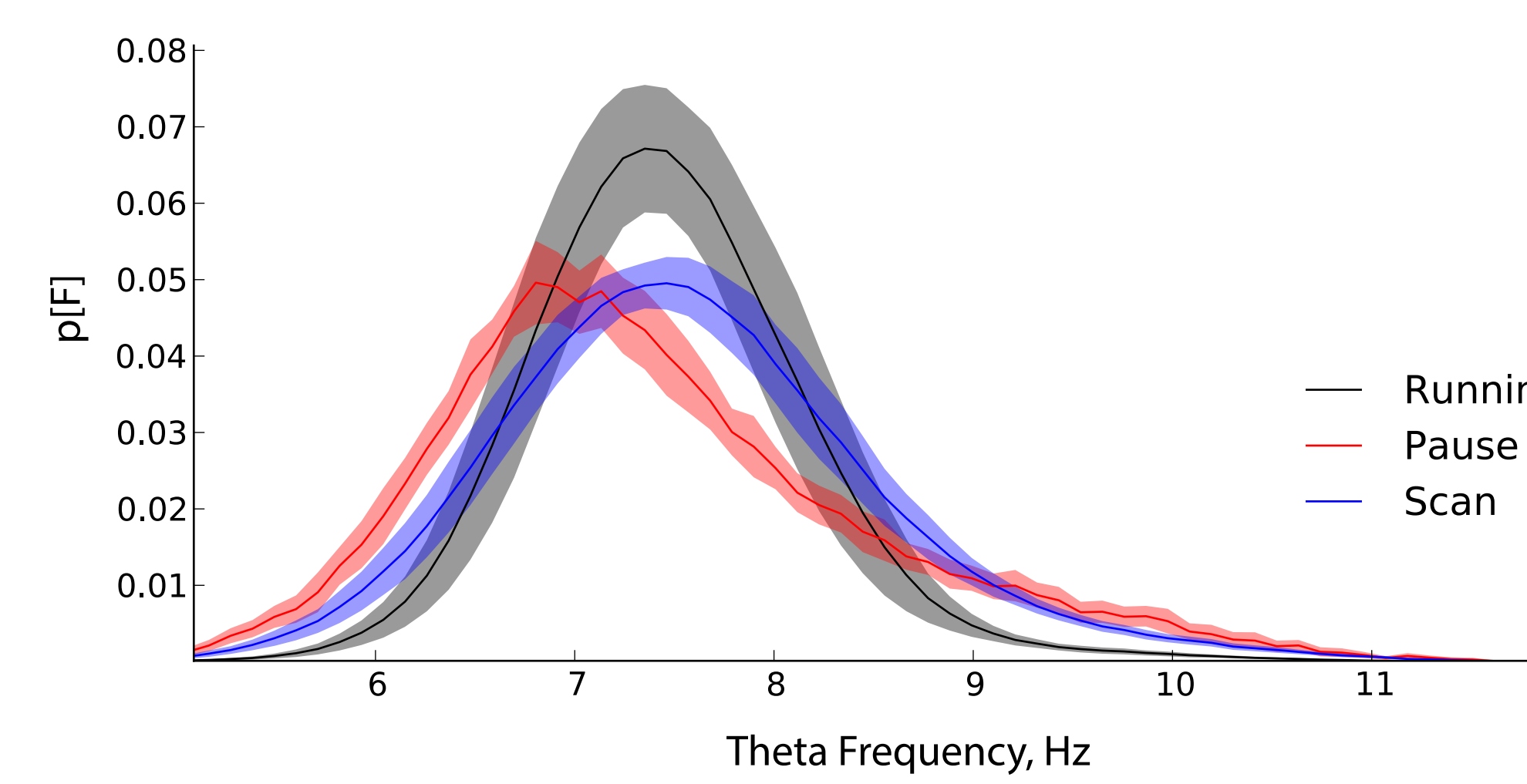
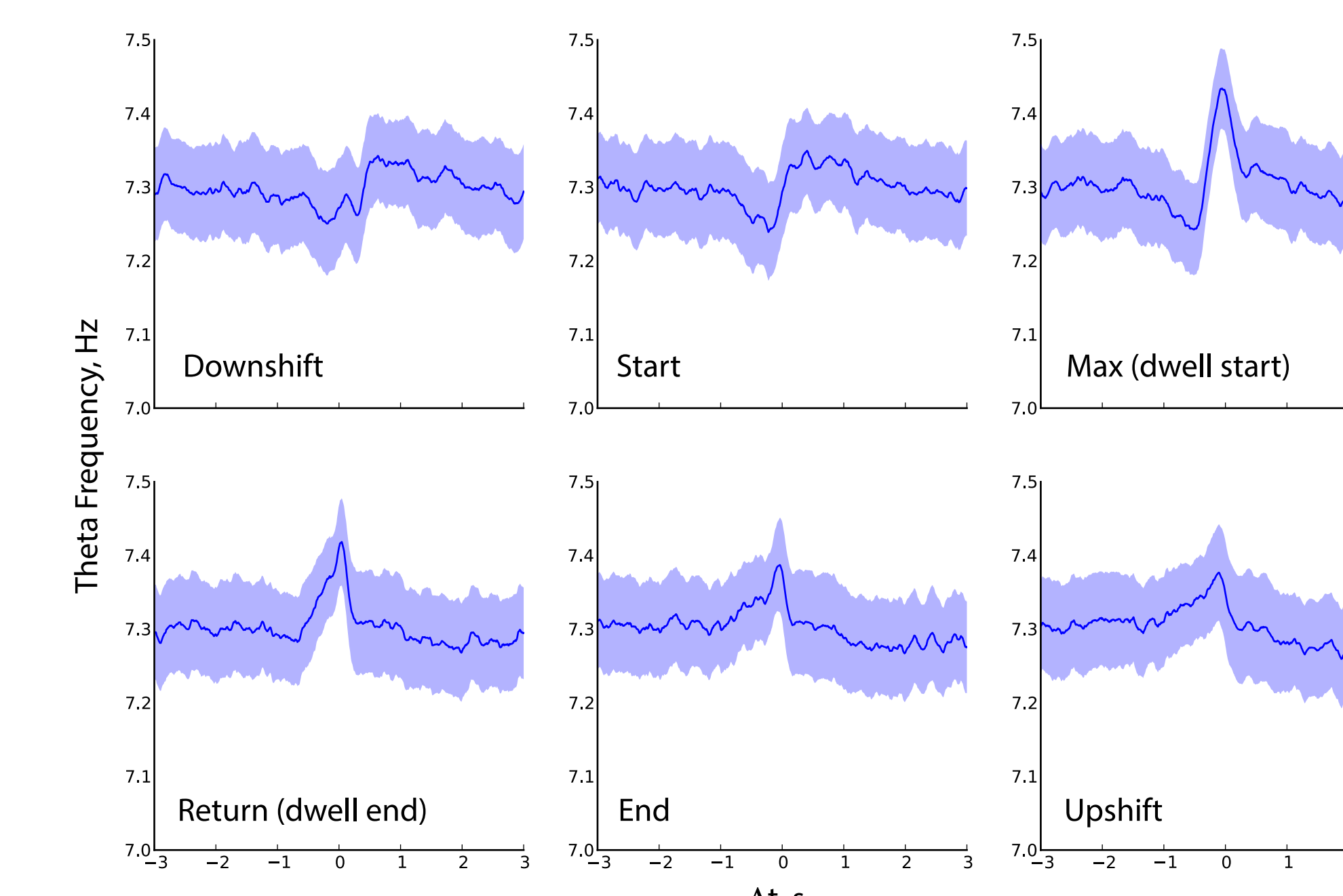


Fig. 4. Distributions of instantaneous theta frequency for scanning, forward running, and non-scanning pause behaviors. Lines and shaded regions are means and 95% confidence intervals across rats. The frequency mode for scanning is similar to the mode for running, but significantly faster than pauses.

The instantaneous frequency of the theta rhythm is modulated higher on the outbound phase of head scans



During non-scanning pauses, theta frequency is momentarily reduced

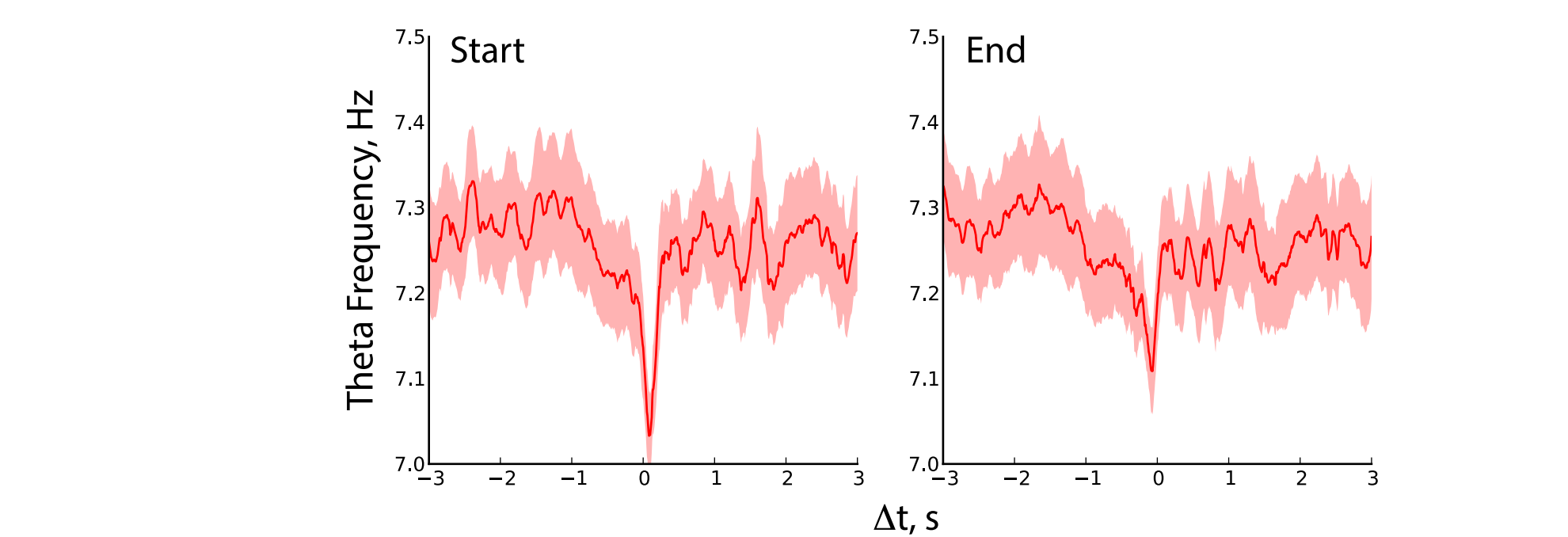
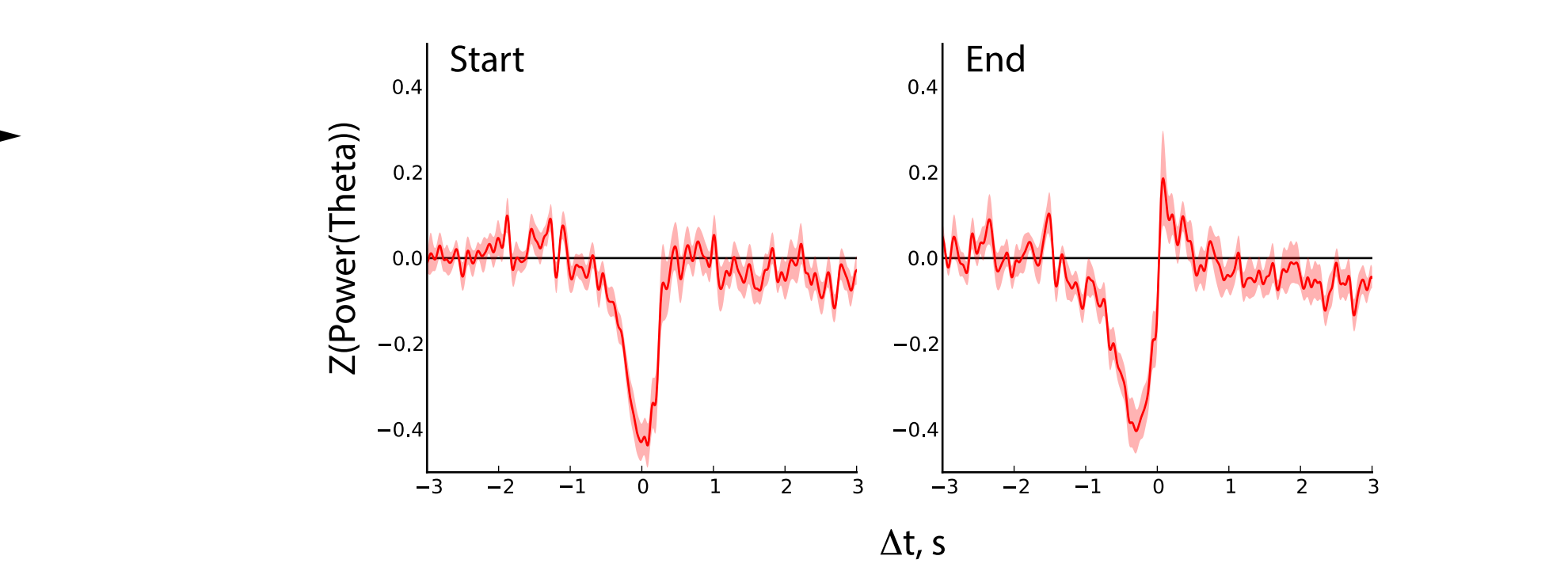


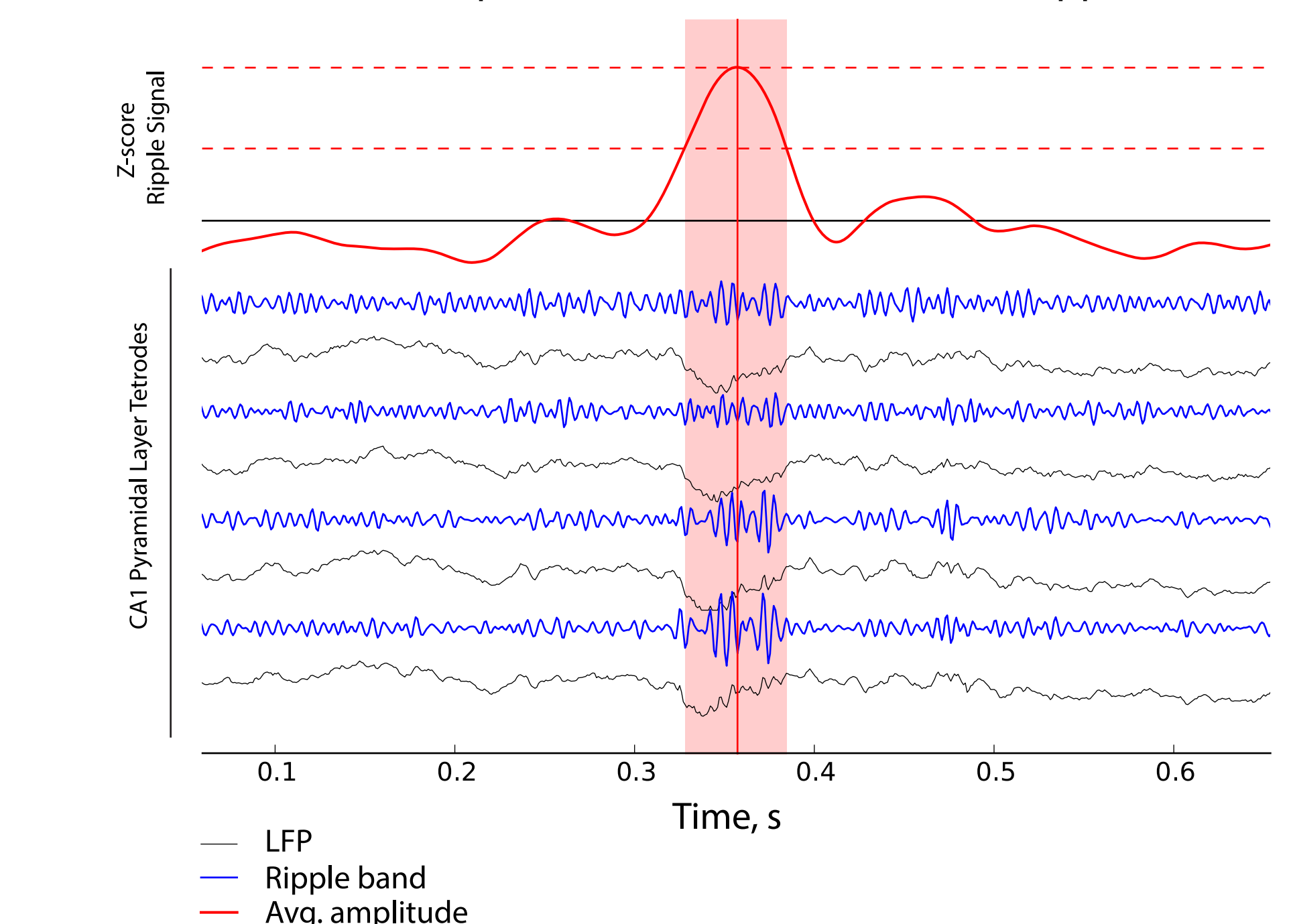
Fig. 5. (top) Cross-correlations, as in Fig. 3, of instantaneous theta frequency are shown for each of the six points defining the phases of head-scan movements. The primary outbound lateral movement begins at "Start" and ends at "Max", and the dwell period begins at "Max" and ends at "Return". (bottom) Correlations are shown for non-scanning pauses, characterized primarily by a sharp reduction in frequency.

Theta power during non-scanning pauses

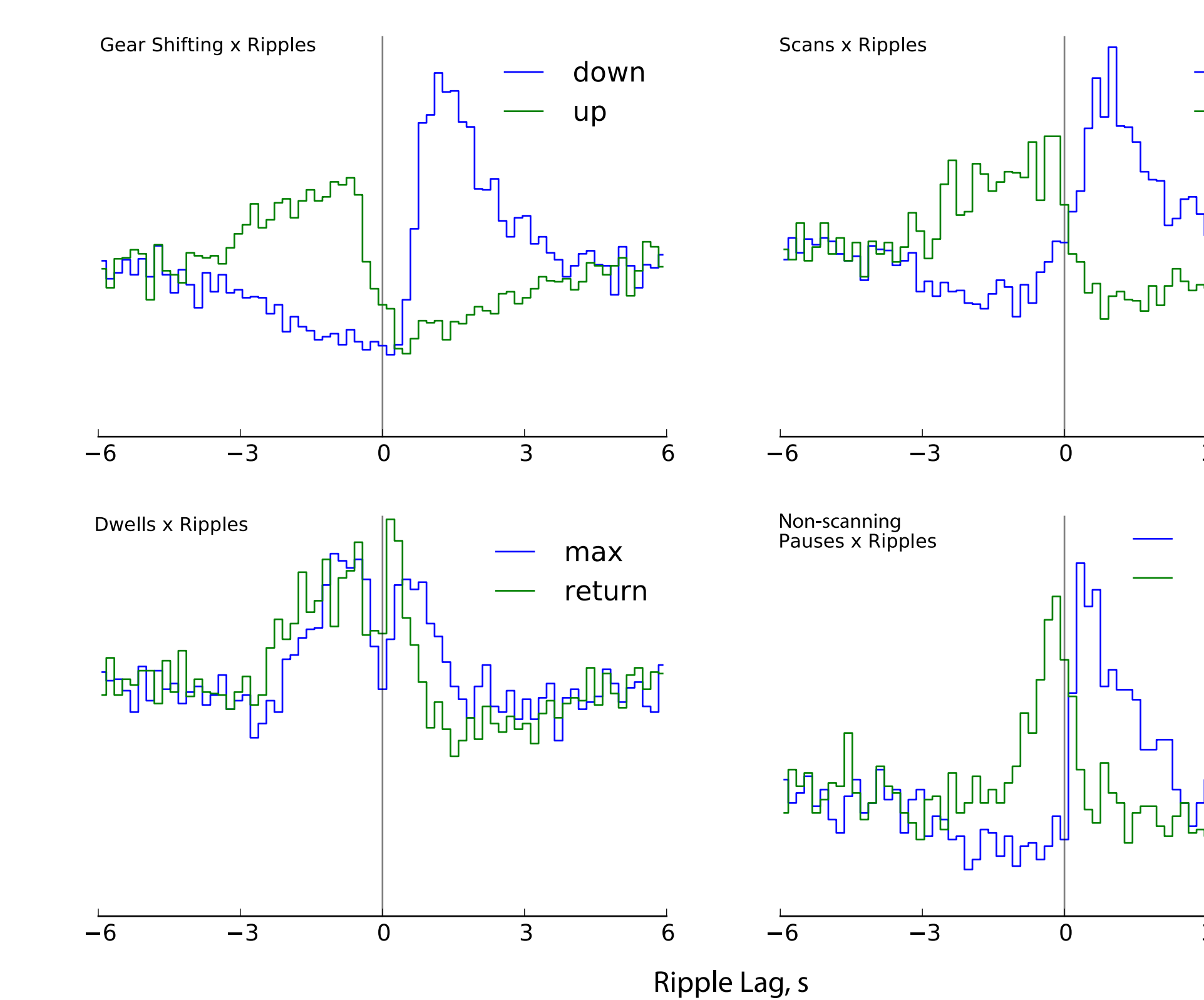


Ripple Oscillations and Scanning

Double-threshold amplitude method used to detect ripple events



Cross-correlations between ripples and head-scan phases



Distributions of ripples across behavior and experiment type

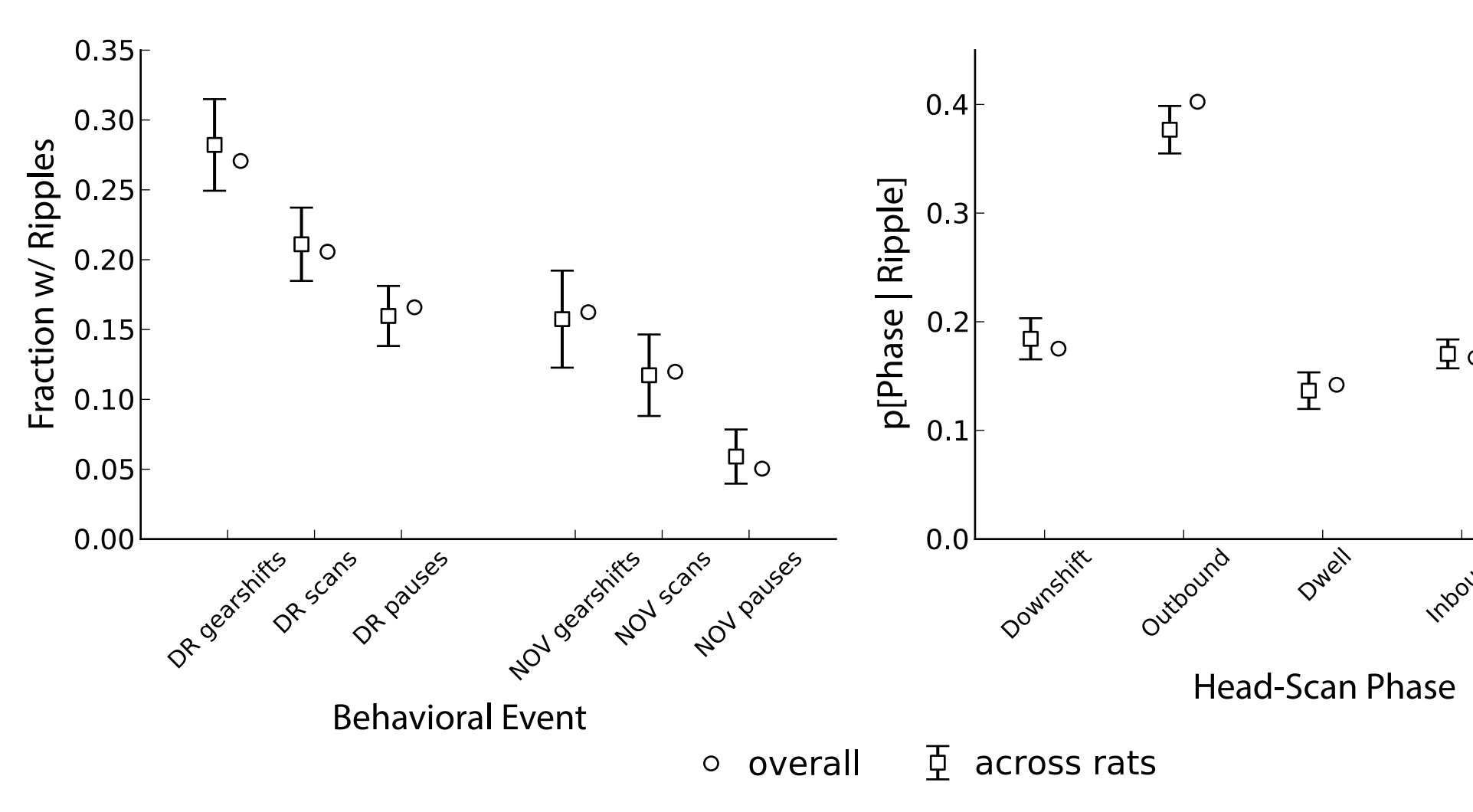


Fig. 7. (top) Ripple events are detected using the double-threshold amplitude method, as described by [5]. Briefly, all tetrodes in the CA1 pyramidal layer are band-pass filtered at 100–250 Hz, the amplitudes computed, averaged, and z-scored, then putative ripple events are determined by the threshold crossings as illustrated. We used a high peak threshold of 4.2 sigma to ensure a low false-positive error rate for detection of ripple events. (middle) Event cross-correlations between the timing of ripple peaks and the end-points of head-scan phases. Gear-shifting (top left), scanning (top right), dwell period (bottom left), and non-scan pauses (bottom right) are shown. Ripple likelihood is strongly modulated by the deceleration ("downshift") into and the initiation ("start") of head scans. (bottom) Prevalence of ripples in behavioral epochs (left) and the distribution of ripples across scan phases (right) show that ripples mostly occur on the outbound phase.

Ripples, Theta, and Scanning

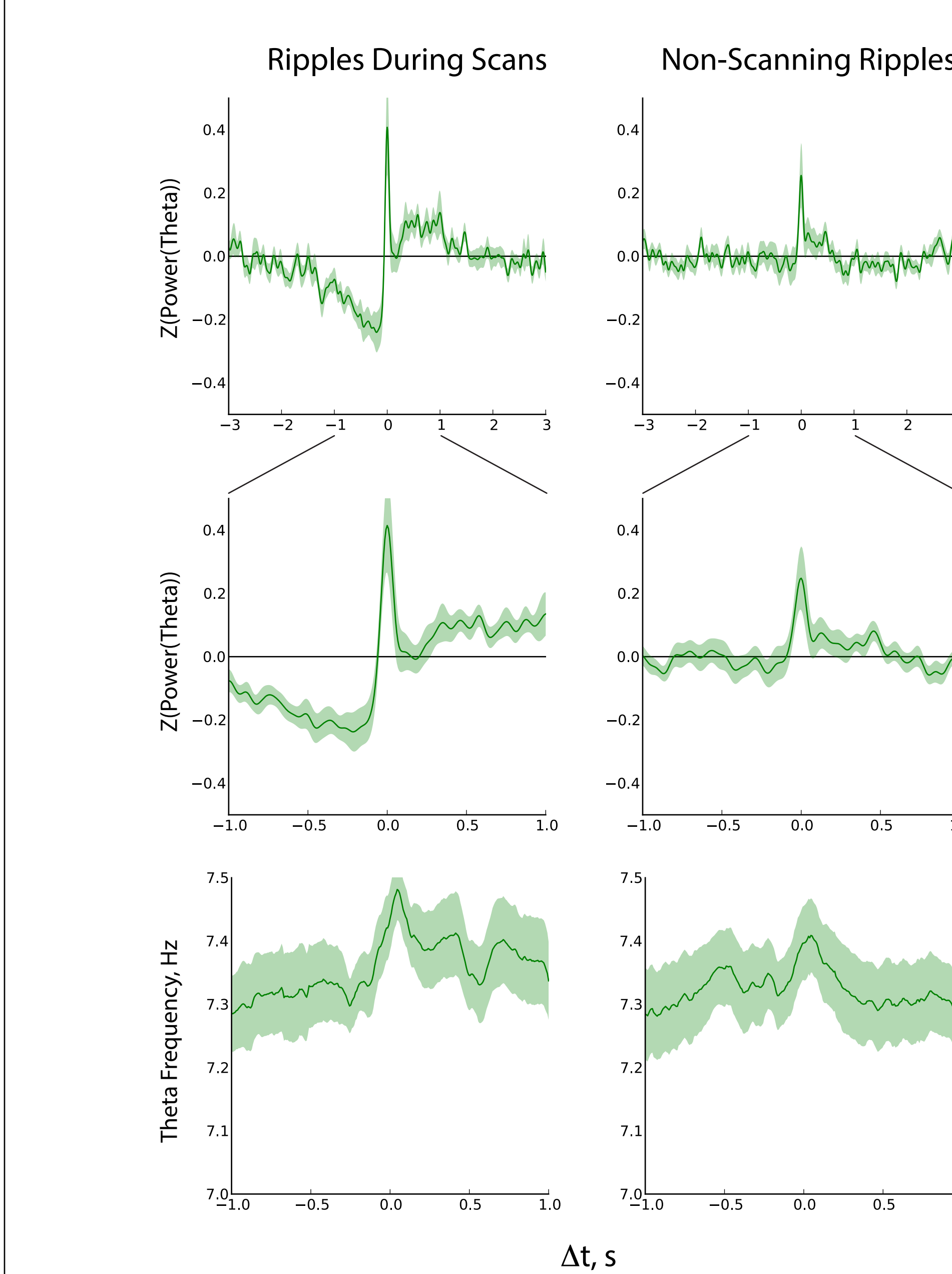


Fig. 7. Event cross-correlations of theta power (top two rows) and frequency for ripples that occurred during scanning (left column, scanning defined to include gear-shifting) and non-scanning epochs (right column). Correlation computed as in Figs. 3 and 5. Ripple timing is defined as the peak of the averaged ripple-band amplitude during the detected ripple event. The narrow central peak represents an increase in LFP power during ripples (possibly due to concurrent sharp waves). Ripples during scans occur during periods where theta power is gradually increasing on a time-scale of 1-second.

Conclusion

While rodent behavior is typically divided into active exploration, dominated by strong theta, and quiescent or consummatory behaviors, characterized by large-amplitude irregular activity and sharp-wave/ripple complexes, head scanning may present an intermediate (or mixed) mode. Theta power and frequency are reduced at the deceleration and initiation of the lateral head movement, but increase across the outbound phase of the scan as the animal looks out to the environment. Around one quarter of scan events contain ripples, which mostly occur on the outbound phase as theta power is increasing. These dynamics are distinct from those of more quiescent pauses that lack scanning movements. The preparation for a head scan resembles a typical pause, but the major lateral head movement outward is associated with both a return to theta and an increased likelihood of ripple oscillations. The temporal coordination evident in the LFP during head scanning may promote the integration of sensory information into the hippocampal spatial map.

Acknowledgements

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