1 Introduction

Recording invasively from human epileptic patients allows us to clearly see oscillations related to cognitively relevant variables [1, 2, 3, 4]. In a virtual taxi driving task, we found human cortical theta oscillations related to virtual movement and type of search. While this is consistent with the extensive rodent literature linking theta oscillations with exploratory behavior [5, 6, 7], an alternate account is that these theta oscillations are related to the classic posterior alpha observed during resting wakefulness. To address this we asked our participants to successively open and close their eyes, then analyzed their intracranial EEG (iEEG), identifying the topographical and spectral pattern of desynchronization with eye opening. We compared this pattern with the topographical/spectral pattern obtained with the task comparisons, to enable us to rule in or out the resting alpha account of our results.

2 Methods

2.1 Patients and recording

We recorded iEEG from subdurally place grids and strips, in three epileptic patients who were undergoing long-term monitoring for planning of subsequent resection surgery. We analyzed iEEG signal from a total of 213 electrode contacts (excluding epilepsy zones), with a sampling rate of 256 Hz, band-pass filtered 0.3–70 Hz (BioLogic Corp.).

2.2 Behavioral procedure

Virtual navigation Participants navigated virtual, 3-D rendered towns, viewed from a first-person perspective and consisting of 3×3 blocks. Participants alternately searched for passengers who could be located anywhere within the town (“foraging” phase) and delivering passengers to their desired location— a specific store within the town (“goal-seeking” phase). There were three stores (possible goal-seeking targets) and six buildings (distractors) that were never targets in each virtual town. Participants made seven deliveries to each store in counterbalanced order, in one environment, town **A**, followed by the same procedure in a distinct environment with different stores, buildings and configuration, town **B**, and finally returned to town **A**. The present results represent analyses averaged across town **B** and the first exposure to town **A**.

Resting alpha protocol A computer-recorded voice instructed participants to alternately close and open their eyes for five-second intervals, and for five iterations.

2.3 Oscillation analysis

All iEEG signal was transformed with Morlet wavelets (6 cycles/packet, in steps of base $2^{1/4}$) over the range 2–45 Hz.

For movement-related oscillations in virtual navigation, we applied an oscillatory episode detection algorithm [2] that accounts for the background colored noise spectrum, identifying epochs of heightened power (95^{th} percentile based on the noise distribution) over a minimum duration (3 cycles of overlapping wavelet windows). Percentage of time occupied by oscillations at frequency f, or $P_{episode}(f)$ was compared between epochs of movement (forward, left or right) and epochs standing still (only epochs of uniform behavior between 0.5 and 30 s were included). The analysis was performed separately for the foraging and goal-seeking phases, using a two-tailed Mann-Whitney U test.

For resting alpha, we compared wavelet power during the eyes-open condition with that during the eyes-closed condition, excluding the first 0.5 s to account for the participant's response time to the instruction. The analysis was performed with a two-tailed Mann-Whitney U test, correcting the degrees of freedom for overlapping wavelet windows.

3 Results and Discussion

Figure 1 (left) shows the frequency distribution of movement-related oscillations during foraging. Note the prevalence of this effect in the theta band (4–8 Hz) across all three participants. Figure 1 (right) shows the frequency distribution of resting alpha. Here as well, there is an effect in the theta band, but also at other frequencies. In particular, some brain areas show desynchronization upon eye opening, but others show *synchronization*. Differences across participants is most likely due to substantial differences in electrode placement.

To test whether movement-related oscillations could be related to the resting alpha rhythm, we evaluated correlation between the two statistical tests. We first z-transformed the statistics (Mann-Whitney U scores). Then we masked our analyses by requiring that an electrode/frequency must show at least one of the two effects to $p < 0.01$ to be included in the correlation. We then computed the Pearson correlation between the z-scores for the virtual movement effect and resting alpha effect across all such included electrode/frequencies and evaluated the correlation against the null hypothesis of independence. A small value of r would suggest that the two effects are independent. A large, positive value of r would suggest that the effect occur at the *same* brain locations and frequencies as each other. A large, negative value of r would suggest that the two effect are mutually exclusive.

Table 1 shows the resulting Pearson correlation values. Only for participant 2 did the correlation reach significance, and it did so both within the theta band (4–8 Hz) and across the entire band analyzed (2–45 Hz), in both cases the correlation being positive. However, even when significant, the magnitude of the correlation is small, suggesting that while there is overlap between the

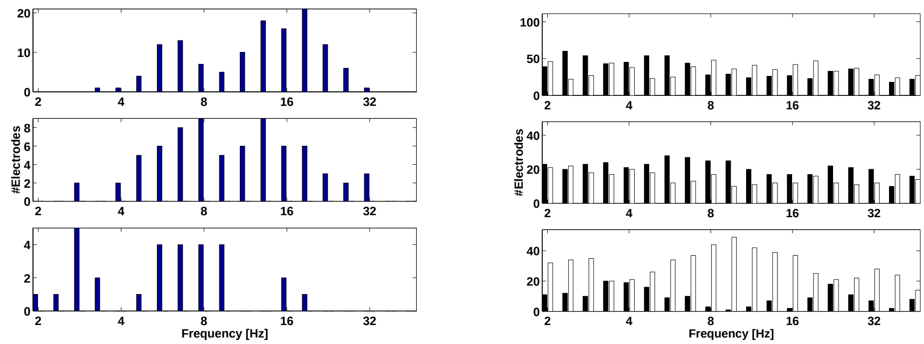

Figure 1: Frequency dependence of oscillations. **Left panels**, Movement-related oscillations during foraging. Each histograms shows the number of recording sites that show more oscillations during virtual movement than standing still, during foraging, as a function of frequency ($p < 0.001$). **Right panels**, Oscillations that desynchronize upon eye opening as a function of frequency ($p < 0.001$). Unfilled bars denote more wavelet power during eyes closed than eyes open (desynchronization upon eye opening); filled bars denote the reverse effect. Panels in rows denote participants 1–3, respectively. Total number of electrodes included in the analyses were 111, 48 and 54 for participants 1–3, respectively.

Participant	**r(df), θ-band**		**r(df), broad-band**	
1	0.003 (438)		0.047 (1519)	
2	0.187 (209)	$**$	0.157 (702)	$***$
3	0.061 (224)		0.026 (760)	

Table 1: Pearson correlations between z-transformed tests for movement- and resting-alpha-related oscillations. $*\ p < 0.05$, $**\ p < 0.01$, $***\ p < 0.001$.

two statistical tests, resting alpha cannot explain the entire movement-related oscillation effect, either within or outside the theta band.

These findings suggest that virtual movement-related oscillations in the human cortex represent an oscillatory correlate of exploratory behavior that is distinct from resting posterior alpha.

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