Theta Oscillations and Human Navigation: A Magnetoencephalography Study

Dráulio B. de Araújo¹,², Oswaldo Baffa², and Ronald T. Wakai¹

Abstract

Magnetoencephalography (MEG) was used to study alpha and theta activity while subjects navigated through a computer-generated virtual reality town. The subjects were first allowed to explore the environment freely. They then had to navigate from a starting point to a destination, knowing that an obstruction would appear at one of several possible locations along the main route and force them to take a detour. Spatiotemporal analysis of the theta and alpha bands were performed (1) prior to the start of navigation, (2) from the start of navigation until the obstruction was encountered, (3) during the time subjects were contemplating a detour and were not navigating, and (4) from the resumption of navigation until the destination was reached. In all subjects, theta power was strongest during the two periods of navigation. The peak frequency of the oscillations was approximately 3.7 Hz. Control studies consisted of a motor task similar to that required for navigation, passive viewing of a tour through the same virtual reality town, and a mental concentration task. No consistent increases in theta power were seen in the MEG during any of the control tasks. The results suggest an association between theta rhythm and the performance of navigational tasks in humans.

INTRODUCTION

Rhythmic slow activity, or theta rhythm, consisting of 4–12-Hz oscillations, is the dominant rhythmic neuronal activity in lower mammals. Perhaps the best-known aspect of this type of oscillation is its relationship to encoding and retrieval of spatial information in rodents. The activity of so-called place cells in the hippocampal formations of freely moving rats depends strongly on the specific location of the animal in its environment (O’Keefe & Dostrovsky, 1971). Animal studies also suggest that hippocampal theta rhythm is involved in the formation of memory, through its role in the facilitation of long-term potentiation (Stanton & Sejnowski, 1989).

In humans, however, theta activity is less prominent. It occupies a narrower frequency band (4–7 Hz) and generally is dominated by the alpha rhythm. The role of theta and other brain rhythms is still not understood. Studies of theta rhythm report a wide variety of task-dependency, primarily involving nonspatial memory and learning tasks (Teshe & Karhu, 2000; Klimesch, 1999; Teshe, 1997). An important example is an electroencephalography (EEG) study by Gevins, Smith, McEvoy, and Yu (1997), which showed a relationship between theta rhythm and memory load. An increase in memory load was followed by an increase in theta band oscillation, mainly in the frontal electrodes. This type of activity was studied systematically in 1969 by Legewie, Simonova, and Creutzfeldt. Because of the increase in theta power in the frontal midline region during concentrated mental activity, the oscillations were termed frontal midline theta activity (Fmθ). Recently, Fmθ has been reported in a large number of different tasks such as arithmetic calculation, sensory imagery, and attention (Ishii et al., 1999).

Few human studies have reported an association between theta oscillations and navigational tasks. This would seem to imply that theta oscillations do not play an important role in spatial cognition tasks, such as orienting, navigating, encoding, and retrieving of spatial memory (Grunwald et al., 1999), as it does in rodents. But an alternative explanation is that most prior studies failed to use an appropriate paradigm to elicit theta rhythm. A recent report lends support to the latter. Using arrays of subdural electrodes implanted in different parts of the cortex of three epileptic patients, Kahana, Sekuler, Caplan, Kirschen, and Madsen (1999) recorded theta activity in the operating room while the subjects moved through 6- and 12-turn virtual reality mazes. They found that for the longer maze theta power was significantly greater and the length of theta bursts was significantly longer. Although the sources of this activity could not be located precisely, theta rhythm was present in widely separated cortical regions, including temporal and parietal cortex.

Encouraged by this result, we decided to investigate whether a similar protocol could be implemented with magnetoencephalography (MEG), a noninvasive functional brain imaging technique with high temporal res-
olution. This would allow study of normal subjects under ordinary laboratory conditions. Among the main advantages of such a study is the ability to extend the duration of the sessions to include appropriate control measurements. Signals can also be mapped over the same brain region in each subject to facilitate intersubject comparisons. In the study of Kahana et al. (1999), clinical considerations determined the extent and placement of the electrode grid, and undoubtedly limited the duration of the recording sessions.

For several reasons, we chose to use a different navigational task than the one used by Kahana et al. (1999). One possible interpretation of their results is that the increased theta power for the longer maze is the result of increased memory load or increased task difficulty, and is not related to navigation per se. We, therefore, sought to maintain memory load constant throughout the task and to compare theta activity between periods when subjects were navigating and periods when they were not. Another problem we encountered in preliminary studies was that subjects reported difficulty orienting in mazes due to the absence of landmarks. We, therefore, decided to use a virtual reality city (Figure 1), which simulates a commonplace environment and allows the subject to more easily build an internal representation of the environment.

Studies of navigation protocols in humans through the use of conventional functional neuroimaging, such as positron emission tomography (PET) and functional MRI (fMRI), have been reported since the late 1990s (Maguire, Frackowiak, & Frith, 1997; Maguire et al., 1998). However, the temporal resolution of such techniques is inadequate for studying the association between navigation and high-frequency brain activity, such as theta activity.

The goal of the present study was to use MEG to characterize the spatiotemporal patterns of theta activity evoked while normal human subjects navigated through a virtual reality environment and performed various control tasks, and to investigate the relationship between theta rhythm and cognitive aspects of navigation.

**RESULTS**

Figure 2a,b shows the power spectral densities (PSD) during the four epochs from two different subjects. All subjects showed a large theta peak near 4 Hz. Notice that the peak frequency of the theta rhythm is outside the classically defined range of 4–7 Hz. The mean peak frequencies were 3.7 and 10.5 Hz for theta and alpha oscillations, respectively. Alpha peaks were prominent in some subjects (Figure 2a), but were barely visible in others (Figure 2b).

![Figure 1. View of a landmark within the virtual reality city. An overview of the city is shown in the inset.](image)
In all subjects theta power was greater during navigation (Epochs 2 and 4) than during the baseline period prior to the start of navigation (Epoch 1) or during the time when navigation was suspended upon encountering the obstruction (Epoch 3; Figure 2c). The percentage of increase of theta power (4–7 Hz) from the baseline period, Epoch 1, to the first period of navigation, Epoch 2, ranged from 7% to 98%, with a mean of 45% (Figure 2c). Most subjects (Figure 2a) also showed alpha desynchronization during navigation, i.e., the amplitude of the PSD in the alpha band (8–12 Hz) was lower during the second and fourth epochs.

Time–frequency analysis (Figure 3) shows how the patterns of theta and alpha activity vary throughout the run and, in particular, between the four epochs comprising the run. The first and third epochs, when subjects were not navigating, were dominated by alpha activity (Figure 3b,d). In contrast, the second and fourth epochs, when subjects were navigating, were dominated by theta oscillations (Figure 3a,c). The average duration of theta bursts was approximately 600 msec. No unusually large bursts of theta were seen during navigation; rather, the oscillations were present continually and were not associated strongly with any particular event or action. The same was true of the alpha rhythm during the first and third epochs. In addition, the changes in alpha and theta power during transition between the epochs were relatively smooth and continuous.

A single dipole model was used to determine the location of the magnetic field generators. Although this model generally does not provide accurate localization of sources of spontaneous activity, studies show that dipole fitting yields reasonable source locations for times when the field topography is highly dipolar (Benzel, Lewine, Bucholz, & Orrison, 1993). For our data, clusters of dipoles were found primarily near the superior temporal gyrus and the deeper temporal structures of both hemispheres (Figure 4).

The time evolution of the magnetic field topography during periods of large theta oscillations was observed using specialized computer software (Swerdloff, Ruegsegger, & Wakai, 1993), as shown in Figure 5. Magnetic field strength is displayed on a realistic head shape using false coloration: red corresponds to a large positive field, blue corresponds to a large negative field, and green to zero field. The topography implicated source locations mainly in temporal regions, consistent with the dipole fits. In addition to these relatively stationary dipoles, a distinctive spatiotemporal pattern of theta activity appeared repeatedly in the data (Figure 5a–c), in which a dipolar pattern propagated from front-to-back. The pattern started at the front edge of the sensor array, over the superior frontal region, and propagated toward the back edge, over the parietal lobe, in a time of about 200 msec.

In the first of the control studies, Fm could be seen at electrode Fz during arithmetic calculation; however, no similar increase in theta activity was detected by either of the MEG probes, which were positioned over the temporal regions (Figure 6). The mean peak

---

**Figure 2.** PSD by epoch from two different subjects. The data were averaged over all 37 MEG channels and all four runs. (a–b) Theta peaks were prominent in all subjects; alpha peaks were visible in all subjects, but were more variable in amplitude. (c) Power in the theta band (4–7 Hz) by epoch for four subjects, and the grand average. Theta power increased markedly when subjects were navigating (Epochs 2 and 4), compared with when they were not (Epochs 1 and 3).

In all subjects theta power was greater during navigation (Epochs 2 and 4) than during the baseline period prior to the start of navigation (Epoch 1) or during the time when navigation was suspended upon encountering the obstruction (Epoch 3; Figure 2c). The percentage of increase of theta power (4–7 Hz) from the baseline period, Epoch 1, to the first period of navigation, Epoch 2, ranged from 7% to 98%, with a mean of 45% (Figure 2c). Most subjects (Figure 2a) also showed alpha desynchronization during navigation, i.e., the amplitude of the PSD in the alpha band (8–12 Hz) was lower during the second and fourth epochs.

Time–frequency analysis (Figure 3) shows how the patterns of theta and alpha activity vary throughout the run and, in particular, between the four epochs comprising the run. The first and third epochs, when subjects were not navigating, were dominated by alpha activity (Figure 3b,d). In contrast, the second and fourth epochs, when subjects were navigating, were dominated by theta oscillations (Figure 3a,c). The average duration of theta bursts was approximately 600 msec. No unusually large bursts of theta were seen during navigation; rather, the oscillations were present continually and were not associated strongly with any particular event or action. The same was true of the alpha rhythm during the first and third epochs. In addition, the changes in alpha and theta power during transition between the epochs were relatively smooth and continuous.

A single dipole model was used to determine the location of the magnetic field generators. Although this model generally does not provide accurate localization of sources of spontaneous activity, studies show that dipole fitting yields reasonable source locations for times when the field topography is highly dipolar (Benzel, Lewine, Bucholz, & Orrison, 1993). For our data, clusters of dipoles were found primarily near the superior temporal gyrus and the deeper temporal structures of both hemispheres (Figure 4).

The time evolution of the magnetic field topography during periods of large theta oscillations was observed using specialized computer software (Swerdloff, Ruegsegger, & Wakai, 1993), as shown in Figure 5. Magnetic field strength is displayed on a realistic head shape using false coloration: red corresponds to a large positive field, blue corresponds to a large negative field, and green to zero field. The topography implicated source locations mainly in temporal regions, consistent with the dipole fits. In addition to these relatively stationary dipoles, a distinctive spatiotemporal pattern of theta activity appeared repeatedly in the data (Figure 5a–c), in which a dipolar pattern propagated from front-to-back. The pattern started at the front edge of the sensor array, over the superior frontal region, and propagated toward the back edge, over the parietal lobe, in a time of about 200 msec.

In the first of the control studies, Fm could be seen at electrode Fz during arithmetic calculation; however, no similar increase in theta activity was detected by either of the MEG probes, which were positioned over the temporal regions (Figure 6). The mean peak
The frequency of theta in the EEG and in the MEG was slightly higher for Fm than for theta evoked by the navigational task. The frequency of the alpha oscillations was the same as during the navigational task.

In the passive viewing task, the power in the theta band increased slightly, but not nearly enough to account for the large increase seen during navigation. The last control study, involving a motor task, showed no increase in theta power.

For all three control studies, the power in the alpha band decreased relative to the resting state.

**DISCUSSION**

The results of this study support the hypothesis that theta oscillations are associated with navigational tasks in normal adult humans, as they are in lower mammals. Specifically, we have shown that spontaneous MEG activity with an approximate frequency 4 Hz was stronger during navigation than during periods when subjects were not navigating. The consistency of this finding was remarkable. In every subject, theta power was greater during both periods when subjects were navigating than during either period when they were not. A question raised by the Kahana et al. (1999) study, which is answered here, is whether the increase in theta they observe is due to the fact that all of the patients they studied had epilepsy. It is well known that epilepsy can be associated with a general increase in low-frequency components of the EEG. Here we show that it is possible to observe increased theta associated with navigation in normal volunteers.

The peak frequency of the oscillations associated with the navigational task was only about 3.7 Hz, which is slightly outside the 4–7-Hz frequency band that is commonly associated with theta oscillations. In order to show that the effects reported here could be demonstrated using the conventional definition of theta, the bar graphs of total theta power were computed with a 4–7-Hz frequency band (Figure 2c). If instead theta power had been computed using bands centered about the peak frequency, then the relative increase in theta power during periods of navigation would have been even greater.

Designing an appropriate experimental protocol for studying the association of theta oscillations and navigation is challenging because synchronization and desynchronization of theta can be elicited by a number of...
Rather than comparing theta between periods in which subjects were navigating under different conditions, as in the study of Kahana et al. (1999), our protocol was designed to allow comparison between periods when subjects were navigating and when they were not. An effort was made to minimize the effects of memory load, attentional demands, and task difficulty. Memory load was constant throughout the study. Subjects were required at the beginning to store into memory the paths from the starting point to the destination, including alternate routes, and to retain this information for the duration of the study, which was relatively brief (approximately 20 min). Attentional demands were relatively constant throughout. Even during the baseline period, prior to navigation, subjects were required to be alert for the starting signal. Lastly, the difficulty of the navigational task was made low so that all subjects were able to successfully reach the destination in a similar amount of time and the difference in task difficulty between periods of navigation and other periods was lessened.

Due to the complexity of the experimental protocol, there are many alternative explanations for the observed increase in theta power, and it is impossible to control for all of them. In our control studies, we attempted to rule out three of the most obvious ones. First, it is well known that various tasks involving mental concentration evoke $F_{\mu}$ (Sasaki, Tsujimoto, Nishikawa, Nishitani, & Ishihara, 1996). Second, subjects were subjected to complex, streaming visual stimulation as they navigated through the virtual reality environment. Third, navigation required the performance of a precise motor task, consisting of manipulation of a computer mouse. However, the control studies showed that none of these could account for the observed theta activity. Only a very small increase in theta was seen during the passive viewing protocol. Even the mental concentration tasks did not show a significant increase in MEG (Figure 6b) theta amplitude, despite an increase in EEG theta amplitude (Figure 6a), apparently because the MEG sensors were situated over the temporal region, rather than frontally, where $F_{\mu}$ theta typically is maximal for both EEG and MEG (Doppelmayr, Klimesch, Schwaiger, Auinger, & Winkler, 1998; Klimesch, Doppelmayr, Schimke, & Ripper, 1997). This implies that the theta evoked by the navigational task and $F_{\mu}$ arise from different generators.

A major component of navigation is retrieval of episodic memory, that is, memory of events that happened at a specific place and time. Some studies support the hypothesis that event-related synchronization (Plurtscheller & Aranibar, 1977) in the theta band has a direct correlation with the retrieval of episodic memory (Doppelmayr et al., 1998; Klimesch et al., 1997). In our study, however, theta activity was much less during the third epoch, when subjects were attempting to retrieve a map from memory, than during navigation. This suggests that the increase in theta during navigation is due to causes other than the retrieval of episodic memory.

The magnetic field topography associated with the theta oscillations was often highly dipolar, and implicated temporal and parietal sources. In the navigation study of Kahana et al. (1999), theta oscillations were recorded over many widely separated regions of cortex, including temporal and parietal hemispheres. fMRI and PET studies have also demonstrated the participation of several brain regions in navigation protocols, including medial temporal structures, and medial parietal lobe (Grön, Wunderlich, Spitzer, Tomczak, & Riepe, 2000; Maguire et al., 1997, 1998). Thus, the topographies of the signals detected in this study are compatible with the fMRI and PET findings. More sophisticated MEG source modeling may allow precise comparisons; however, poor knowledge of the relationships between

---

**Figure 4.** Localization of dipole clusters from a typical subject, using a single current dipole model. In (a), the dipoles cluster along the left superior temporal gyrus (STG) and deep insula; a large deeper cluster lies along the choroid fissure and medial hippocampus. In (b), the dipoles cluster primarily in the left and right STG. Smaller clusters localize to the white matter stem of the left temporal lobe and bilaterally overlying the cerebral peduncles.
blood flow and metabolism and spontaneous electrical brain activity may preclude meaningful comparisons between our results and those from fMRI and PET studies.

Previous studies (Grön et al., 2000; Maguire et al., 1997, 1998) have suggested that two distinct cognitive processes are required for successful navigation. The first one, governed by mesial temporal structures, mainly the hippocampus, is involved in the formation of an allocentric representation of the environment. The second one, residing in inferior parietal cortex, uses this information to create an egocentric representation, which is essential to compute body turns and other movements necessary for the act of navigation. This suggestion is supported by neuroanatomical tracing studies (Suzuki & Amaral, 1994), which have demonstrated strong projections between inferior parietal lobe and mesial temporal structures, implying functional connectivity between these areas. Given that much of the theta we observe appears to arise from sources in these regions, the decrease in theta during Epoch 3, when subjects are retrieving a map from memory without navigating, implies diminished activity in these regions, presumably due to nonparticipation of inferior parietal cortex. An alternative explanation is that theta is involved in the binding of these areas during navigation. The observed front-to-back propagation of the theta dipole pattern is compatible with a proposed role of brain oscillations as a means of “scanning” the brain. A previous MEG study suggested such a role for gamma oscillations, which showed a sweep-like pattern due to a front-to-back shift in phase (Ribary et al., 1992). The reduction in theta during Epoch 3 then implies that binding of these areas ceases in the absence of navigation.

In conclusion, using MEG we demonstrated increased activity of signals in the theta band while subjects...
navigated through a virtual reality town. The findings support the hypothesis that theta oscillations and their underlying generators are involved in navigation in humans, as they are in lower mammals.

METHODS

Subjects

The subjects were 11 young adults (9 men, 2 women; 10 right-handed, 1 left-handed) with a mean age 28.8 years.

Recordings

The recordings were made with a 74-channel first-order gradiometer (Magnes II, Biomagnetic Technologies) housed within a high-magnetic permeability-shielded room. The signals were passed through analog filters with passband of 0.1–100 Hz and digitized at 297.6 Hz.

Procedure

By design, the complexity of the virtual reality city and the level of difficulty of the navigational task were not high, so that all subjects were able to successfully complete the task in a similar amount of time. This was deemed advantageous because in preliminary studies with complex mazes it was problematic to compare data between subjects who completed the task easily and subjects who got lost.

The virtual reality city was built using commercial software (Duke Nukem 3D), which allows the user to design their own environment (Figure 1). The town consisted of two main avenues and 10 secondary streets. Distinctive buildings were placed in strategic locations, such as corners, to serve as reference points. The game could be recorded and replayed, allowing the movements of the subjects and the time of events to be determined precisely.

For the navigational task, subjects had to navigate from the designated starting point to the destination, but in order to reach the destination, they would be required to navigate around one of four possible obstructions. They were told that they should stop navigating upon encountering the obstacle and attempt to visualize a complete detour to the destination. Only then should they resume navigating to the destination.

The subjects lay on their sides throughout the study. The probes were positioned bilaterally over the temporal regions and were not repositioned during the session. Using a mouse to navigate, subjects were first allowed to explore freely on their own in order to build an internal representation of the city. As they navigated through the city, they were shown the starting point and destination, the locations of the four possible obstructions, and detours from each obstruction to the destination. Subjects were asked to navigate from the starting point to the destination to make sure that they could accomplish this without difficulty.

At the start of each of run, the subjects viewed a static scene of the starting point while awaiting a visual signal to begin navigation. The MEG was recorded continuously, from prior to the start of navigation until the time when the subject arrived at the destination. Four runs were recorded from each subject.

Analysis

For analysis, each run was divided into four contiguous epochs. The first epoch was a baseline period prior to the start of navigation, lasting 3–15 sec. The second epoch started when navigation was initiated and ended when the subject encountered the obstruction and...
stopped navigating. The third epoch corresponded to the period when the subject was visualizing a detour and was not navigating. During this time, subjects presumably were retrieving from memory their internal representation of the city and evoking the mental representation of the navigation act without physically navigating. The last epoch started when navigation was resumed and ended when the destination was reached. Artifact rejection was performed to remove segments of the recordings contaminated with eye blinks and eye movement artifacts. After bandpass filtering the data from 1 to 30 Hz, the PSD (256-point fast-Fourier transforms of nonoverlapping Kaiser window) was computed in each epoch and averaged over all channels and all four runs. Time-frequency analysis was used to identify theta and alpha bursts in the time domain. Single dipole fitting was employed to compute the location of sources of theta activity. The dipoles were overlaid onto magnetic resonance (MR) images to identify the relevant structures. The MR images were generated using a 1.5-T GE Horizon MR scanner (3D SPGR whole-brain volume; 21/7 msec TR/TE; 40° flip angle; 24 cm FOV; 256 × 256 matrix; 124 contiguous axial slices including vertex through cerebellum; 1.2 mm slice thickness).

Control Studies

Three control studies were performed in order to determine whether aspects of the protocol unrelated to navigation could increase theta activity. The studies were intended to control for the effects of mental concentration, visual stimulation, and motor task performance. The three control studies were performed on 4 of the 11 subjects in a separate session. The MEG sensors were placed bilaterally over the temporal lobes, just as in the experimental condition. Two runs of each control measurement were recorded from each subject.

In the first control study, the subjects were asked to perform two different mathematical calculations that would evoke Fmθ activity: counting backwards from 1000 in steps of seven and computing $2^n$ for integer $n$. For this study, an EEG electrode was placed at international 10–20 electrode position Fz, where Fmθ activity typically is strongest.

The second control study was intended to assess whether theta is increased by the performance of a motor task that involves the manipulation of a computer mouse. First, the subjects were instructed to remain motionless and to not think of anything. Then, they were instructed to trace the lines of a triangle that was displayed on a computer screen. Lastly, they were instructed to trace out a triangle with their eyes closed.

The third control study was intended to assess whether theta activity is increased during passive viewing of a visual stimulus similar to that experienced during the experimental condition. The subjects passively viewed a tour through a virtual environment similar to the one that they had navigated. This was preceded by a baseline recording in which the subjects viewed a static scene of the starting location.

Acknowledgments

This work was partially supported by CNPq and FAPESP. We thank Dr. Howard Rowley for assistance with the interpretation of the magnetic source images.

Reprints requests should be sent to Dráulio de Araújo, DFM-FFCLRP, Av. Bandeirantes 3900, 14040-901 Ribeirão Preto, SP, Brazil, or via e-mail: draulio@fisicamedica.com.br.

REFERENCES


de Araújo, Baffa, and Wakai


