

Working-memory related theta (4-7Hz) frequency oscillations observed in monkey
extrastriate visual cortex

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0. Abstract

Working memory has been linked to elevated activity in single neurons in monkeys, as well as to oscillatory phenomena in the human EEG. To understand the relation between these findings, we explore here whether working-memory oscillations can also be observed in monkey cortex. We indeed found working-memory related oscillations in the theta frequency band in monkey visual cortex, which were correlated to monkeys' behavioral performance on a contrast discrimination task. We discuss possible functional interpretations of this finding.

1. Introduction

Working memory is the process by which the brain stores information for brief periods. Studies of the neural basis of working memory in monkeys have focused on the prefrontal cortex, which contains many neurons that exhibit delay activity – elevated firing during memory periods of cognitive tasks¹⁻³. Working memory is thought to rely on the coordinated interaction of distributed networks involved in sensory as well as mnemonic processing. Indeed, EEG studies in humans have linked brain oscillations in the theta (4-7Hz) and alpha (8-13Hz) ranges in frontal and occipital areas with working memory⁴⁻⁷. It is not known whether or how these oscillations observed in different brain regions and elevated activity in prefrontal and other areas interact to support working memory. To begin to address this question, we recorded local field potentials (LFP) from multiple sites in occipital extrastriate visual cortex of awake behaving monkeys. Here, we report variations of oscillations in the theta range (4-7Hz) of the LFP at occipital visual sites related to working memory.

2. Results

Monkeys performed a delayed matching to sample (DMS) task, with natural images 10deg by 10deg in size, presented at the center of gaze as stimuli. After a fixation period (1000ms), they viewed a sample stimulus for a brief period (300ms). The sample stimuli were presented at different contrast levels (5%, 10%, 25%, 50%, 75% and 100%). After a brief delay (1000 ms), a probe stimulus was presented at 100% contrast, and monkeys were required to release a lever if this probe matched the sample to obtain a juice reward. As expected, monkeys' behavioral performance varied systematically and monotonically with contrast. Performance was at chance (50% correct) for 5% and 10% contrast, indicating that monkeys were not able to discriminate the stimuli at these low contrast levels. Performance was near 80% correct at 25% contrast, and at ceiling (above 90% correct) for the three highest contrast levels.

During performance of the task, we collected LFPs from up to eight single electrodes placed simultaneously in occipital extrastriate area V4. Electrodes were manipulated in pairs, and recording sites were separated from each other by at least 1mm. Signals were amplified, filtered (0.1Hz-1kHz) and digitized at 2kHz. To estimate power in a particular frequency band (we focus here on theta power TP; power in the theta band from 4-7Hz), the raw A/D traces collected on each trial were digitally band-pass filtered (Butterworth 4-pole filter, 4-7Hz), rectified and low pass filtered (convolution with 200ms boxcar). We report results from a total of 38 datasets obtained in six sessions from two monkeys with 3-7 channels per session.

An example LFP recorded in V4 during the course of a trial with a 100% contrast sample stimulus is shown in Figure 1. During the second half of the delay period (between the hatched areas representing the presentation of sample and probe stimuli), several cycles of oscillation in the theta range can be seen in the raw (solid line) and theta-band filtered (dotted line) signals (Fig.1a). This is reflected in elevated levels of theta power (TP) during this period, compared to levels during the fixation period before the onset of the sample stimulus (Fig.1b). The TP level as a function of time and sample stimulus contrast for an example recording site, averaged across all repetitions for each sample contrast level, is shown in Figure 2. Sample stimulus presentation was associated with transient changes in TP at contrast levels of 10% and higher. These effects are consequences of the visually evoked potential (VEP). During the delay period, we observed a sustained reduction in TP relative to levels during the fixation period for 5% contrast sample stimuli, whereas TP was elevated for high contrast levels. To quantify these effects, we computed the average theta power (TP) during the last 700ms of the delay period for each contrast level, and compared it to theta power during the last 700ms of the fixation period. For the example session shown in Fig.2, TP was significantly reduced at 5% contrast (t-test, $P < 0.05$), and significantly elevated at contrast levels of 25% or greater (t-tests, $P < 0.05$).

This trend was also apparent when looking at the entire population of recorded sites, as shown in Fig.3. At 5% contrast, significant reductions in TP during the delay period were seen at the majority of recorded sites (30/38 or 79%; t-tests, $P < 0.05$), and at no site did we observe significant increases. At contrast levels of 25% or higher we observed significant increases at the majority of recorded sites. For example, for sample stimuli at 50% contrast we saw significant increases in TP at 24/38 sites (63%), whereas only significant decreases were observed in only a minority of sites (5/38 or 13%).

3. Discussion

We found task-dependent variations in theta oscillations during a delay period in occipital extrastriate visual cortex. Presentation of stimuli at contrasts that did not allow monkeys to discriminate the stimuli resulted in robust long lasting decreases in theta power. At high contrasts where monkeys had no trouble in stimulus discrimination and performance of the DMS task, we observed increases in theta power during the delay relative to fixation. We conclude that the variations in theta oscillations were correlated with behavioral performance. Note that there is a large shift in performance at the 25% contrast level, and this is also where there is the most profound change in the LFP. That is, in addition to an overall correlation between performance and LFP theta power, the theta band of the LFP also reflects the non-linear part of the performance/contrast function. We note that increased theta power does not appear to reflect anticipatory or prospective coding of the probe stimulus as is often observed in prefrontal cortex ⁸, because it is absent at low contrast despite the anticipation of a high-contrast probe stimulus. By contrast, increased theta power during the delay period reflects sensory stimulation provided during the sample period, consistent with an involvement of theta oscillations in working memory. Our data are consistent with two functional interpretations. On the one hand, these oscillations may reflect coordinated working-memory related reverberations of neural activity within visual cortex or between visual cortex and other regions involved in visual working memory. Another possibility is that the delay-

specific oscillations serve to isolate higher level areas from sensory input, thus protecting working-memory related elevated activity levels from disruption. A related possibility is that theta reflects the maintenance of a local cortical state. This is not the same as idling, which refers to interruption of function, but rather a mode of protection of cortical representation or state. This maintenance function would be consistent with the decrease in TP immediately preceding the arrival of the probe stimulus, allowing the extrastriate cortex to process the incoming probe information. Further studies examining multiple areas as well as single unit activity are needed to address this issue.

4. Literature

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5. Figure Legends

Figure 1: (a) The local field potential (LFP), as well as the LFP signal filtered in the theta band (4-7Hz) is shown for an example single behavioral trial. Horizontally hatched areas mark the periods of sample and probe stimulus presentation. (b) Theta power (TP) for this same behavioral trial is shown, revealing elevated levels during the delay period.

Figure 2: Theta power (TP) is shown as a function of sample stimulus contrast and time during the behavioral trial, for an example recording site. Note the systematic variation of TP with sample stimulus contrast during the delay period.

Figure 3: The bar graphs summarize the number of recording sites for which we observed increases, decreases or no significant differences in TP between the fixation and delay periods (t-tests, $P < 0.05$).

6. Biographical Information

Gregor Rainer is a DFG Heisenberg Investigator at the Max Planck Institute for biological cybernetics and a faculty member at the Tübingen University Medical School. He is interested in understanding the neural mechanisms visual perception and memory, using electrophysiological and fMRI methods.

Hahn Lee is a graduate student at the Max Planck Institute for biological cybernetics. He is writing his Ph.D. thesis on perceptual learning in V4.

Gregory V. Simpson is the Director of the Dynamic Neuroimaging Laboratory, Department of Radiology, University of California San Francisco. He is interested in the brain networks that underlie attention and working memory and studies these with EEG, MEG and fMRI methods.

Nikos K. Logothetis is a Director at the Max Planck Institute for biological cybernetics. His recent work includes the studying the physiological mechanisms underlying visual perception and object recognition, the application of functional imaging techniques to monkeys and measurement of how the functional magnetic resonance imaging signal relates to neural activity.





