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

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Working memory is the process by which the brain stores information for brief delays. 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 tasks[1,2]. 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 memory [3-6]. It is not known whether or how these oscillations observed in many brain regions and elevated activity in prefrontal or other areas interact to support working memory. To address this question, we recorded both single-unit activity (SUA) and local field potentials (LFP) simultaneously from multiple sites in occipital extrastriate visual cortex. Here, we report variations of oscillations in the theta range (4-7Hz) of the LFP at many occipital visual sites related to working memory.

Monkeys performed a delayed matching to sample (DMS) task, with natural images 10deg by 10deg in size and presented at the center of gaze as stimuli. After a fixation period (1000ms), they viewed a sample stimulus for a brief period (300ms). The 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 of 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 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 the theta band from 4-7Hz), the raw A/D traces collected on each trial were digitally bandpass filtered (Butterworth 4-pole filter, 4-7Hz), rectified and low pass filtered (convolution with 200ms boxcar). We report average results from a total of 37 datasets obtained in six sessions from two monkeys with 3-7 channels per session.

We found that sample stimulus presentation was associated with transient reductions in theta power (TP), which were inversely correlated with stimulus contrast. TP reductions were thus largest (~30% decrease) at the lowest contrast level (5%). At 5% contrast, TP did not recover and remained at low levels throughout the delay period. At 10% contrast, TP recovered only to reach levels during the fixation period, whereas there was a robust sustained increase of TP compared to fixation for the remaining contrast levels (25%, 50%, 75%, 100%). Statistical analyses comparing TP during the last 800ms of the delay with an equal period during fixation confirmed significance of these effects (paired t-tests, $P<0.01$). There was some variability in the results when looking at individual sites. We observed greater TP during delay than fixation at high contrast at a majority of sites (70%), but the remaining sites showed decreased TP. The reduction in TP after low contrast sample stimuli was seen at almost all sites (98%). Topographic analyses suggest that cortical depth as well as the location of the recording site may account for some of the observed heterogeneity.

Taken together, we find 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 are correlated with behavioral performance. Note that there is a large shift in performance at the 25% 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 [7], 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 suggests that 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.


**1** Fuster, J.M. (1990) Prefrontal cortex and the bridging of temporal gaps in the perception-action cycle. *Ann N Y Acad Sci* 608, 318-316

**2** Goldman-Rakic, P.S. (1995) Cellular basis of working memory. *Neuron* 14 (3), 477-485

**3** von Stein, A. and Sarnthein, J. (2000) Different frequencies for different scales of cortical integration: from local gamma to long range alpha/theta synchronization. *Int J Psychophysiol* 38 (3), 301-313

**4** Klimesch, W. (1999) EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Res Brain Res Rev* 29 (2-3), 169-195

**5** Jensen, O. et al. (2002) Oscillations in the alpha band (9-12 Hz) increase with memory load during retention in a short-term memory task. *Cereb Cortex* 12 (8), 877-882

**6** Raghavachari, S. et al. (2001) Gating of human theta oscillations by a working memory task. *J Neurosci* 21 (9), 3175-3183

**7** Rainer, G. et al. (1999) Prospective coding for objects in primate prefrontal cortex. *J Neurosci* 19, 5493-5505