# LARGE-SCALE NEURAL SYNCHRONY ASSOCIATED WITH TOP-DOWN SELECTIVE ATTENTIONAL MODULATION OF NECKER CUBE PERCEPTION

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## Abstract

*We investigated top-down selective attentional modulation of bistable perception. Sixteen healthy human observers were presented with the Necker cube on a black background. Observers reported perceptual switches between two possible interpretations by pressing one of two keys. Observers were instructed either to passively view the Necker cube or to try to attend to one of the two possible interpretations. Observers showed strong selective attentional modulation of dominance durations. We measured brain electrical activity by 62ch EEG and used phase locking value to evaluate large-scale phase synchrony between pairs of EEG signals. We observed stronger long-lasting large-scale synchrony at 3-4 Hz among the frontal, parietal and occipital areas associated with perceptual switches in the attentional control condition than in the passive view condition. These results suggest that top-down selective attentional modulation of Necker cube perception is mediated by frontal-parietal-occipital synchrony networks in the theta frequency range.*

Large-scale neural synchrony is proposed as a mechanism for perceptual binding and functional integration of neural assemblies across brain regions (Varela et al., 2001, Ward, 2003). For example, Brain-wide, frequency-specific neural synchrony has been associated with meaningful perception of "Mooney face" (Rodriguez et al., 1999), perceptual awareness during binocular rivalry (Doesburg et al. 2005) and central executive function in a mental arithmetic task (Mizuhara and Yamaguchi, 2007).

Multistable visual stimuli like the Necker cube offer unique tools for dissociating perceptual changes from stimulus driven (bottom-up) changes in visual processing. A previous behavioral study of Necker cube perception demonstrated that the effect of top-down selective attention was powerful in Necker cube perception (Meng and Tong 2004). It is not well known, however, how the top-down modulation is implemented by synchronization networks in multiple frequency bands.

To investigate the mechanism of top-down modulation of Necker cube perception, we analyzed endogenous changes in EEG synchrony during top-down control and passive view of Necker cube perception.

## Method

16 adult observers with normal or corrected-to-normal vision (mean age, 24.7 years; SD, 4.7 years) gave informed consent. Observers were presented with the Necker cube (width = 4.22°) in the dark on a black background in the center of a 19" CRT monitor (100 Hz refresh rate) at a distance of 95 cm. A chin rest maintained observers' head position throughout the experiment. Observers were instructed to maintain fixation throughout each 180-s block and to avoid making eye movements and eye blinks.
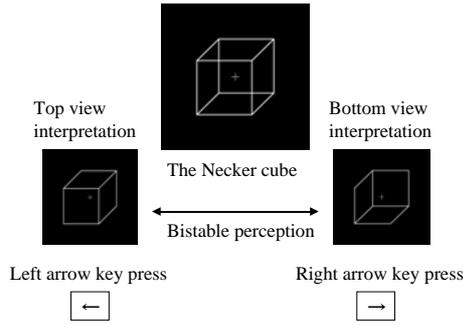
Fig. 1. The Necker cube and two possible interpretations.

Observers held down the left arrow key with their right index finger when they perceived the "top view" and held down the right arrow key with their right middle finger when they perceived the "bottom view", and made no response when they perceived an intermediate or flat interpretation of the Necker cube (Fig. 1). The following 4 experimental conditions and instructions were given to each observer.

*(1)Passive view condition: "Just look at the cube passively";*

*(2)Top view biasing condition "Try to perceive the cube from the top view for as long as possible" (i.e., as if seen from above);*

*(3)Bottom view biasing condition "Try to perceive the cube from the bottom view for as long as possible" (i.e., as if seen from below);*

*(4)Self-paced key pressing condition without the Necker cube: "Press the keys at your own pace."*

After one practice block for each condition and a resting block, observers received the 4 conditions in a mixed randomized order (5 blocks/condition). Observers took a break between blocks.

The electroencephalogram (EEG) was recorded from 62 electrodes, placed according to the standard 10-10 placement system. The electrooculogram (EOG) was recorded bipolarly with electrodes positioned 1 cm from the outer canthi of both eyes and above and below the left eye. Electrode impedances were kept below 5k ohm. EEG and EOG were amplified, band-pass filtered between 0.1 and 100 Hz, digitized at 500 Hz, and stored on disk for offline analysis. Scalp voltages were referenced to an average mastoid reference.

EEG epochs were extracted in which perception of the rivaling views persisted for 1 s or longer both before and after the perceptual switching. Epochs were analyzed from 1000ms before the observers pressed the key to indicate a particular view was dominant until 1000ms after the key press. Epochs with artifacts caused by blinks or eye movements (vertical and horizontal), amplifier saturation, were detected and excluded from further analysis. For each subject, the number of epochs was the same for all conditions and for two switches (top view to bottom view, bottom view to top view). Epochs from 16 observers were combined for the analysis (398 epochs). In order to control for volume conduction from time-varying sources, we calculated scalp current density (SCD), a reference-free measure that reduces spurious synchronies (Lachaux et al. 1999, Kayser 2006).

We first band-pass filtered the EEG SCD data using a two-way, least-squares, finite-impulse-response filter around central frequencies (cf) from 3 to 60 Hz in 1-Hz steps with filter relative bandwidth of 0.9 cf to 1.1 cf (Fig. 1c). Next, we obtained the instantaneous amplitude, A(t), and phase, $\phi$(t), of the filtered signal, f(t), from the analytic signal,

$$\varsigma(t) = f(t) + i\,\tilde{f}(t) = A(t)e^{i\phi(t)}$$

where $\tilde{f}(t)$ is the Hilbert transform of $f(t)$.

Phase locking value (PLV; Lachaux et al., 1999) between the instantaneous phases of pairs of filtered EEG SCD time series was calculated for all pairs of electrodes using the set of EEG SCD epochs accumulated across 16 observers as,

$$PLV(t) = \frac{1}{N}\left|\sum_{n=1}^{N} e^{i\theta(t,n)}\right|,$$

where $\theta(t,n) = \phi_1(t,n) - \phi_2(t,n)$ (t, n) and $\phi_1$ and $\phi_2$ are respectively the instantaneous phases of EEG SCD time series from electrodes 1 and 2, and N is the number of epochs included in the calculation. PLV is a real value between 0 (random phase difference, no phase locking) and 1 (constant phase difference, maximum phase locking). To detect signal-related changes in synchrony, we standardized the PLV values relative to a resting block at each frequency. The raw PLVs during the resting baseline period varied across electrode pairs (larger for closer electrodes) and frequencies. Standardized PLV values, PLVz(t), were computed from

$$PLV_z(t) = \frac{PLV(t) - PLV_{Bmean}}{PLV_{Bsd}}$$

where $PLV_{Bmean}$ and $PLV_{Bsd}$ are the mean and standard deviation of the PLVs computed from the resting period baseline at each frequency. The resulting index, PLVz, indicates standardized changes in the direction of increased synchrony (positive values) or decreased synchrony (negative values). Standardized instantaneous amplitude was computed in the same way. To assess statistical reliability of the PLVz, we controlled for the statistical effects of multiple comparisons by choosing a very conservative significance threshold ($p < 0.00005$) .

## Results and Discussion

*Behavioral results*
Figure 2 shows the dominance durations for bottom view (left) and top view (right) for all 16 observers in all conditions. We found very strong top-down modulation effects on the distribution of dominance durations in the top view biasing (Mann-Whitney U test, p<0.00001) and bottom view biasing (p<0.00001) conditions.
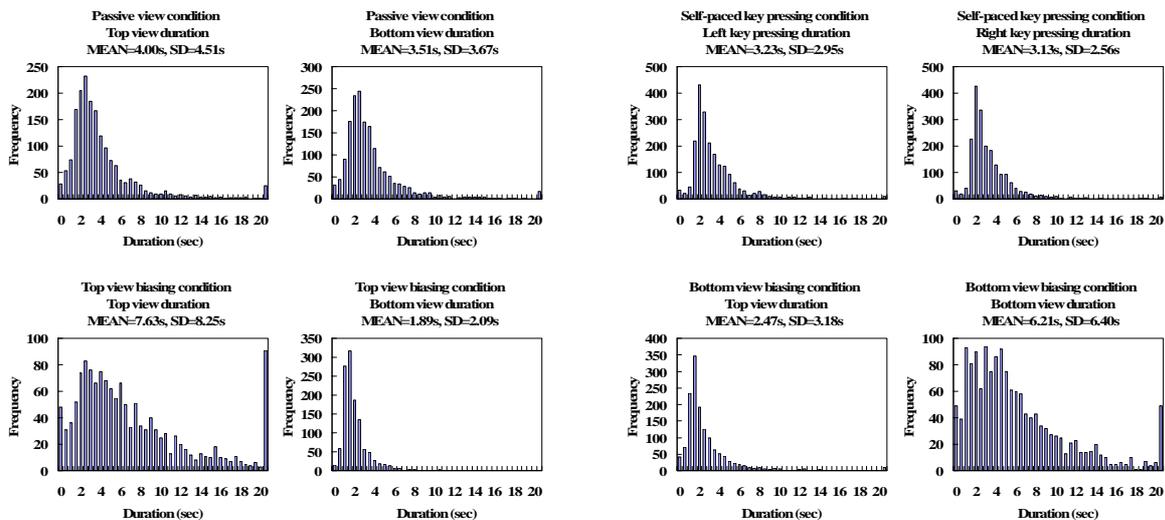


Fig. 2. Distribution of perceptual dominance durations
Top view durations and bottom view durations in top view biasing condition, passive view condition, bottom view biasing condition, and self-paced key pressing condition.

Observers could selectively enhance the dominance duration of the attended interpretation and decrease the dominance of the unattended interpretation. Moreover, top view interpretation was longer and more stable than bottom view interpretation in passive view condition (p<0.0005). The results are consistent with a previous study, which also found that the effect of top-down selective attention was powerful in Necker cube perception (Meng & Tong, 2004).

*EEG results*

Fig. 3(a) and fig. 4(a) show the average PLVz across all 1891 pairs of the 62 electrodes over 16 observers for the bottom view to top view switch in top view biasing condition (Fig. 3(a)) and passive view condition (Fig. 4(a)), respectively.

We observed relatively long-lasting increases in large-scale synchrony, most prominently in top view biasing condition around the key press in the theta band (3Hz to 4 Hz). Fig. 3(b) and fig. 4(b) show topography of phase synchronization/de-synchronization and spherical-spline-interpolated standardized instantaneous amplitude at 4Hz and 35Hz. Increases in the long-lasting synchrony in the theta band were widespread across the scalp and were accompanied by increased instantaneous amplitude in frontal, parietal and occipital areas. We also observed transient gamma synchronization around -400 ms most prominently in the top-view biasing condition. Increases in the transient gamma synchrony were accompanied by increased instantaneous amplitude in frontal and occipital areas.

To determine the effects of top-down attentional modulation on large-scale phase synchrony, we computed differences in synchrony between top-view biasing condition and passive view condition (Fig. 5). Increases in large scale phase synchrony were more prominent for some frontal-parietal-occipital pairs from -400ms to +600ms in the theta band (3-4Hz) in top view biasing condition than in passive view condition, whereas before -600ms increases in synchrony were more prominent in passive view condition. The synchrony increases after -400ms were accompanied by increased amplitude in frontal, parietal and occipital areas (Fig. 5 (b)).
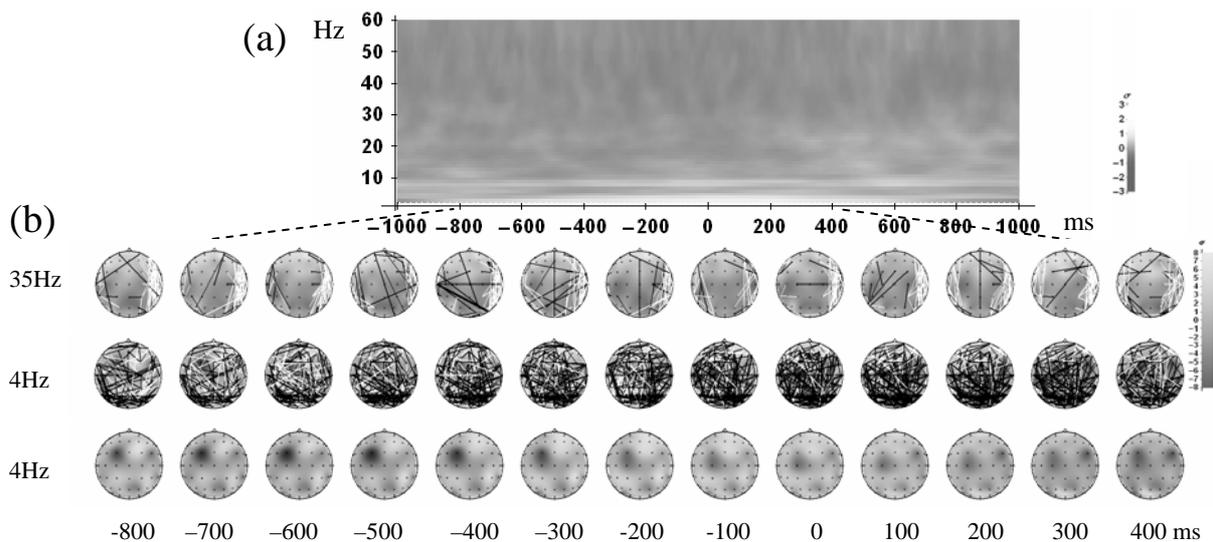


Fig. 3. (a) Time-frequency diagram of PLVz averaged across all 1891 electrode pairs and 16 observers for the bottom view to top view switch in top view biasing condition. Observers pressed the left key at 0ms. (b) Significant (p<0.00005) increases (black lines) and decreases (white lines) in synchrony between electrode sites at 4 Hz and 35 Hz. Grayscale-coded areas on head maps refer to spherical-spline-interpolated standardized instantaneous amplitude.
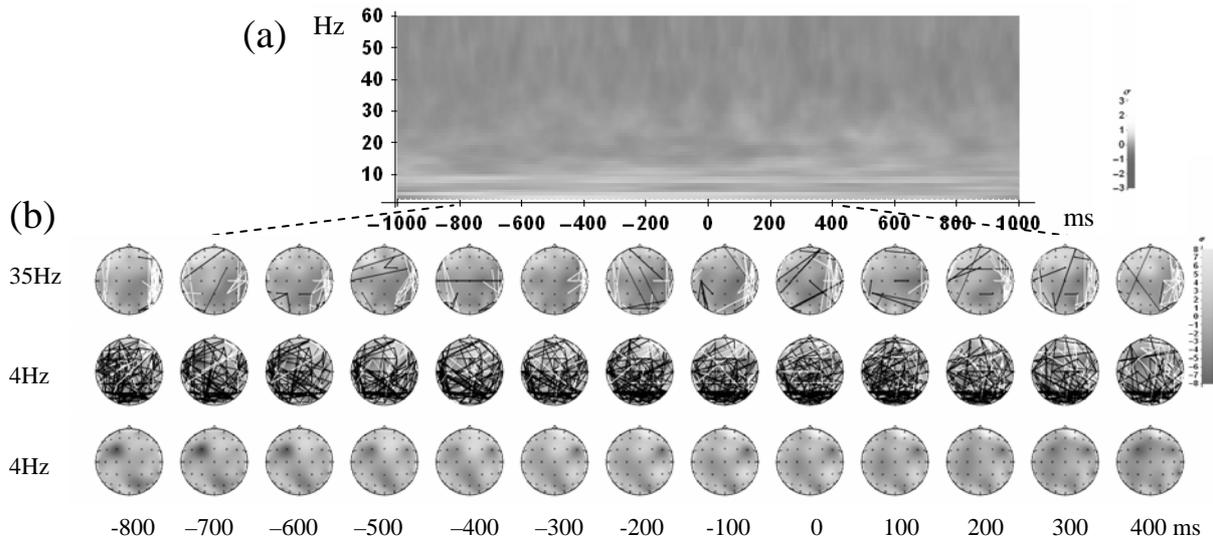
Fig.4 (a) Time-frequency diagram of PLVz for the bottom view to top view switch in passive view condition. (b) Significant (p<0.00005) increases (black lines) and decreases (white lines) in synchrony between electrode sites at 4 Hz and 35 Hz and spherical-spline-interpolated standardized instantaneous amplitude.
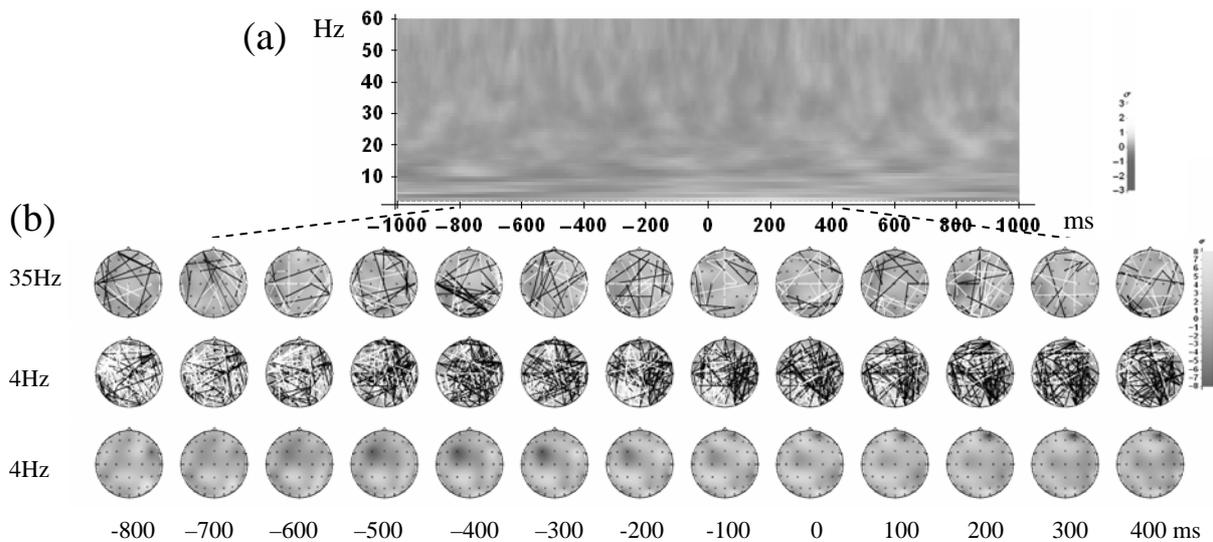


Fig.5 (a) Difference of time-frequency diagrams of PLVz between top view biasing condition and passive view condition for the bottom view to top view switch. (b) Difference in synchrony and instantaneous amplitude between top view biasing condition and passive view condition.

These results suggest that top-down selective attentional modulation of Necker cube perception is mediated by frontal-parietal-occipital synchrony networks in the theta frequency range. Large-scale synchrony in the theta band has been proposed as a mechanism for the implementation of top-down executive processes, dynamically linking task-relevant brain regions (Doesburg et al., 2005; von Stein and Sarnthein, 2000). Moreover, top-down selection theory predicts that attention-related frontal-parietal areas are responsible for initiating perceptual alternations by sending top-down signals to guide activity in visual

cortex toward one representation or another (Leopold & Logothetis, 1999, Meng & Tong 2004). Consistent with these studies, the observed theta-band synchronization associated with perceptual switches may reflect top-down influences on visual areas responsible for the perception of the Necker cube. Because of conduction delays, low frequency oscillations, such as theta rhythm, are particularly suited for synchronization over long distances, whereas fast oscillations, such as the gamma rhythm, are thought to synchronize cell assemblies over relatively short spatial scales (Jensen, 2007). The transient gamma patterns suggest that this burst of gamma-band synchrony is not associated with top-down modulation as observer's top-down modulation presumably extends beyond the termination of this gamma burst.

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