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Spatial attention enhances steady-state visual evoked responses in the gamma band

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Abstract. We carried out a cued spatial attention experiment in order to investigate the effects of attention on gamma band (20 Hz or greater) networks processing visual stimuli. Subjects were cued to direct attention to one of two visual stimuli in opposing hemifields which were flickering at 20 and 30 Hz respectively, while maintaining center fixation. Simultaneously recorded magneto- and electroencephalogram (MEG/EEG) revealed steady-state responses, localized to occipital and parietal areas, which were enhanced during trials in which the associated flicker was attended. Moreover, this attentional enhancement was also evident in the responses at higher order flicker harmonics. These results indicate that SSVEP responses from early visual areas reflect the effects of attention on visual information processing.

Keywords: MEG, Spatial Attention, Gamma-band, SSVEP

1. Introduction

Numerous studies have shown that selective spatial attention has the effect of enhancing neural responses to an attended visual stimulus [see Kastner & Ungerlaider, 2000 for review]. In EEG specifically, spatial attention increases the amplitude of early components of the visual evoked potential (VEP) induced by a visual stimulus [Hillyard & Anllo-Vento, 1998]. In addition, Gruber et al. [1999] demonstrated that attention to a visual stimulus results in increased levels of induced gamma-band power over pariteto-occipital electrodes. Such results are consistent with the hypothesis, advanced by Singer [1993], that attention serves to increase gamma-band synchronization in local neural assemblies to facilitate binding of visual information into coherent perecepts. However, recent studies have shown that it is often difficult to distinguish between authentic gamma-band EEG activity and that generated by scalp musculature and oculomotor sources [Nunez & Srinivasan 2010]. In this study we make use of steady-state methods which are uniquely robust to this type of broad-band artifact. Our goal is to gain an understanding of the dynamical interaction between local neural populations in visual cortex, which presumably have resonant frequencies in the gamma band, with globally distributed spatial attention networks which operate at lower frequencies in the alpha and theta bands. In this study we demonstrate that spatial attention enhances gamma band steady-state responses at both the fundamental flicker frequency as well as higher order harmonics.

2. Methods

Three subjects (2 male, 0 left-handed, 3 native English speaking) participated in the experiment. There were three experimental conditions: attend left (AL), attend right (AR) and attenional switching (AS). At the start of each trial the subject was instructed to either “Attend LEFT”, “Attend RIGHT”, or “Attend SWITCH”. On each trial the subject observed a pair of flickering stimuli presented symmetrically in each visual hemifield (eccentricity of the inner edge from center was 2.275 degrees of visual angle). The stimulus in each field consisted of a circular region (6.5 dva) containing randomly oriented bars (unit length for each of 0.56 dva) which appeared for a single frame (refreshed at 60 Hz). After a fixed period corresponding to the given flicker frequency, a new array was presented. On the fixed attention trials (AL/AR), the stimulus in the attended field was bounded by a green annulus, and the unattended stimulus was bounded by a red annulus throughout the entirety of the 50 second trial. On attention switching trials (AS), the subject was instructed to attend to the region bounded in green. At random intervals (roughly every 6-12 seconds) throughout the 100 second trial, the colors of the annuli in the respective hemispheres switched, prompting the subject to switch attention to the opposite hemifield.

The subject's task was to maintain center fixation (indicated by a gray fixation square) while simultaneously detecting targets in the attended hemifield and ignoring targets in the unattended hemifield. A target consisted of a 250 ms interval in which each field of randomly oriented bars contained an iso-oriented subset. The fraction of this subset as a percentage of the whole field was determined by a psychophysical staircasing procedure for each subject. In a separate session, subjects they were asked to detect the presence of a target in the cued hemifield within a three second interval. Subjects completed 100 such trials for each of four stimulus types (20/30 Hz Left/Right, attend Left/Right). Each time the subject responded correctly the fraction of iso-oriented bars on the successive target trial decreased by 1%, whereas the fraction increased 3% on incorrect trials. In order to facilitate accuracy on the more difficult task of sustained attention, the target level for each stimulus type was defined as that of the 95th percentile of all incorrect responses on each respective staircase.

An example of a target frame in which the subjects attention was directed left is shown in figure 1 (center). Note that for convenience in the source analysis we placed the pair of stimuli in the lower visual field in order to stimulate local networks along the dorsal surface of visual cortex. There were 36 total trials (2 x 3 x 6) corresponding to a single pair of flicker frequencies (20 and 30 Hz) presented in each of two visual hemispheres (Left/Right) for each of 3 attention conditions (attend Left/Right/Switch), with each trial type repeated six times throughout the experiment in random order.

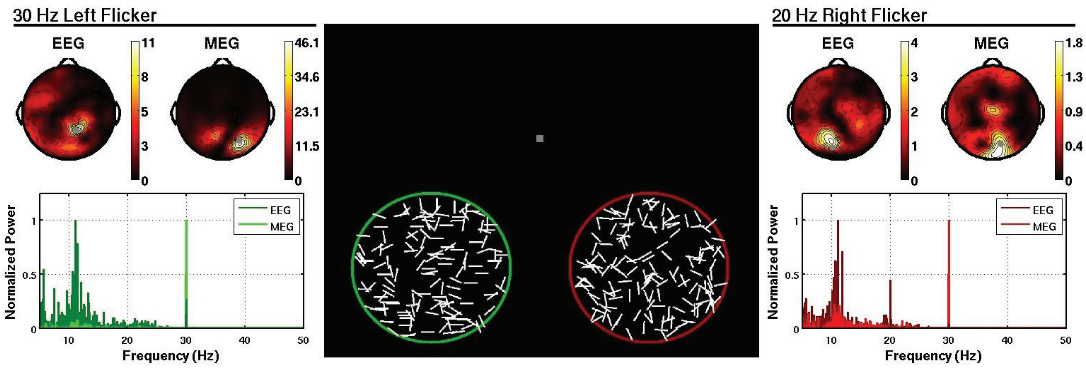

Figure 1. The Stimulus Display. *An example target frame is shown for an attend Left trial (center) in which the left and right patterns were updated (flickered) at 30 and 20 Hz, respectively. Each flicker gives rise to an independent steady state response in the EEG/MEG (magnetometer) localized over occipito-parietal areas (shown in upper left/right for a single trial in SNR units). Raw power spectra for the peak channels (indicated by gray dots) are shown for this same trial (lower left/right) to illustrate the spectral peaks at each frequency. Note that spectra were normalized by their respective maxima in order to show MEG and EEG spectral structure on the same scale.*

MEG/EEG recording. Simultaneous MEG/EEG signals were measured with an Elekta/Neuromag whole head neuromagnetometer at USCD Radiology Imaging Lab in San Diego, California. This system records field fluctuations using two planar gradiometers and one scalar magnetometer at each of 102 locations. In this paper we only report the magnetometer data. 128 channels of EEG were simultaneously recorded. Both signals were sampled at 1000 Hz. The locations of the EEG electrodes and MEG sensors were coregistered with respect to anatomical features of the subjects head using a Polhemus FastTrack 3-D digitizer. MEG data for each trial was artifact edited offline using a signal space correction algorithm (see Song et al., 2009), which uses spherical harmonic decomposition to separate MEG signals emanating from within the brain from noise sources external to the sensor array. For each subject, EEG channels containing high amplitude broad-band signals uncharacteristic of human EEG were recognized as artifact. These were identified as those channels for which spectral power on a given trial was in the 95th percentile (of all channels) *for each frequency* from 0-100 Hz. Since data were to be averaged across trials of similar types, channels which were recognized as artifact on *any* trial were excluded from analysis on *all* trials. This procedure resulted in a unique subset of 3-10 bad EEG channels per subject.

Analysis of steady-state visual evoked responses. MEG/EEG data from each trial were alligned on the onset of the flicker and Fourier coefficients were computed using the Matlab Fast-Fourier transform. Coefficients for each trial were then averaged across the six trials of each type. For each flicker frequency and its first two harmonics, we defined the signal to noise ratio (SNR) for each channel as the ratio of the power (squared modulus) in the bin corresponding to the flicker frequency and the 95th percentile of power in a window of 100 adjacent bins. We disregarded data for the first harmonic of our 30 Hz flicker, as well as the second harmonic of our 20 Hz, due to the fact that these both correspond to 60 Hz which is notoriously contaminated with electrical line noise.

In order to assess differences in steady-state responses related to attention, we first compared the 20 and 30 Hz responses in each hemisphere for both EEG and MEG magnetometer data by ranking the SNR computed over non-switching trials for each sensor. We analyzed scalp topographies of SNR for each data type and confirmed that the channels with the highest SNR tended to cluster into single groups of adjacent occipto-parietal channels in the EEG and symmetric bilateral groups of occipito-parietal sensors for the MEG (see figure 2). For each data type we compared the mean SNR in the top ranked 5-7 sensors (depending on whether these sensors fell naturally into adjacent groups) between trials where the flicker was attended vs those where it was unattended. An identical analysis was then done for the steady state responses at the second harmonic of the 20 Hz flicker (40 Hz) and the third harmonic of the 30 Hz flicker (90 Hz).

3. Results

Behavioral Results. Subjects were consistently able to detect targets throughout the experiment, with mean detection rates of 78.8%, 70.8%, and 77.8% (standard deviation 16.8%, 16.3%, 12.4%) for subjects 1-3 respectively. Accuracy did not generally vary by attentional condition; subjects performed comparably whether attending left or right, and on switching vs. non-switching trials. The one exception to this was subject 1, who showed a strong accuracy bias towards attending left (93.7% vs 63.52% for attend left/right respectively).

Effects of attention on the steady-state response. Figure 2 shows the topography of EEG and MEG SNR for each stimulus configuration for subject 1, and the corresponding effects of attention on the steady state response. For this subject, peaks in EEG SNR are visible for each stimulus type in a single cluster of electrodes which lateralizes very slightly over occipito-parietal areas contraletral to the hemifield containing the flicker. The MEG responses peak in two bilateral groups of occipito-parietal sensors. Like the EEG, the SNR of the MEG in response to the 30 Hz stimuli (Figure 2, C and D) is greater over areas contralateral to the hemifield containing the flicker. Moreover, both EEG and MEG SNR is generally higher in response to the 30 Hz stimuli (figure 2, C, and D) than for the 20 Hz stimuli (A, and B); a finding that is true across subjects as well. Comparing the average SNR at peak channels (indicated by gray dots), we see that for both the EEG and MEG, steady-state response to each flicker frequency in each hemifield is greater when the stimulus is attended (indicated in green bars) then when it is unattended (red bars).

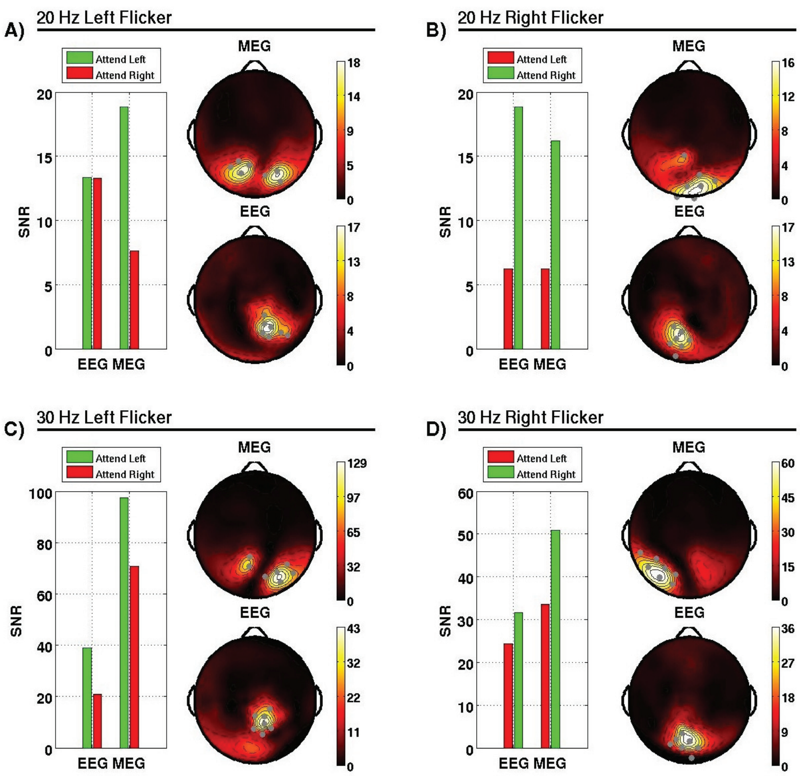

Figure 2. Effect of attention on the steady-state response at the fundamental. *EEG/MEG responses for subject 1 are shown (in SNR units) for one stimulus configuration. EEG responses tended to*

localize over a single cluster of occipito-parietal channels whereas MEG responses were bilateral. The 30 Hz stimulus response evoked a larger response than the 20 Hz across all subjects. For this subject, the response to the attended flicker was greater than the response to the unattended flicker for all stimulus configurations.

Figure 3 shows similar topographies and attentional effects for the same subject at 40 (Figure 3, A and B) and 90 Hz (C and D). Interestingly, the steady-state responses at the 40 Hz harmonic to stimuli in both hemifields is much larger than the corresponding responses at the 20 Hz fundamental (Figure 2, A and B). This is true for both EEG and MEG data. The peak MEG response at 40 Hz when the flicker is in the Left Hemifield (3A) is larger and more widespread than the corresponding 20 Hz response, and the peak response to the opposite field flicker (3B) occurs in completely non-overlapping sensors with those of the corresponding 20 Hz peak. The structure of the EEG topographies at 40 Hz also varies with respect to those of the 20 Hz response. We see again that the EEG response is larger, more widespread, and shows a greater degree of lateralization at 40 Hz. The response for this subject at the 90 Hz harmonic (Figure 3, B and C) shows a different relationship to the response at the 30 Hz. Response peaks at 90 Hz in the EEG data occur in almost entirely overlapping areas as those at the 30 Hz fundamental (Figure 2, C and D), and are clearly comparatively smaller. Likewise, the response peaks at 90 Hz in the MEG are also smaller than the corresponding peaks at the 30 Hz fundamental, and show a comparatively smaller degree of contra-lateral hemispheric lateralization. One fact remains consistent across both harmonics, however. Larger steady-state responses are observed in both the EEG and MEG for each stimulus configuration when the flicker is attended.

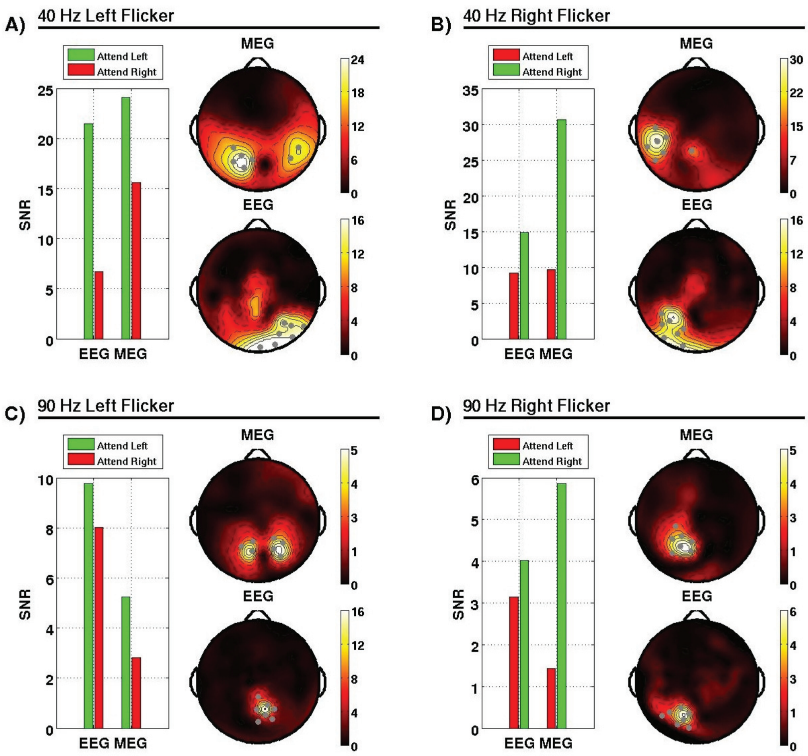

Figure 3. Effect of attention on gamma-band response harmonics. *EEG/MEG responses for subject 1 are shown (in SNR units) at the first harmonic of the 20 Hz stimulus (40 Hz, A and B), and the second harmonic of the 30 Hz flicker (90 Hz, C and D). For this subject the 40 Hz harmonic response was much larger, and more widespread than that at the 20 Hz fundamental, and showed a greater degree of contrlateral hemispheric lateralization in the EEG. Again, for this subject the harmonic response when the fundamental flicker was attended was always greater than the response when it was unattended.*

Figure 4 shows similar peak SNRs and attentional effects for subjects 2 (4A) and 3 (4B) as those observed for subject 1 in previous figures. In general, SNR at peak channels is greater for all subjects in response to the 30 Hz flicker than to the 20 Hz in both the EEG and MEG data. Moreover, for subject 2 we see that SNR over peak channels is much higher at the 40 Hz harmonic than at the 20 Hz fundamental in both the EEG and MEG data (whereas for subject 3 the SNRs are comparable). However, for all subjects the response at the 30 Hz fundamental is far larger than the 90 Hz harmonic response. Finally, we see that the effects of attention on the steady-state responses are more complicated for subjects 2 and 3 than was observed for subject 1, specifically for the 20 Hz fundamental and 40 Hz harmonic responses. Attention to flicker at this fundamental sometimes induced greater peak SNR for both data types (subject 2, 20 Hz left hemifield), sometimes resulted in greater SNR in one data type and less in the other (subject 2, 20 Hz left hemifield), and even sometimes resulted in less peak SNR for both data types (subject 3, 20 Hz right hemifield). However, the attentional effects at the 30 Hz fundamental and 90 Hz harmonic are much simpler. In all subjects, attention to this flicker induces greater peak SNR in both the EEG and MEG data.

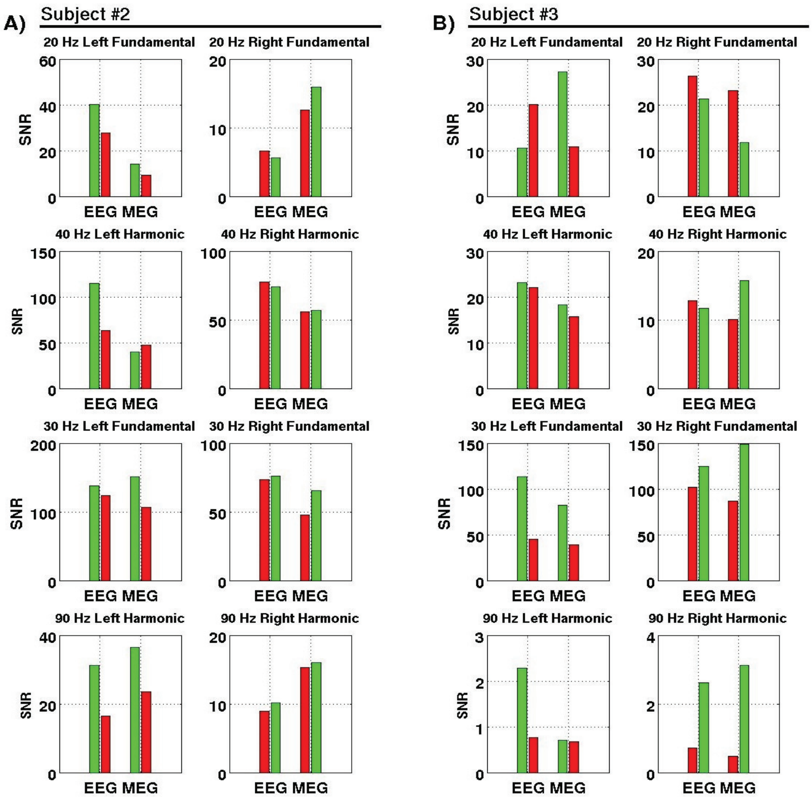

Figure 4. Effect of attention on the fundamental and harmonics responses for Subjects 2 and 3. *For all subjects the response to the 30 Hz flicker was greater than the response at 20 Hz. For subject 2, the response at the 40 Hz harmonic is greater than the response at the 20 Hz fundamental; the same relationship was observed for subject 1. For subjects 2 and 3, the effects of attention on the 20 Hz fundamental and 40 Hz harmonic responses are not straightforward. However, for the 30 Hz fundamental and 90 hz harmonic responses the attended response was larger than the unattended for each stimulus configuration.*

4. Discussion

We have seen that spatial attention promotes enhanced steady-state responses both at the fundamental gamma frequency and its harmonics. The observation that in two of three subjects the 40 Hz harmonic response far exceeded the response at the fundamental lends support to the hypothesis that information processing populations in early stages of the visual hierarchy may have a resonance around this frequency. Understanding the interaction between these gamma-resonant populations and lower-frequency endogenous attention signals acting on larger spatial scales in networks spanning parietal and frontal cortex is one goal of our ongoing and future research. The other goal is the localization of these gamma-band SSVEP networks by the simultaneous source analysis of the EEG and MEG.

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