Using steady state responses in MEG to study information integration within and across the senses

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Introduction:

How does the brain integrate information within and across sensory modalities to form a unified percept? This question has previously been addressed using transient stimuli, analyzed in the time domain. Alternatively, sensory interactions can be investigated using frequency analyses of steady state responses (SSRs). SSRs are elicited by periodic sensory stimulation (such as frequency modulated tones). In the frequency domain, 'true' signal integration is reflected by non-linear crossmodulation terms (i.e. the sums and differences of the individual SSR frequencies). In addition, two signals may modulate the amplitude of the fundamental and harmonic frequencies of one another. Using visual (V) and auditory (A) SSRs, we investigated whether A and V signals are truly integrated as indexed by crossmodulation terms or simply modulate the expression of each other's dominant frequencies. To manipulate perceptual synchrony, we imposed additional slow modulations on the auditory and visual SSRs either at same or different frequencies. This also enabled us to investigate the integration of two dynamic features within one sensory modality.

Methods:

14 subjects participated in this MEG study (whole-head CTF MEG 275 System, SPM8 for data analysis). The experiment conformed to a 3x3 design, manipulating (1) modality (A, V, AV) and (2) temporal dynamics (static, dynamic1, dynamic2). In the static conditions, subjects were presented with (1) gratings, luminance modulated at 6Hz and/or (2) pure tones, frequency modulated at 40 Hz (Figure 1a & b). In the dynamic conditions, the grating's diameter and the tone's amplitude were additionally modulated (i) both at 0.2Hz (dynamic1 = synchronous for AV) or (ii) at 0.2Hz (V) and 0.7Hz (A) (dynamic2 = asynchronous for AV) (Figure 1c). Source reconstruction was performed using a multiple sparse priors (MSP) inversion. In sensor and source space, we compared (i) A, V or AV > baseline, (ii) A or V ≠ AV, (iii) synchronous ≠ asynchronous at fundamental, harmonic and crossmodulation frequencies in paired t-tests at the random effects level ($p<0.05$ SVC for sensory cortices (source space) and frequencies of interest).

Results:

In sensor space, the amplitude at fundamental and harmonic frequencies was significantly greater for A V & AV than baseline conditions, over temporal and occipital regions. Crossmodulation terms were observed only for within- (e.g.: 6Hz + 0.2Hz) but not across-modalities (e.g.: 40Hz + 6Hz) (Figure 2). In source space, V SSR was located in visual cortices and A SSR in auditory cortices. More importantly, source activity at 6Hz was significantly greater in visual cortices for synchronous conditions relative to unisensory V (Figure 3a) and asynchronous AV conditions (Figure 3b).

Conclusions:

Over the past decade, evidence has accumulated for AV interactions already at the primary cortical level. Yet, using A and V SSRs, we did not observe non-linear AV interactions as indexed by crossmodulation terms. Instead AV interplay emerged only as increased source activity in visual cortices for synchronous relative to asynchronous and unisensory visual conditions. These findings suggest that the previously reported AV interactions in primary sensory areas may mediate low level saliency effects by detecting spatiotemporal co-occurrence of transients such as onset/offsets that are less relevant for sustained SSR responses.
In contrast, crossmodulation terms were observed when two stimulus features within the same sensory modality were modulated at different frequencies (e.g. auditory: 40Hz + 0.2 Hz). These results suggest that indeed frequency and amplitude coding within the visual and auditory systems interact already at the primary cortical level.
In conclusion, our results suggest that information in SSR is integrated at the primary cortical level within but not across sensory modalities.

Perception and Attention:

Perception: Multisensory and Crossmodal

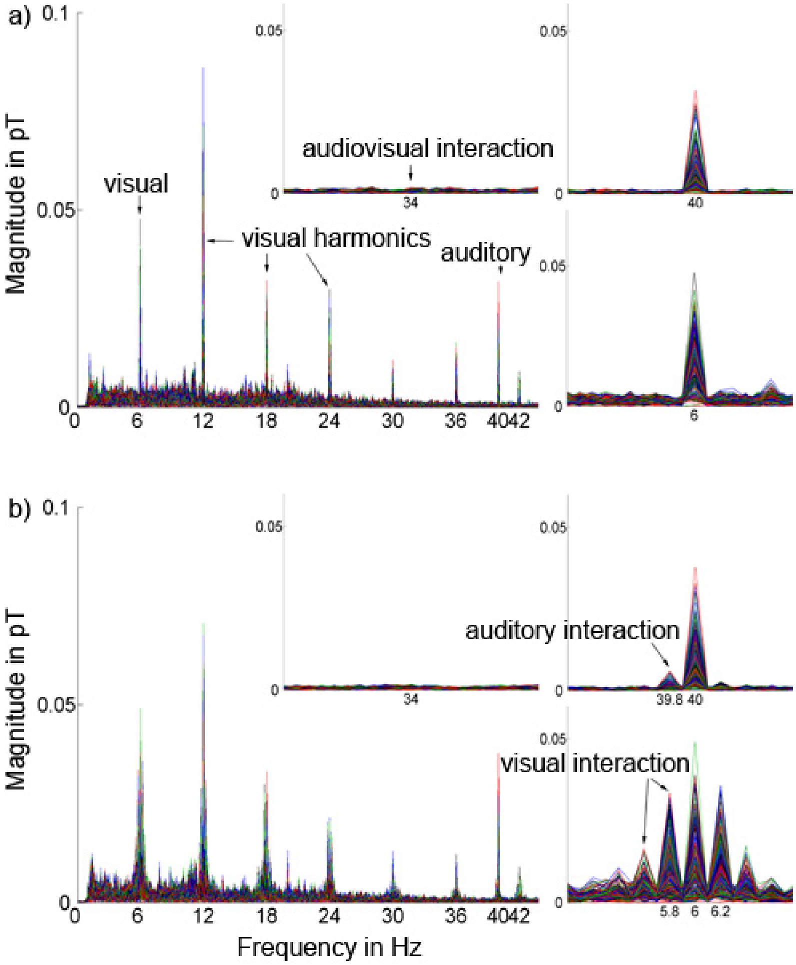

Figure 2: Mean magnitude (pT) as a function of frequency (Hz) over all channels at static (a) and dynamic congruent (b) conditions, for one representative subject. The figure shows clear peaks at the stimulation frequencies (auditory = 40 Hz and visual = 6 Hz) and their higher harmonics. Moreover, clear unimodal visual interactions (e.g., at 5.8 Hz and 6.2 Hz) and unimodal auditory interactions (e.g., at 39.8 Hz) can be seen for the dynamic congruent stimulation. However, there are no peaks at audiovisual interaction frequencies (e.g., at 34 Hz).

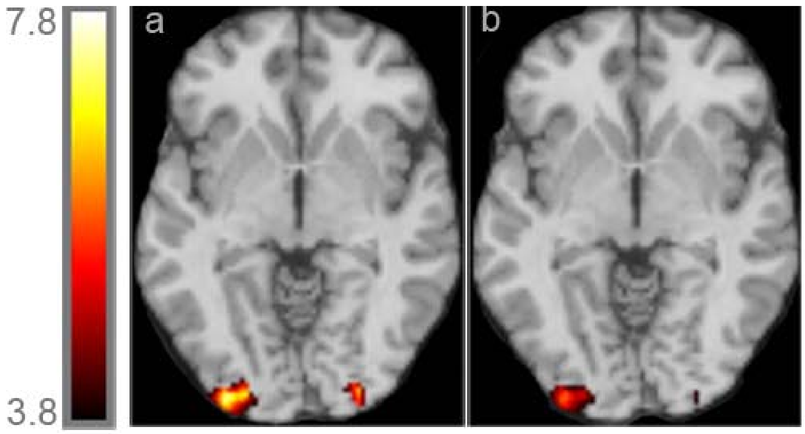

Figure 3: Source level results (*t*-map): Significant differences in source energy at 6 Hz for AV synchronous relative to unisensory V (a) and AV asynchronous (b). Displayed on transverse sections of a canonical MNI brain at $t > 3.8$, $p < 0.001$ uncorrected, voxel threshold = 20.

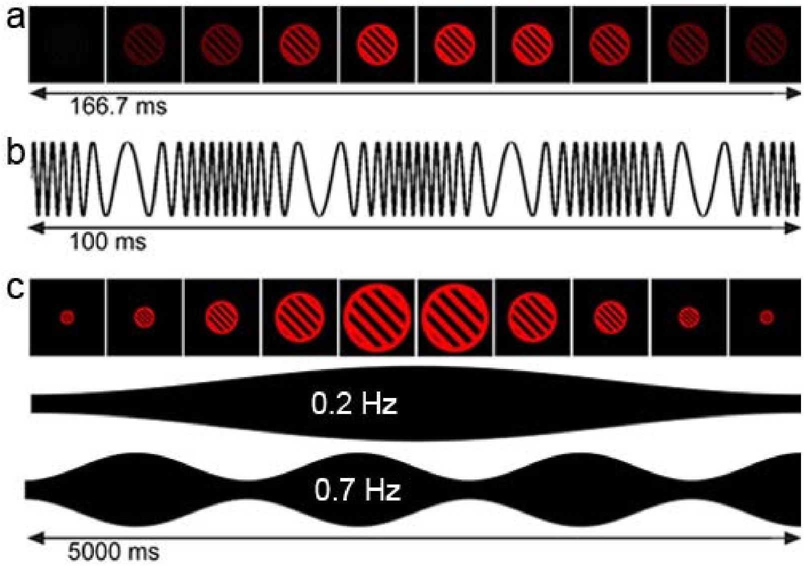

Figure 1: Experimental stimuli and conditions:
a) Visual: Grating luminance modulated at 6Hz
b) Auditory: Pure tone frequency modulated at 40Hz
c) Dynamic condition 1: Visual: Grating luminance modulated at 6Hz and diameter modulated at 0.2 Hz Auditory: Pure tone frequency modulated at 40Hz and amplitude modulated at 0.2 H
c) Dynamic condition 2: Visual: Grating luminance modulated at 6Hz and diameter modulated at 0.2 Hz. Auditory: Pure tone frequency modulated at 40Hz and amplitude modulated at 0.7 H

Abstract Information

References