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# Early modulation of visual cortex by sound: an MEG study

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## Abstract

Sound can alter visual perception. This has been recently demonstrated by a strong illusion in which a single flash is perceived as multiple flashes when accompanied by multiple brief sounds. While psychophysical findings on this sound-induced flash illusion indicate that the modulations of visual percept by sound occur at a perceptual processing level, it remains unclear at what level of perceptual processing these interactions occur and what mechanisms mediate them. Here we investigated these questions using MEG. We found modulation of activity in occipital and parietal scalp locations, when comparing illusion trials with visual-alone and auditory-alone trials. This modulation occurred as early as 35–65 ms from the onset of the visual stimulus. Activity was also modulated in the occipital and parietal areas as well as anterior areas at a later (∼150 ms post-stimulus) onset. No significant interactions were observed in occipital and parietal areas in trials in which illusion was not perceived. These results indicate that the auditory alteration of visual perception as reflected by the illusion is associated with modulation of activity in visual cortex. The early onset of these modulations suggests that a feed-forward or lateral circuitry is at least partially involved in these interactions.

*Keywords:* Multisensory integration; Sound-induced flash illusion; Auditory–visual interactions; Multisensory perception; MEG; Cross-modal interactions

The discovery of various cross-modal interactions in recent years (e.g., [7–9,20,21,23,35,37,40,41]) suggests that these interactions are the rule rather than exception in human perceptual processing. Even the visual modality, which has long been viewed as the dominant modality, has been shown to be affected by signals of other sensory modalities (e.g., [35,37]). While it has been known for some time that sound can influence the perceived temporal aspects of the visual stimuli [15,25,32,39,44,45], recent studies have revealed that this influence is not limited to temporal aspects, and sound can affect the visual percept qualitatively [35], even when there is no apparent ambiguity in the visual stimulus [37,38]. It is not clear at what level of perceptual processing these cross-modal effects take place, however. These interactions may occur at brainstem, at early or late visual cortical areas, or at polysensory associative cortical areas.

Schröger and Widmann [34] used ERP to explore the sites of audio-visual interactions. They employed an odd-ball paradigm, and found no early interactions between the auditory and visual processes. They interpreted their results as suggesting that the audio-visual integration occurs somewhere beyond the modality-specific areas but before the decision-making stage. Giard and Peronnet [16] used ERP for tackling the same question employing a pattern recognition task. They reported very early cross-modal effects in the occipital area, and interpreted these results as modulation of activity in the "sensory-specific" visual cortical areas by sound. In their study, however, they used two visual deformation patterns, which unfolded over a course of 230 ms, and the subjects were trained in advance to associate each of the two visual patterns with a specific tone. It is not clear whether their results generalize to situations

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in which subjects are not trained to associate specific visual stimuli with specific auditory stimuli, or in which the visual stimulus is a static image as opposed a deforming pattern. In a more recent ERP study [24], auditory–visual interactions were examined in a reaction-time task. A pattern of early cross-modal effects similar to that reported by Giard and Peronnet was found in the parieto-occipital regions, suggesting cross-modal interactions during early sensory processing. Calvert et al. [4] reported enhanced activation of visual area V5 during bi-modal auditory–visual speech perception, compared to either unimodal auditory or visual speech perception. This provides evidence that visual cortex can be affected by auditory stimuli, but it remains to be seen whether such auditory influences on visual cortex can occur in earlier visual cortical areas that do not immediately precede known multimodal areas (as area V5 does).

None of these earlier studies has employed a paradigm in which the signal in one modality causes a strong qualitative change in the percept in the other modality. We used an illusion, known as sound-induced flash illusion, in which sound radically alters visual perception, as a testbed for investigating the underlying mechanisms of auditory–visual interactions. When a single flash is accompanied by two auditory beeps, the single flash is mis-perceived as two flashes [38]. The simplicity of the eliciting stimuli together with the robustness of the illusion with respect to a number of parameters (e.g., the shape, color, brightness and size of the visual flash, the frequency and intensity of the auditory beeps, the spatial disparity between beeps and flash, etc.) suggest that this illusion reflects a fundamental mechanism subtending auditory–visual interactions. Several psychophysical findings indicate that the illusion reflects a genuine perceptual phenomenon as opposed to a cognitive effect. These characteristics render the flash illusion an ideal tool for investigating mechanisms underlying auditory–visual perceptual interactions in general.

We have previously sought to identify the brain mechanisms underlying auditory–visual integration using the flash illusion in an ERP study, showing that visually evoked potentials can be modulated by sound [3,36]. However, this study used only recordings from three occipital electrodes. In the present study, we aimed to examine the time course of auditory–visual interactions at various scalp locations using MEG in order to gain further insight into the circuitry involved in auditory–visual integration. This study takes advantage of recordings from 122 channels distributed across the scalp. The larger number of channels together with the much higher signal-to-noise ratio provided by MEG enabled this study to assess the time course of the cross-modal interactions more accurately, and across different brain regions.

Eleven adult volunteers (eight males, three females, ages ranging 22–40 years) participated in the study. The study was conducted in accordance with the Declaration of Helsinki and was approved by the Internal Review Board. All subjects were without a history of neurological or psychiatric disorders and had normal or corrected to normal visual acuity, and normal hearing. Subjects gave informed consent to participate, and were paid for their participation.

The magnetic signals of the brain were measured with a 122-channel whole-scalp neuromagnetometer (Neuromag) in a magnetically shielded room. The instrument measured two orthogonal tangential derivatives of the magnetic field at 61 scalp locations. In all conditions in which there was a visual stimulus, the event trigger was synchronized to the onset of the (first) flash. In the auditory condition, the event trigger was synchronized with the onset of the first beep. The subjects were instructed to fixate on a cross on the screen, and not to blink during trials. MEG signals were band-pass filtered at 0.03–100 Hz and digitized at 550 Hz, and stored for off-line analysis.

The experiment consisted of four conditions: V: a visual flash, AV: a flash accompanied with two beeps, A: two beeps and no flashes, and a control condition $V^2$: two physical flashes. The flashing stimulus was a uniform white disk subtending a visual angle of 2° in the periphery at 8.5° eccentricity for a duration of 20 ms. In the physical double-flash condition, the SOA of the two flashes was set to 50 ms. The auditory stimulus consisted of two brief beeps each lasting 10 ms and separated by 50 ms. The sound stimulus (1 kHz frequency at 70 dB SPL) was presented from headphones. In the bimodal condition, the flash onset was 14 ms after the onset of the first beep. There were 80 trials for each condition and the order of trials was random. The inter-trial interval was varied randomly between 1500 and 2000 ms. The participant's task was to judge the number of flashes they saw on the screen at the end of each trial in a three-response-category paradigm—zero, one, or two flashes. They responded by pressing keys on a keypad.

The continuous MEG signals were divided into epochs (−100 ms pre- to 500 ms post-stimulus onset) and were digitally low-pass filtered at 30 Hz cutoff frequency. The epochs containing eye blinks or excessive movements were excluded based on amplitude criteria [26]. It has been argued that anticipation of stimuli can lead to slow (or anticipatory) potentials [42]. These potentials can lead to artifacts, which can be mistakenly interpreted as early interaction. Our random inter-trial interval helps minimize the anticipation of the stimuli, and hence the incidence of anticipatory potentials. However, in order to completely avoid this artifact, each epoch was further band-pass filtered at 2–25 Hz. The low-pass filtering was performed due to the presence of oscillations of Helium cylinders during the recording of MEG signals, which required high frequencies in the gamma range to be filtered out. Filtering out of these high frequency components does not amount to a significant loss as they would be attenuated by conventional averaging techniques to obtain ERF in any case. The choice of bandpass filter settings is in line with those used in previous studies [11,16,17,22].

For the bimodal condition AV, illusion trials (two flashes perceived) were separated from the non-illusion trials (one flash perceived) because of our previous ERP finding that audio-visual interaction was strongly correlated with the perception of the illusion [3,36]. This resulted in 389 illusion trials over all subjects. For visual-alone conditions (V and $V^2$), only trials in which the subject's response was correct (i.e., the number of perceived flashes was the same as the number of physically presented flashes) were used for further analysis. Because these criteria led to an imbalance in the number of trials across different conditions (e.g., 800 in condition A versus 389 in AV), we removed trials from conditions A, V, and $V^2$ to match the number of trials in the AV illusion condition (389). The MEG signals for each condition were averaged and baseline corrected to produce event related magnetic field (ERF) responses.

The auditory–visual interaction was investigated by examining the differential ERF response obtained by subtracting the sum of the ERFs to the auditory and the visual stimuli from the ERF to the bimodal stimuli: $\mathrm{ERF(AV)} - [\mathrm{ERF(A)} + \mathrm{ERF(V)}]$. This procedure has traditionally been used by cross-modal studies [11,12,18,26,29,36]. In this analysis, any deviation from zero would reflect a cross-modal interaction. The direction of deviation, whether it is positive or negative, cannot be directly interpreted as excitation and inhibition, however, because these changes in the magnitude can be caused by a change in the *orientation* of the source dipole as well.

The differential responses were statistically compared against zero using point-wise two-tailed Student's *t*-tests for each sensor location separately. Significant audiovisual interaction was defined as intervals of at least 30 ms (17 successive samples) that meet the statistical significance criterion ($p < 0.05$). As discussed by Molholm et al. [24], this criterion is more stringent than the traditional Bonferroni corrections for multiple comparison, thus making it appropriate when a large number of *t*-tests are calculated across many sensors and ERF epochs. Our statistical significance criterion is more conservative than some previous studies (which have used 10 significant successive points as a criterion) in order to minimize the chance of obtaining early interactions due to Type I error.

The flash illusion occurred in 62% of the auditory–visual trials. Figs. 1–5 show the results of the MEG recordings. In all figures, time zero denotes the onset of the visual stimulus. In Fig. 1, the activity in auditory-alone, visual-alone, and auditory–visual illusion trials are shown for the entire scalp at different latencies in three different rows. As can be seen, the auditory–visual activity is considerably different from each of the unisensory activities. In order to examine cross-modal interactions, the activity in bimodal condition has to be contrasted with the sum of the unimodal conditions. As described above, the time intervals in which the difference wave is significantly different from zero are considered the periods of cross-modal interaction. Significant intervals of cross-modal interaction at all channels are shown in Fig. 2. As can be seen, cross-modal interactions occur at different times in different scalp locations, with the occipital channels showing the earliest interactions, followed by anterior channels, followed by a global effect exhibited across most of the scalp. Fig. 3 shows a topographic map of the neuromagnetic response associated with the difference wave in the same time span.

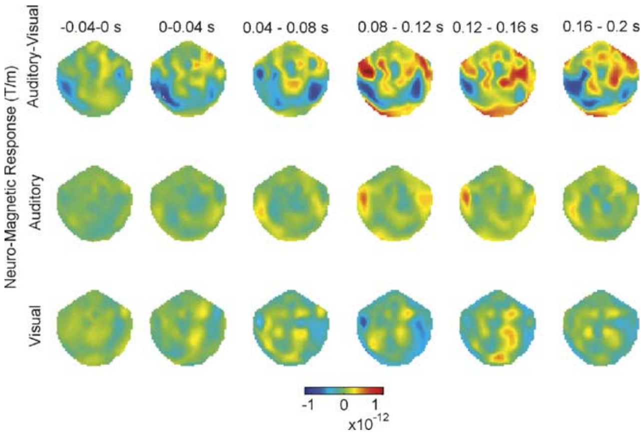

Fig. 1. Topographic progression of neuro-magnetic response in the three conditions. The responses corresponding to the auditory–visual illusion, auditory-alone, and visual-alone conditions are shown in the top row, middle row, and bottom row, respectively. The view is one looking down on cortex. Zero denotes the stimulus onset time.

In order to examine whether the observed significant auditory–visual interactions are correlated with the percept of the illusion or occur irrespective of the percept, we also analyzed the trials of AV condition in which no illusion occurred. As in Fig. 2, Fig. 4 shows the significant intervals of cross-modal interaction, however, for trials in which no illusion occurred. Note that the AV trials examined in this figure are identical to those examined in Fig. 2 in terms of the physical stimuli. These trials only differ from those examined in Fig. 2 in terms of the observers' percept, and yet the results are substantially different. In contrast to extensive interactions observed in illusion trials, interaction is found in only a few channels in these trials. More importantly, there is no interaction in the occipital and parietal regions at any time. This suggests that there is no *perceptual* interaction between the two modalities in these trials. Most of the interaction is found in the frontal areas and some in central areas. These interactions probably reflect influences in cognitive or decision-making processes.

Finally, in order to examine whether there is any similarity between the pattern of activity associated with the percept of the illusory second flash and that of a physical second flash, we examined $V^2 - V$. Fig. 5 shows the time intervals in which $V^2 - V$ is significantly different from zero. Comparing Figs. 2 and 5, it can be seen that there are some similarities between the patterns of activity. There are activations in the left occipital, right parietal, left and right frontal regions around ∼145 ms latency in both cases. The somewhat global late activation (∼350–450 ms) seen in Fig. 2, although to a lesser extent, is also present in Fig. 5. The discrepancies between the two include the lack of very early activation (35–65 ms) in the right occipital region, and the presence of early activity instead in the frontal and temporal areas.

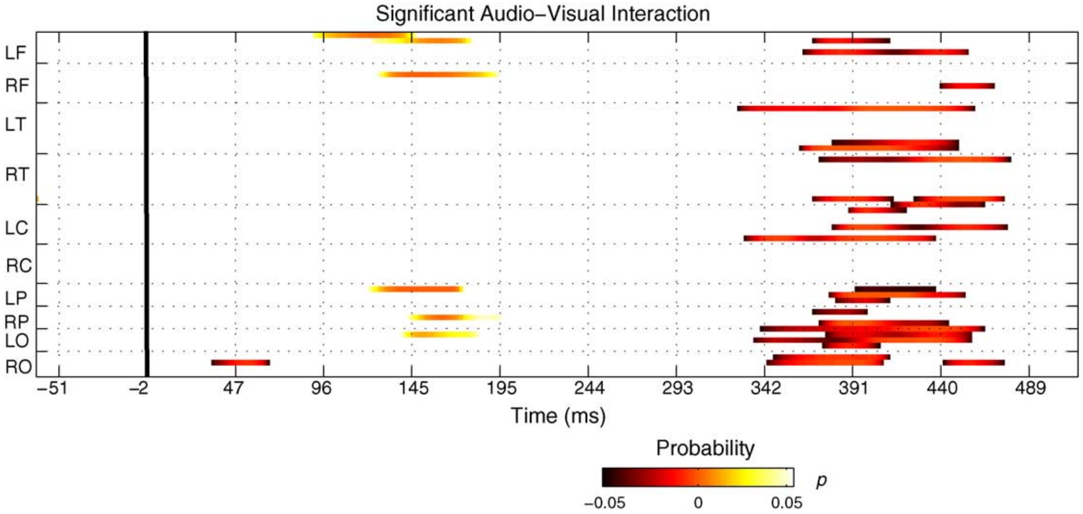

Fig. 2. Probability map for significant auditory–visual interactions across all channels. Each row represents the activity in one of the 61 channels. The channels are grouped and labeled according to their cortical location. The abbreviated labels on the *y*-axis represent the location of the channels. The first letter denotes the hemisphere (L: left, R: right) and the second letter denotes cortical region with O, P, C, T, and F representing occipital, parietal, central, temporal, and frontal, respectively. The probability map has been color coded such that the negative and positive values can be distinguished. The earliest interaction is observed in the right occipital region during 35–65 ms post-flash onset. Moderately early interactions are found in left occipital (140–182 ms), right parietal (144–195 ms), left parietal (122–175 ms), right frontal (127–193 ms), and left frontal (91–147 ms and 124–178 ms) regions. Late interactions occur more globally and in more extended time intervals ranging from 327 to 478 ms in latency.

The important findings are summarized below.

(i) Activity in the visual cortex got modulated in the auditory–visual illusion trials as compared to the sum of activity in visual-alone and auditory-alone trials.
(ii) Many anterior regions also show modulated activity.
(iii) The earliest significant interaction effect was found in sensors over right occipital region at 35–65 ms post-stimulus.
(iv) More robust interaction was found later with average onset latency of 125 ms over occipital, parietal, temporal, and frontal cortical areas.
(v) The most global interaction was found later at 327 ms onwards.
(vi) The last moment of interaction was 478 ms.
(vii) No significant auditory–visual interaction was found in occipital and parietal regions when no illusion occurred in the auditory–visual condition.

Recently, it has been pointed out that using the difference wave as a means of examining cross-modal interactions can be misleading if certain conditions are not met [6,42]. If there

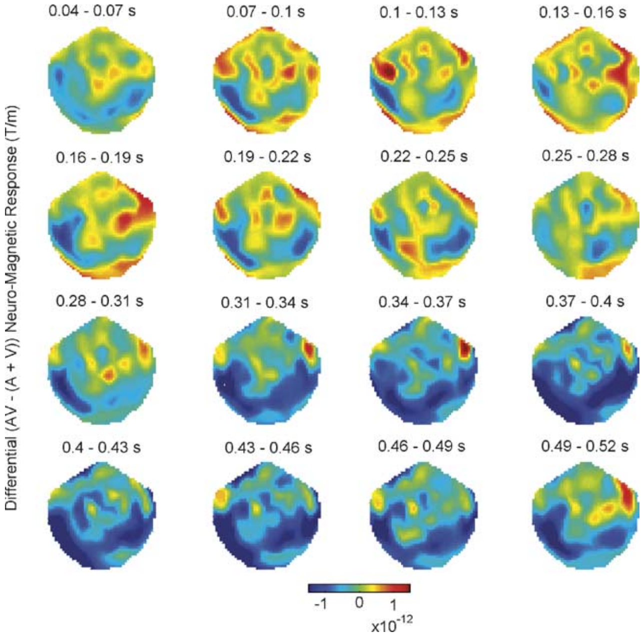

Fig. 3. Topographic progression of neuro-magnetic response corresponding to the difference wave [AV − (A + V)]. The view is one looking down on cortex.

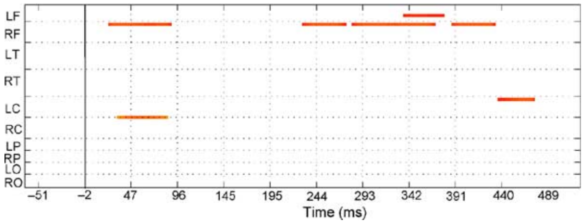

Fig. 4. Probability map for significant auditory–visual interactions in the non-illusion trials across all channels. The channel groupings are the same as those described in Fig. 2. The time intervals in which AV − (A + V) significantly deviates from zero are shown for trials in which subjects did not perceive an illusion, i.e., they reported seeing one flash. In contrast to the illusion trials (shown in Fig. 2) there is very little interaction indicated for the non-illusion trials. The interaction in the occipital and parietal regions observed for the illusion trials is completely absent when no illusion is perceived.

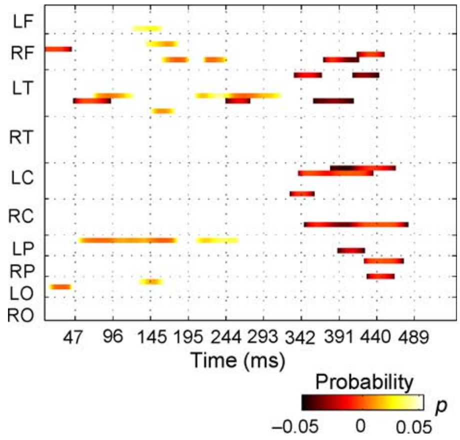

Fig. 5. Activation associated with the percept of a second *physical* flash. The statistically significant differences between the double flash and single flash conditions (i.e., $V^2 - V$ compared against 0) is plotted for each of the 61 channels. See Fig. 2 caption for description of the notation. These results are to be contrasted with the significant $AV - (A + V)$ interactions shown in Fig. 2 which can be interpreted as activity associated with the percept of an *illusory* second flash.

is a common activation component among the three conditions (A, V, and AV), this component is subtracted twice and added once, thus resulting in a non-zero activation even when there are no interactions between the unimodal processes. It has been argued that the slow potentials due to expectation of the sensory stimuli, which are common in all three conditions can lead to this artifact. As mentioned in the data analysis section, we excluded the slow potentials from the data by high-pass filtering the signals, in order to avoid such artifactual interactions. Therefore, it is unlikely that the observed early interactions in the occipital region is due to such artifacts. There is a possibility that the late interactions, observed between ∼350 and ∼450 ms, are due to processes involved in decision-making and motor responses, which are common to all three conditions. However, the pattern of the results are not quite consistent with this interpretation. The significant interactions are highly localized in time (between ∼350 and ∼450 ms) and occur somewhat globally, from sensory areas, all the way to frontal areas. Therefore, it appears that these late modulations reflect cross-modal interactions.

Perhaps the most important finding of this study is the modulation of activity in occipital channels as early as 50 ms (center of the interval) post-visual stimulus onset. This finding suggests that the visual cortex can be modulated by extra-visual signals even in a task, which does not involve spatial attention. More surprisingly, the early onset of these interactions suggests a fairly direct pathway mediating the interactions, as opposed to a second-order effect due merely to feedback modulations from higher-order cortical areas. Recent neuroanatomical studies in monkey have reported direct projections from primary and parabelt auditory cortex and STP to the peripheral representations in the V1 and V2 [10,28]. These pathways are likely to exist in humans as well, and would provide a plausible circuitry for the observed auditory modulations of the visual cortex.

The modulation of visual cortex by sound found in this study is consistent with the results of our ERP study of the flash illusion which also suggested the involvement of the visual cortex in the representation of the illusion [3,36], as well as a more recent ERP study of the illusion confirming the role of early visual cortical areas in the illusion [2].

The excellent temporal resolution as well as the high signal to noise ratio of the MEG method allowed a more precise temporal localization of these interactions in the present study. Interestingly, the timing and location of the early interactions found in this study are remarkably consistent with those reported by two earlier ERP studies of auditory–visual interactions which employed quite different paradigms. We found the auditory–visual interactions occurring as early as 35–65 ms in right occipital scalp. Giard and Peronnet [16] used an identification task, and reported auditory–visual interactions with an onset of 40 ms post-stimulus in the right parieto-occipital scalp. In a reaction-time study, Molholm et al. [24] found auditory–visual interactions in the right parieto-occipital regions with an onset of 46 ms. The right hemispheric dominance found in our study as well as these previous studies, suggests that the right hemisphere may play a greater role in housing the network for early audio-visual processing. However, it is to be noted that opposite (i.e., left) hemispheric dominance has been observed during audio-tactile interaction [18].

The finding that AV interactions are correlated with the percept of the illusion has interesting implications for the debate about how early in the sensory processing is neuronal activity correlated with conscious perception. The results seem to be consistent with some previous findings indicating that conscious visual perception is correlated with early visual cortical activity (e.g., [14,27,43]).

Over the last few years, several studies utilizing various methodologies have reported cross-modal modulation or invocation of activity in early stages of sensory processing in the cortex. Our present results together with these recent studies [1–3,5,13,16,19,30,31,33,36,46] provide accumulating evidence for cross-modal interactions occurring at early stages of perceptual process; areas that have long been viewed as “sensory-specific.” These findings seriously challenge the notion of modularity of perceptual processing and provide further ground for a shift to a more interactive and integrative paradigm of perceptual processing.

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