

## Good times for multisensory integration: Effects of the precision of temporal synchrony as revealed by gamma-band oscillations

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### Abstract

The synchronous occurrence of the unisensory components of a multisensory stimulus contributes to their successful merging into a coherent perceptual representation. Oscillatory gamma-band responses (GBRs, 30–80 Hz) have been linked to feature integration mechanisms and to multisensory processing, suggesting they may also be sensitive to the temporal alignment of multisensory stimulus components. Here we examined the effects on early oscillatory GBR brain activity of varying the precision of the temporal synchrony of the unisensory components of an audio-visual stimulus. Audio-visual stimuli were presented with stimulus onset asynchronies ranging from  $-125$  to  $+125$  ms. Randomized streams of auditory (A), visual (V), and audio-visual (AV) stimuli were presented centrally while subjects attended to either the auditory or visual modality to detect occasional targets. GBRs to auditory and visual components of multisensory AV stimuli were extracted for five subranges of asynchrony (e.g., A preceded by V by  $100 \pm 25$  ms, by  $50 \pm 25$  ms, etc.) and compared with GBRs to unisensory control stimuli. Robust multisensory interactions were observed in the early GBRs when the auditory and visual stimuli were presented with the closest synchrony. These effects were found over medial-frontal brain areas after 30–80 ms and over occipital brain areas after 60–120 ms. A second integration effect, possibly reflecting the perceptual separation of the two sensory inputs, was found over occipital areas when auditory inputs preceded visual by  $100 \pm 25$  ms. No significant interactions were observed for the other subranges of asynchrony. These results show that the precision of temporal synchrony can have an impact on early cross-modal interactions in human cortex.

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In many real-world situations, information from multisensory objects needs to be integrated by our cognitive system. The stimulus onset asynchrony (SOA; i.e., the relative timing of the onsets) of inputs from multiple sensory modalities appears to be a critical factor that influences the integration of such objects (Bushara, Grafman, & Hallett, 2001; Calvert, Hansen, Iversen, & Brammer, 2001; Eimer, 2001; Wallace et al., 2004). For example, during a thunderstorm lightning is often perceived much earlier

than the sound of thunder, because light travels substantially faster than sound. As the storm draws near, the visual image of lightning and sound of the thunder reach the senses at increasingly similar times. Consequently, the separate percepts start to merge into a single coherent percept. This implies that our sensory system is able to integrate inputs from the multiple senses even if these inputs arrive at the system with a temporal disparity. The neural mechanisms underlying the temporal integration of multisensory stimuli are thus far not well understood.

One mechanism that is likely to be involved in temporal multisensory processing is the synchronization of the oscillatory responses of cell assemblies in the high frequency gamma range (Galambos, 1992; Gray, König, Engel, & Singer, 1989).

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Oscillatory gamma-band responses (GBRs) have been closely linked to binding and feature integration mechanisms in the auditory and in the visual modality (Engel & Singer, 2001; Gallinat, Winterer, Herrmann, & Senkowski, 2004; Herrmann, Munk, & Engel, 2004; Singer & Gray, 1995). These relationships have been reported in both animal (Konig, Engel, & Singer, 1995; Castelo-Branco, Neuenschwander, & Singer, 1998; Engel, Kreiter, Konig, & Singer, 1991) and in human studies (Bertrand & Tallon-Baudry, 2000; Herrmann, Mecklinger, & Pfeifer, 1999; Tallon-Baudry & Bertrand, 1999). Moreover, recent studies have reported an association between early high frequency gamma oscillations and integrative multisensory processing for simultaneously presented auditory and visual inputs (Sakowitz, Quian Quiroga, Schurmann, & Basar, 2001; Sakowitz, Quian Quiroga, Schurmann, & Basar, 2005; Senkowski, Talsma, Herrmann, & Woldorff, 2005; Kaiser, Hertrich, Ackermann, Mathiak, & Lutzenberger, 2005). Here we present a study in which we systematically examined SOA effects on early evoked GBRs for asynchronies of  $-125$  to  $+125$  ms between the auditory and visual components of multisensory stimulation.

The relationship between temporal processing in the unisensory-auditory modality and GBRs has previously been shown in a magnetoencephalography (MEG) study (Joliot, Ribary, & Llinas, 1994). In that study a direct correlation between GBRs and the perception of two temporally distinct unisensory-auditory stimuli was found. For short SOAs between two unisensory-auditory stimuli ( $<14$  ms) only one single gamma burst was observed, thus correlating to the subjects' reports of perceiving just one single tone. However, for longer SOAs ( $>14$  ms) where subjects identified two tones, two distinct gamma bursts were observed. The link between GBRs and temporal integration in the auditory modality suggests that GBRs might also be involved in temporal aspects of multisensory processing. Single cell recordings in the superior colliculus of cats have shown reliable multisensory interactions when auditory and visual stimuli are presented simultaneously or nearly simultaneously in time (Meredith, Nemitz, & Stein, 1987). For this reason, we expected to also find early interactions for simultaneously presented audio-visual stimuli. Since recent electrophysiological studies using event-related potentials (ERPs) have reported audio-visual interactions at early stages of cortical information processing ( $<100$  ms), we expected that possible effects of stimulus asynchrony might occur at early time latencies (e.g., Giard & Peronnet, 1999; Molholm et al., 2002; Talsma & Woldorff, 2005).

In addition to the analysis of temporal audio-visual interactions, a secondary goal of the present study was to investigate the influence of attention on multisensory temporal integration processes. We and others have recently demonstrated that selective attention can influence audio-visual neural interactions under specific circumstances (Eimer, van Velzen, & Driver, 2004; Eimer & Schroger, 1998; Talsma & Kok, 2001; Talsma & Woldorff, 2005; Senkowski et al., 2005). For example, Talsma and Woldorff (2005) and Senkowski et al. (2005) found larger multisensory integration effects in the ERPs and in the GBRs, respectively, when stimuli occurred in a selectively attended location in space. However, subjects were explicitly instructed to

direct their spatial attention to both modalities simultaneously. Thus, the contribution of attending to one specific modality during simultaneous multisensory stimulation remains to be elucidated.

## 1. Materials and methods

The experiment consisted of a behavioral prestudy and a main experiment. The prestudy was conducted to examine whether the SOAs between the auditory and visual stimulus components were experienced at the perceptual level. The focus of the main experiment was on the analysis of early multisensory interactions in the evoked GBRs as a function of the audio-visual temporal asynchrony and how such effects were modulated by attention.

### 1.1. Subjects

Twenty healthy subjects ( $25.4 \pm 3.8$  years, 10 male, 10 female) participated in the prestudy and the main experiment. All subjects were recruited through advertisements at the campus of Duke University and were compensated for participating. Two subjects were excluded from the analysis because of excessive high-frequency noise in their EEG data due to muscle activity. The remaining 18 subjects ( $25.4 \pm 4$  years, 9 male, 9 female) were included in the complete data analysis. Seventeen of these subjects were right-handed and one was left-handed. All subjects had normal or corrected-to-normal vision and gave written informed consent to participate in the study. None of the subjects reported having any history of neurological or psychiatric disorders.

### 1.2. Procedure of the prestudy

A stream of multisensory (audio-visual) stimuli with varying SOAs between the auditory and the visual components was presented at central locations directly in front of the subject. Subjects were instructed to indicate when they perceived an asynchrony in the stimulus components by pressing a button with their right index finger (the order with which auditory and visual stimuli appeared was not required to be noted). Pilot studies showed that subjects were mostly not able to detect any asynchrony in the  $\pm 125$  ms range (in both directions). Since subjects in these pilot studies perceived most of the stimuli as simultaneous, they often had a tendency to cease responding entirely. Therefore, in order to provide several contrasting conditions, multisensory stimuli with asynchronies in two additional SOA subranges that were perceptually unbound were included in the prestudy—namely, V preceding A by 275–325 ms and A preceding V by 200–250 ms). Trials were presented with inter-trial-intervals (ITIs) between 1200 and 1400 ms. For each of the seven SOA subranges, 30 trials were presented. The focus of the analyses was on the “hit” rate, which corresponded to the percentage of trials in each condition in which the subject thought they perceived an asynchrony. A repeated measure analysis of variance (ANOVA) was calculated for the hit rate using the within-subject factor ‘stimulus asynchrony’ (seven SOA subranges).

### 1.3. Procedure of the main experiment

The subjects' task in the main experiment was to attend to either the auditory or the visual stimuli ('attend auditory' or 'attend visual' conditions) in a continuous stream of randomly mixed unisensory-auditory, unisensory-visual, and multisensory audio-visual stimuli in order to detect occasional target stimuli in that modality (see target description in Section 1.5). Multisensory target stimuli could be composed of either a visual standard paired with an auditory target, or a visual target paired with an auditory standard, but could never be composed of both a visual and an auditory target.

Multisensory stimuli were presented with temporal onset asynchronies of the auditory and visual inputs ranging between  $\pm 125$  ms. Effects of SOA were investigated for five different 50 ms subranges as shown in Fig. 1. The reason for analyzing SOA subranges was to control for overlapping GBR activity (see below). For each of the five SOA subranges, a total number of 160 standard multisensory trials and 96 target multisensory trials (half of which contained a visual target, the other half an auditory target) was presented in each condition ('attend visual',

**Five 50 ms stimulus onset asynchrony subranges for visual and auditory stimuli**

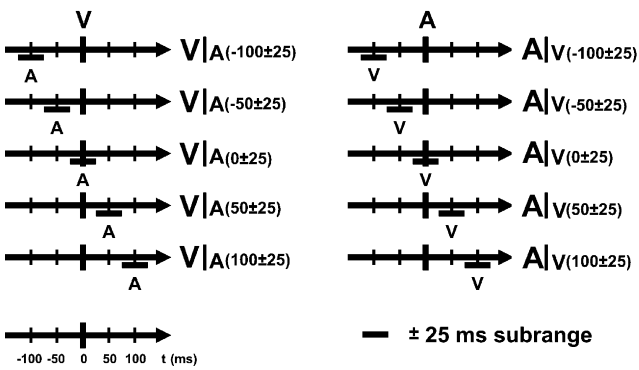


Fig. 1. Five different 50 ms stimulus onset asynchrony (SOA) subranges were investigated for visual (left side) and auditory stimuli (right side). The average SOA time of the five subranges was  $-100$ ,  $-50$ ,  $0$ ,  $50$ , and  $100$  ms. For example, for the  $V|_{A(-100\pm 25)}$  subrange, visual stimuli with a preceding auditory stimulus by  $-125$ ,  $-124$ , ...,  $76$  ms were averaged together. Thus, the auditory stimuli were jittered between  $\pm 25$  ms relative to the visual stimuli.

‘attend auditory’). In addition, included in randomized order, 160 unisensory-auditory and 160 unisensory-visual standards, and 32 unisensory-auditory and 32 unisensory-visual targets were presented in each condition. All stimuli were presented at ITIs between 500 and 800 ms (mean 650 ms) equally divided in 16 separate blocks. In addition, in each condition 400 “no stim” (i.e., omitted) trials (Busse & Woldorff, 2003; Talsma & Woldorff, 2005) were randomly inserted into the stream of stimuli, further reducing the predictability of the experimental stimuli. The two experimental conditions (‘attend visual’, ‘attend auditory’) alternated every two blocks and the starting condition was randomized over subjects. One practice block in both conditions was run prior to the experiment. The focus of the analyses was on the examination of early multisensory interactions on standard stimuli.

*1.4. Control of overlapping activity*

For the study of multisensory interactions of different stimulus asynchronies, there is an issue with overlapping activity from adjacent trials. For instance, GBRs to multisensory stimuli in which a visual input precedes the auditory by 100 ms cannot be simply compared with GBRs to multisensory stimuli in which a visual input precedes the auditory by 50 ms. This is because the overlap of activity in response to visual and to auditory inputs would differ for multisensory stimuli with different SOAs (Woldorff, 1993). To address this issue of overlapping GBR activity, trials within each of five different 50 ms SOA subranges were

**Event-related GBRs: Simulation of a 50 ms time jitter Multisensory stimuli**

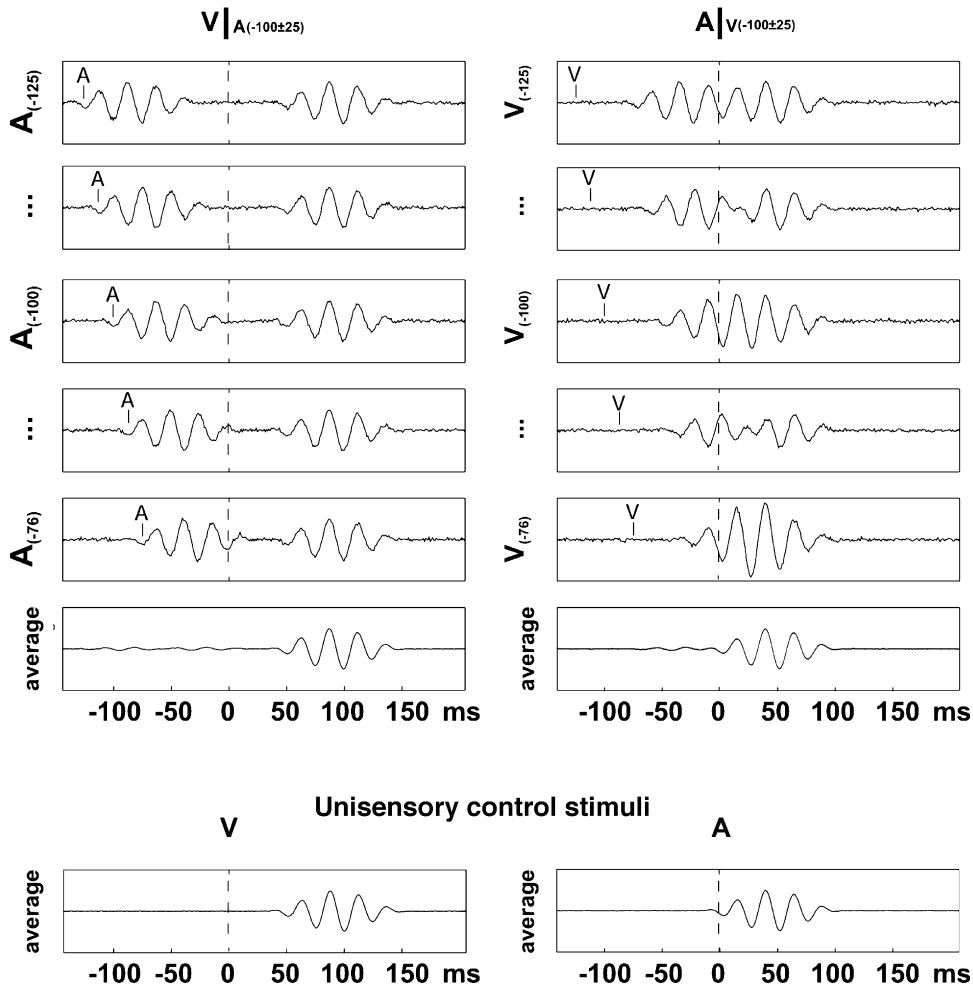


Fig. 2. Simulation of event-related GBRs for a time jitter of 50 ms. The figure illustrates the effects of averaged SOA subranges for multisensory  $A|_{V(-100\pm 25)}$  and  $V|_{A(-100\pm 25)}$  stimuli. The averaged GBRs to jittered stimuli are very similar to the mean response of the unisensory control stimuli, confirming that a main part of overlapping event-related GBR activity is cancelled out during averaging when multisensory stimuli with a relative time jitter of 50 ms in one modality are averaged.

averaged (Fig. 1). For example, all the trials where a visual stimulus preceded the auditory by  $100 \pm 25$  ms (i.e., the visual stimulus preceded the auditory by SOAs ranging from 125 to 75 ms) were averaged together. For temporally proximal stimuli such as these, Woldorff (1993) suggested that a jitter of at least the period of the frequencies of overlap will be effective at canceling out most of that overlapping activity. Thus, a jitter of  $\pm 25$  or 50 ms (e.g., two times the 25 ms period of a 40 Hz oscillation) should lead to an effective cancellation of the overlapping GBRs during time-locked averaging. Indeed, for activity at right around 40 Hz, a jitter of 50 ms (and thus exactly twice the period of the frequency of the overlapping activity), the cancellation would be expected to be essentially complete. Fig. 2 shows a simulation of a  $\pm 25$  ms time jitter for a typical activity pattern of event-related oscillatory GBRs that has been reported before (Gallinat et al., 2004; Senkowski & Herrmann, 2002). The figure illustrates that overlapping event-related oscillatory GBRs are almost completely cancelled out during time locked averaging when stimuli were jittered within a  $\pm 25$  ms time window.

### 1.5. Stimuli

Visual standard stimuli in the prestudy and in the main experiment consisted of white horizontal gratings which were presented on a black background ( $5.4^\circ \times 4.8^\circ$  visual angle) with a duration of 100 ms (Fig. 3, left panel). Visual target stimuli in the main experiment were highly similar to standards, but the intensity of the stimulus (contrast between the gratings) was reduced for 33 ms midway through the stimulus presentation. Auditory standards in the prestudy and in the main experiment consisted of 1600 Hz sinusoidal tones, which were presented at a sound pressure level of 65 dB and with a duration of 100 ms (10 ms linear rise and fall times). The auditory targets in the main experiment were similar to the standards, but were reduced in amplitude for 33 ms midway through the presentation, analogous to the defining feature for the visual targets.

### 1.6. Control of task difficulty

To balance the target-discrimination task difficulty over subjects and conditions, the stimulus discrimination threshold for each subject was measured prior to the main experiment. This was done in a unisensory-visual and a unisensory-auditory discrimination task. For the auditory stimuli, participants were presented randomly (50% probability) either a standard or a target tone (i.e., with or without the mid-duration intensity dip) and were instructed to indicate whether the stimulus was a standard or a target. The required accuracy was set to 90% correct trials for both modalities. If a subject's accuracy fell below this criterion, task difficulty was decreased by decreasing the intensity level of the mid-duration amplitude dip of the target stimuli. If a subject's accuracy was above 90%, task difficulty was increased by increasing the intensity level of the mid-duration dip of the targets towards the level of the rest of the stimulus. In order to keep the difficulty constant during the experimental task, the intensity of the mid-duration amplitude dip was also adapted between blocks when the performance had changed substantially over the previous several blocks. An analogous procedure was performed for visual targets.

### 1.7. Data acquisition

EEG and behavioral data were recorded in a sound attenuated, electrically shielded chamber. Stimulus presentation was controlled using the "Presentation" software package (Neurobehavioral Systems). EEG was recorded using 64 channels (Fig. 3, right panel) mounted at equi-spaced positions in a customized configured electrocap (Electrocap International) and referenced to the right mastoid during recording. Horizontal eye movements were monitored by two electrodes at the outer canthi of the eyes referenced to each other. Vertical eye movements and eye blinks were recorded by electrodes placed below the orbital ridge of each eye, relative to electrodes at frontopolar sites (Fp1, Fp2). Impedances were kept below 10 k $\Omega$  for the eye electrodes, 2 k $\Omega$  for the mastoid and ground electrodes, and 5 k $\Omega$  for all other electrodes. The EEG was recorded using a NeuroScan (SynAmps) acquisition system with a sampling rate of 500 Hz and analog-filtered with a 0.01 Hz high-pass and 100 Hz low-pass filter. To suppress high frequency line noise, the EEG data were filtered off-line

with a 60 Hz notch filter ( $-3$  dB points at 57.7 and 62.3 Hz). All EEG channels were re-referenced to the algebraic average of the two mastoid electrodes. Data were epoched separately for each stimulus type, SOA range, and experimental condition. The epochs lasted from 200 ms before stimulus onset to 500 ms after stimulus onset. Artifact rejection was accomplished by automatically excluding from averaging any trials in which the standard deviation within a moving 200 ms time interval exceeded 30  $\mu$ V in any one of the channels between 200 ms before stimulus onset to 500 ms after stimulus onset. Finally, all trials were visually inspected and rejected if electrode drifts, eye-movement drifts, muscle artifacts were visible.

### 1.8. Wavelet transform

Evoked<sup>1</sup> GBRs were analyzed via Morlet wavelet transforms (see e.g. Herrmann et al., 1999 or Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996), i.e. the ERP signals were convolved with complex Morlet wavelets,  $w(t, f_0) = A \exp(i2\pi f_0 t) \exp(-t^2/2\sigma_t)$  having a Gaussian shape both in the time domain (S.D.  $\sigma_t$ ) as well as in the frequency domain (S.D.  $\sigma_f = (2\pi\sigma_t)^{-1}$ ) around the wavelet's central frequency  $f_0$ . The main advantage of the wavelet transform compared with the classical fast Fourier transform (FFT) is that the wavelet transform reveals information about the temporal dynamics of oscillatory responses. Thus, it is possible to more closely pinpoint the temporal appearance of oscillatory responses. In addition, recent observations have indicated that, for some experimental manipulations, oscillatory responses may be even more sensitive than the broad-band event-related potentials (ERP) (Busch, Schadow, Frund, & Herrmann, 2006; Herrmann & Mecklinger, 2001; Senkowski & Herrmann, 2002; Senkowski et al., 2005). Here we applied wavelets with a constant ratio  $f_0/\sigma_f = 2\pi$ , which corresponds to a temporal wavelet duration ( $2\sigma_t = 2/f_0$ ) of two cycles at the wavelet's center frequency  $f_0$ , and a frequency bandwidth of  $2\sigma_f = f_0/\pi$ . As a measure of gamma-band activity, the modulus of the complex transform coefficients was computed. The frequency-dependent normalization factor was  $A = f_0(2/\pi)^{1/2}$ , which allows the transform modulus of an analyzed time-frequency component to be directly compared to the amplitude of the corresponding signal modulation in the time domain. For the generation of time-frequency representations of gamma-band ERPs, wavelet center frequencies were uniformly distributed on a logarithmic scale, with 13 frequencies per octave, between 20 and 80 Hz. For each wavelet scale, the mean activity over a baseline interval between 150 and 50 ms prior to stimulation was computed and subtracted from pre- and post-stimulus activity in order to compensate for unrelated background activity.

### 1.9. Statistical analysis

For the analysis of evoked GBRs, time-frequency planes were plotted for one central anterior channel and one central posterior channel to estimate the frequency with the highest amplitudes in the gamma range (30–80 Hz). Based on these plots (see Fig. 5), evoked GBRs were analyzed at a center frequency of  $f_0 = 40$  Hz for auditory GBRs (since the highest auditory GBRs were found

<sup>1</sup> Notice that some other studies have also focused on the examination of the induced gamma responses (e.g., Gonzalez Andino, Michel, Thut, Landis, & Grave de Peralta, 2005; Gruber, Trujillo-Barreto, Giabbiconi, Valdes-Sosa, & Muller (2006); Kaiser & Lutzenberger, 2003; Muller, Gruber, & Keil, 2000). Induced and evoked oscillatory activity differ in that the former does not have to be strictly phase and time locked to the onset of each trial, whereas the latter is strictly phase and time locked to the onset of each stimulus. Here we focused on the analysis of evoked responses since the relative time jitter of 50 ms between the inputs of the two modalities leads to an effective cancellation of the evoked but not the induced responses of the other modality. The reason for this is that evoked responses are calculated by wavelet transforming the average response over all EEG epochs (i.e., the ERP), whereas the induced responses are calculated by wavelet transforming single trials before averaging the (non-negative) wavelet activations. As illustrated in Fig. 1, evoked gamma oscillations that are presented with a relative time jitter of 50 ms across trials effectively cancel out in the average. These oscillations would not cancel out if wavelet activities of single trials were averaged, i.e., if the induced responses were calculated.

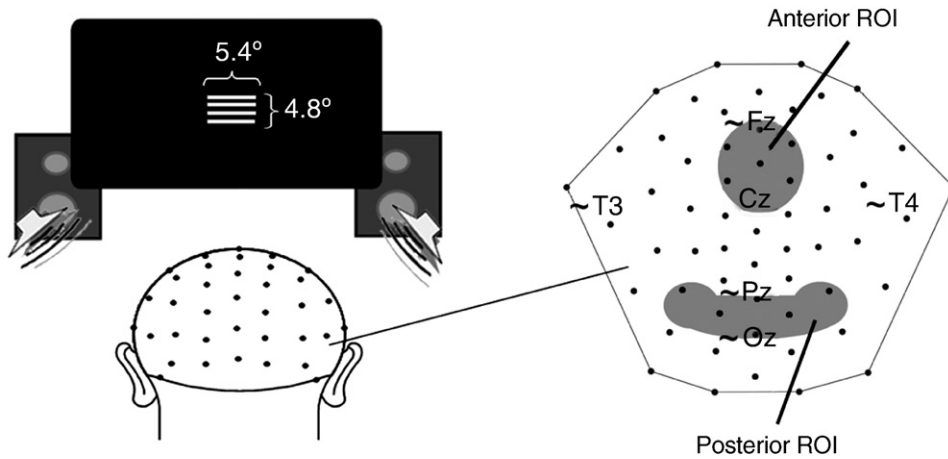


Fig. 3. Left panel: Outline of the experimental setup. Subjects were instructed to detect occasional auditory or visual target stimuli. All stimuli were presented centrally as shown on the figure. Right panel: Topographical map of the 64 EEG channels. One anterior ROI was analyzed for GBRs triggered to auditory inputs and one posterior ROI was analyzed for GBRs triggered to visual inputs.

around 40 Hz) and at a center frequency of  $f_0 = 30$  Hz for visual GBRs (since the highest visual GBRs were found around 30 Hz). The durations ( $2\sigma_t$ ) of the 40 and 30 Hz wavelets were 50 and 67 ms with spectral bandwidth ( $2\sigma_f$ ) of 12.73 and 9.54 Hz, respectively.

Evoked GBRs of auditory and visual inputs were calculated in the ‘attend visual’ and ‘attend auditory’ conditions for the unisensory control stimuli and for five SOA subranges of multisensory stimuli (SOA:  $-100 \pm 25$ ,  $-50 \pm 25$ ,  $0 \pm 25$ ,  $50 \pm 25$ ,  $100 \pm 25$ , see Fig. 1). Multiple repeated measures ANOVAs were implemented to assess statistical effects.

To avoid a loss of power that is inherent when multiple repeated measures ANOVAs are used, the analysis of visual GBRs was focused on the analyses of gamma activity at a posterior region of interest (ROI) that correspond to visual GBRs that have been previously described (Herrmann & Mecklinger, 2001; Senkowski & Herrmann, 2002). This ROI comprises six electrodes that are located over occipito-parietal brain regions typically covered by electrodes at the Oz and Pz scalp sites (Fig. 3, right panel). Since evoked visual GBRs are usually found after about 100 ms (Busch, Debener, Kranczioch, Engel, & Herrmann, 2004), a time window between 60 and 120 ms was chosen for the analysis of posterior visual GBRs.

The examination of GBRs to auditory inputs was focused on the analysis of one anterior ROI that comprises a symmetrically arranged cluster of seven scalp sites spanning a region typically covered by electrodes at the Fz and Cz scalp sites. Previous studies have shown that anterior event-related auditory GBRs occur with an onset response peaking around 40–50 ms after stimulus onset (Tiitinen et al., 1993; Tiitinen, Sinkkonen, May, & Naatanen, 1994). For this reason, anterior GBRs were analyzed in a post-stimulus time window between 30 and 80 ms.

Repeated measures ANOVAs were calculated using the within-subject factors ‘stimulus onset asynchrony’ (five SOA subranges and unisensory-visual or unisensory-auditory control stimuli) and ‘attention’ (attend visual or attend auditory condition) as independent variables. This was done separately for visual and auditory inputs. The mean GBR amplitude within the specified time windows served as the dependent variable. When these ANOVAs revealed a significant effect of the factor ‘SOA’, further ANOVAs were performed to compare GBRs of the five SOA subranges with unisensory control stimuli separately.

## 2. Results

### 2.1. Behavioral prestudy

The results of the prestudy are shown in Fig. 4. An ANOVA using hit rate as the dependent variable and ‘stimulus onset asynchrony’ as a within-subjects factor demonstrated that hit

rates differed between the seven SOA subranges of the prestudy ( $F(6,12) = 82.68$ ,  $p < 0.001$ ). The detection rate of the audio-visual stimulus asynchrony (i.e., the detection that the stimulus components were not synchronous) was high for the two longer SOA time intervals (48% if visual stimuli preceded auditory by  $300 \pm 25$  ms and 64% if auditory stimuli preceded visual by  $225 \pm 25$  ms) relative to the detection rate for the five SOA subranges that were used in the main experimental task (all subranges  $< 17\%$ , four subranges  $< 5\%$ ). This suggests that the stimuli that were used in the main experimental task (i.e., SOAs up to  $\pm 125$  ms) were mostly perceived as simultaneous. However, the detection rate for the  $V|_{A(-100 \pm 25)}$  stimuli (16%) was somewhat higher than the detection rate of the four other stimulus asynchrony windows presented in the main study ( $< 5\%$ ). Further comparisons between  $V|_{A(-100 \pm 25)}$  stimuli with the four other SOAs used in the main experiment revealed a significantly higher detection rate for  $V|_{A(-100 \pm 25)}$  stimuli compared to all other SOAs (all comparisons revealed  $p$  values  $< 0.01$ ). This indicates that this range may have been at, or just under, the perceptual threshold, and that subjects may sometimes have perceived the asynchrony of these stimuli.

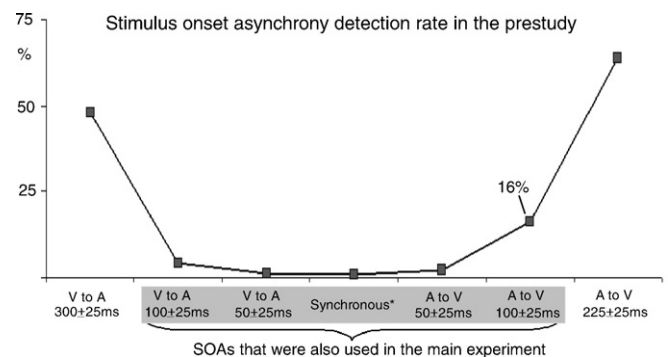


Fig. 4. Detection rate in the behavioral prestudy. Notice the enhanced detection rate if auditory stimuli preceded visual stimuli by  $100 \pm 25$  ms compared to the four other SOA time windows used in the main experiment.

## 2.2. Behavioral data in the main experiment

Repeated measures ANOVAs were performed using the within-subjects factors ‘attention’ (‘attend visual’ and ‘attend auditory’) and ‘SOA’ (six levels consisting of five SOA sub-ranges and either unisensory-visual or unisensory-visual control stimuli). The ANOVA for RTs revealed a significant main effect of ‘attention’ ( $F(1,17)=7.358, p<0.015$ ), indicating faster RTs in the ‘attend visual’ (mean = 483 ms) as compared to the ‘attend auditory’ condition (mean = 500 ms). Moreover, a significant effect of the factor ‘SOA’ was found ( $F(5,13)=3.747, p<0.025$ ). The effects of the ‘SOA’ factor are described below in more detail. No significant interaction between ‘attention’  $\times$  ‘SOA’ was observed. The ANOVA for hit rates revealed a significant effect of the factor ‘SOA’ ( $F(5,13)=3.855, p<0.023$ ), but no effects of the factor ‘attention’ or interaction between ‘attention’  $\times$  ‘SOA’. Repeated measures ANOVAs were performed separately for the ‘attend auditory’ and the ‘attend visual’ condition to further explore the behavioral effects of ‘SOA’.

For RTs of visual stimuli in the ‘attend visual’ condition a significant effect of ‘SOA’ was found ( $F(5,13)=2.86, p<0.02$ ). Separate ANOVAs between RTs to unisensory-visual stimuli (472 ms) with each of the five SOA sub-ranges of multisensory stimuli revealed significantly longer RTs for  $V|_{A(-50\pm 25)}$  (481 ms,  $F(1,17)=7.34, p<0.015$ ,

$V|_{A(0\pm 25)}$  (484 ms,  $F(1,17)=16.66, p<0.001$ ),  $V|_{A(50\pm 25)}$  (488 ms,  $F(1,17)=10.5, p<0.005$ ), and  $V|_{A(100\pm 25)}$  (487 ms,  $F(1,17)=7.95, p<0.012$ ). The differences between RTs to unisensory-visual stimuli and  $V|_{A(-100\pm 25)}$  stimuli approached a trend toward longer RTs (481 ms,  $F(1,17)=2.75, p=0.12$ ). The finding of longer RTs to multisensory stimuli compared to unisensory-visual control stimuli suggests that auditory standards interfered with visual target processing during multisensory stimulation.

The ANOVA for target hit rates in the ‘attend visual’ condition also yielded a significant effect of ‘SOA’ ( $F(5,13)=7.38, p<0.003$ ). Subsequent ANOVAs between the hit rate of unisensory-visual control stimuli (89%) with each hit rate of the five SOA sub-ranges of multisensory stimuli revealed a lower hit rate only when auditory and visual stimuli were presented simultaneously ( $V|_{A(0\pm 25)}=85\%, F(1,17)=5.57, p<0.03$ ). This suggests that the presentation of a non-task-relevant auditory standard stimulus interfered with visual target processing when auditory and visual stimuli were presented simultaneously.

The ANOVAs for the RTs to the auditory targets did not reveal any significant effects. However, for the hit rates a significant effect of the ‘SOA’ factor was observed ( $F(5,13)=2.75, p<0.025$ ). Compared to unisensory-auditory targets (91%), the hit rate was reduced for  $A|_{V(-50\pm 25)}$  (86%,  $F(1,17)=8.38, p<0.01$ ),  $A|_{V(0\pm 25)}$  (86%,  $F(1,17)=5.04, p<0.038$ ), and for

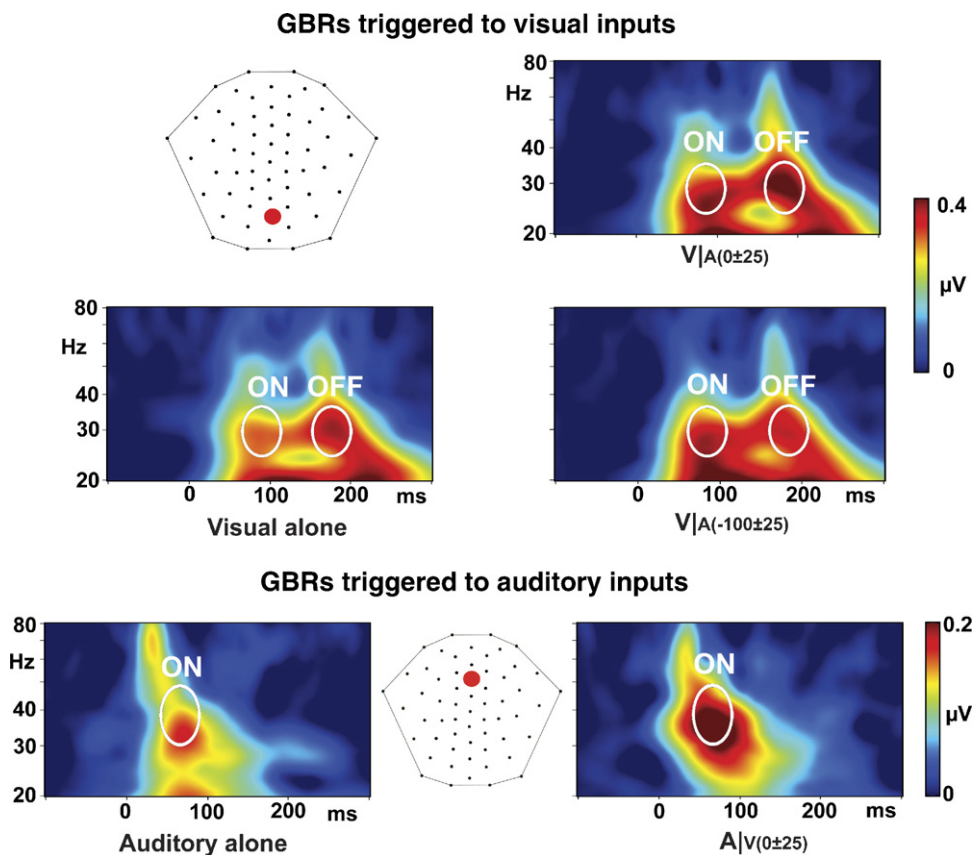


Fig. 5. Time–frequency plots of evoked gamma responses triggered to visual inputs (upper panel) and auditory inputs (lower panel). Upper panel: enhanced ON responses were found at occipital scalp sites for  $V|_{A(0\pm 25)}$  and  $V|_{A(-100\pm 25)}$  stimuli compared to visual alone stimuli (electrode site is marked with a red dot). Lower panel: for medial-frontal GBRs triggered to auditory inputs enhanced responses were observed for  $A|_{V(0\pm 25)}$  stimuli as compared to auditory alone stimuli.

$A|_{V(100\pm 25)}$  stimuli (86%,  $F(1,17)=4.61$ ,  $p<0.046$ ). This suggests that visual standards also interfered with auditory target processing during multisensory stimulation.

### 2.3. Time–frequency representations of evoked gamma responses

Fig. 5 shows time–frequency plots of GBRs triggered to visual inputs (upper panel) and to auditory inputs (lower panel), collapsed over the two attention conditions. The expected time and frequency of all responses were marked graphically in the figures for better understanding of auditory and visual gamma responses. Visual stimuli resulted in clear onset (ON) and offset (OFF) responses. The onset response peaked around 90 ms after stimulus presentation at a frequency around 30 Hz. The offset response peaked around 190 ms (i.e., 90 ms after the end of the stimulus presentation) at about the same frequency. For this reason, the statistical analysis of visual GBRs was performed for 30 Hz Morlet wavelet transformed data. Fig. 5 suggests enhanced anterior onset GBRs to  $V|_{A(0\pm 25)}$  and  $V|_{A(-100\pm 25)}$  stimuli compared to unisensory-visual control stimuli. GBRs triggered to auditory inputs showed only an onset response peaking about 50 ms after stimulus onset with a frequency around 40 Hz over medial-frontal brain regions. Fig. 5 indicates enhanced frontal GBRs to  $A|_{V(0\pm 25)}$  as compared to unisensory-auditory control stimuli. Thus, for the statistical analysis of evoked auditory GBRs a 40 Hz wavelet transform was calculated.

Since a 30 Hz wavelet transform was performed for visual stimuli, it might be that these oscillatory responses did not completely cancel out when a  $\pm 25$  ms (i.e., 50 ms—twice the

length of a 40 Hz oscillation) jitter was used (see Woldorff, 1993). To assess whether the 50 ms jitter did not adequately eliminate the overlapping 30 Hz GBRs, additional analysis was performed in which a random time shift between  $\pm 25$  ms was given for each unisensory-visual trial prior to the computation of the evoked 30 Hz response. The result of this simulated combination of jittered unisensory trials was analyzed for its residual gamma activity in ANOVAs comparing the posterior event-related 30 Hz activity in the baseline interval ( $-150$  to  $-50$  ms) with post-stimulus 30 Hz activity (50 to 150 ms). This was done separately for the ‘attend visual’ and the ‘attend auditory’ condition. The ANOVAs revealed no significant differences between baseline and jittered post-stimulus 30 Hz responses, indicating that a  $\pm 25$  ms time jitter effectively eliminated overlapping GBR activity in the frequency ranges used in the present analyses.

### 2.4. Stimulus asynchrony and attention effects on GBRs

#### 2.4.1. Visual stimuli

An ANOVA using the within-subject factors ‘attention’ (‘attend visual’, ‘attend auditory’) and ‘SOA’ (five SOA sub-ranges and unisensory control stimuli) was performed for posterior visual GBRs. This ANOVA did not reveal a significant main effect of the factor ‘attention’ ( $F(1,17)=0.3$ ,  $p=0.59$ ). Moreover, the interaction between ‘attention’  $\times$  ‘SOA’ did not approach significance ( $F(5,85)=1.74$ ,  $p=0.14$ ), indicating that modality-specific attention did not significantly influence early cortical processing as reflected in the evoked visual GBRs. For this reason, visual stimuli of the ‘attend visual’ and the ‘attend auditory’ condition were combined in the following analysis of SOA effects on visual stimuli.

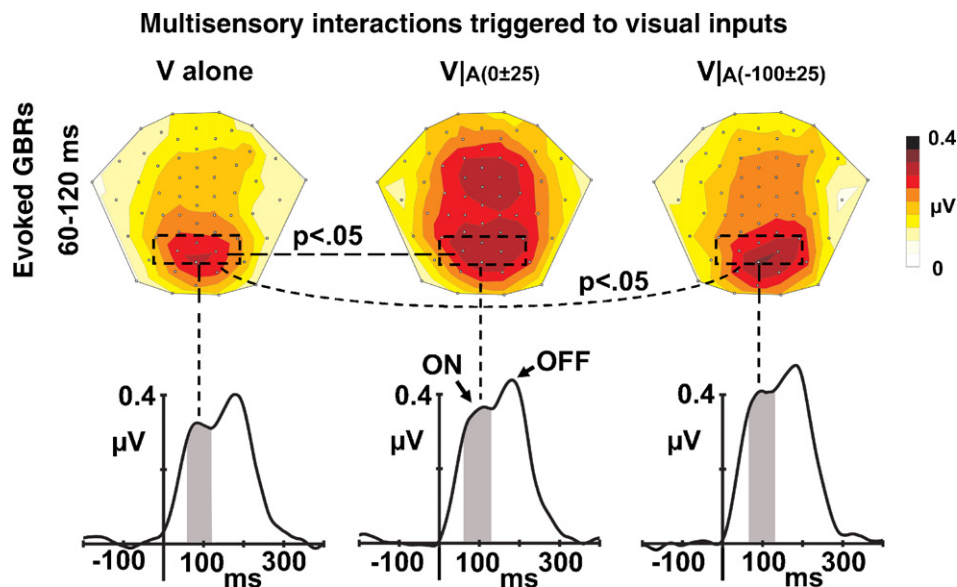


Fig. 6. Topographical maps (60–120 ms) and waveform traces of wavelet transformed evoked GBRs to visual alone,  $V|_{A(0\pm 25)}$ , and  $V|_{A(-100\pm 25)}$  stimuli. GBR peaked about 90 and 190 ms after stimulus onset over occipital brain areas. The first peak reflects the onset response (ON) to the visual input while the second peak reflects the offset response (OFF) of the visual input (stimulus duration was 100 ms). The statistical analysis was focused on early onset responses only. The time window for the statistical analysis is highlighted in gray. GBRs were significantly enhanced for  $V|_{A(0\pm 25)}$  and  $V|_{A(-100\pm 25)}$  stimuli as compared to visual alone stimuli ( $p<0.05$ ), demonstrating multisensory interactions triggered to visual inputs for  $V|_{A(0\pm 25)}$  and  $V|_{A(-100\pm 25)}$  stimuli.

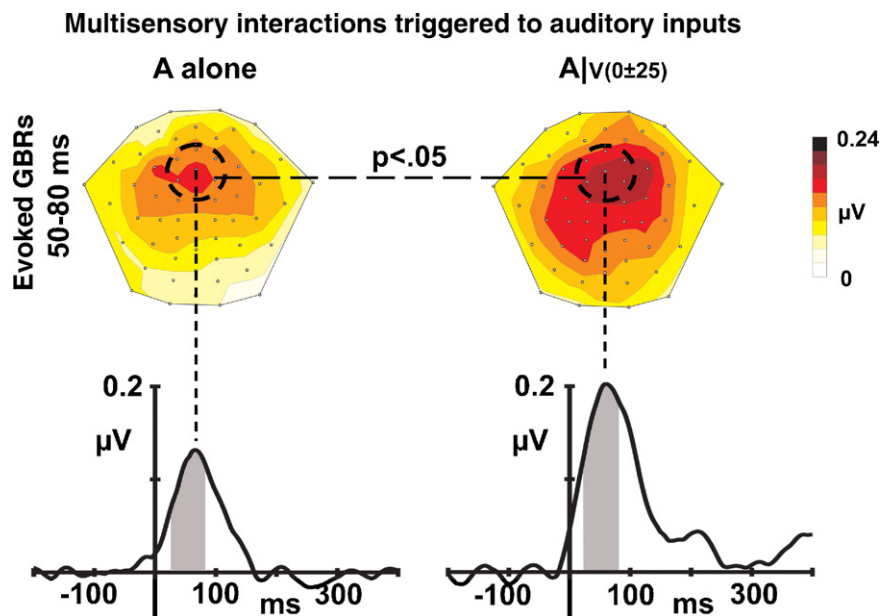


Fig. 7. Topographical maps (50–80 ms) and waveform traces of wavelet transformed evoked GBRs to Aalone and  $A|V(0\pm 25)$  stimuli. Enhanced medial-frontal GBRs were found for  $A|V(0\pm 25)$  as compared to  $A|V(0\pm 25)$  in a time window between 30 and 80 ms (highlighted in gray).

The analysis of the visual-component GBRs collapsed across the two attention conditions revealed a significant main effect of ‘SOA’ ( $F(5,85)=2.8$ ,  $p<0.022$ ). For this reason, separate ANOVAs between unisensory-visual control stimuli and visual inputs of the five different stimulus asynchrony time ranges of multisensory stimuli were performed. Enhanced posterior visual GBRs were observed when auditory and visual stimuli were presented in the most synchronous ‘SOA’ subrange ( $V|A(0\pm 25)=0.33\ \mu\text{V}$ ) compared to unisensory-visual stimuli ( $0.27\ \mu\text{V}$ ,  $F(1,17)=5.47$ ,  $p<0.032$ ) (Fig. 6). In addition, visual GBRs were enhanced when an auditory stimulus preceded the visual by  $100\pm 25$  ms ( $V|A(-100\pm 25)=0.34\ \mu\text{V}$ ) compared to unisensory-visual stimuli ( $F(1,17)=7.3$ ,  $p<0.015$ ). No other significant effects were found for the visual GBRs.

#### 2.4.2. Auditory stimuli

The analyses of the medial-frontal auditory GBRs did not reveal a significant main effect of the factor ‘attention’ ( $F(1,17)=1.72$ ,  $p=0.21$ ) and no significant interaction of ‘attention’  $\times$  ‘SOA’ ( $F(5,85)=0.74$ ,  $p=0.6$ ). This indicates that modality-specific attention did not significantly influence early multisensory processing in the auditory GBRs. In the further analysis of stimulus asynchrony effects, auditory GBRs from the ‘attend visual’ and the ‘attend auditory’ condition were therefore combined.

For the collapsed auditory-component GBRs a main effect of the factor ‘SOA’ was observed, ( $F(5,85)=2.72$ ,  $p<0.025$ ). Further comparisons of auditory GBRs in the context of multisensory stimulation with unisensory control stimuli were performed. In these comparisons enhanced auditory GBRs were found when auditory stimuli were presented the most synchronously with the visual stimuli ( $A|V(0\pm 25)=0.17\ \mu\text{V}$ ) compared to auditory control stimuli ( $0.11\ \mu\text{V}$ ,  $F(1,17)=8.04$ ,  $p<0.014$ ) (Fig. 7). No other significant effects were found.

### 3. Discussion

In this study we present evidence for a highly time-sensitive multisensory network in early cortical audio-visual processing. Using a new electrophysiological analysis strategy for oscillatory responses, we were able to control for overlapping activity from adjacent stimuli, and thus to directly compare integration effects on multisensory inputs with different stimulus asynchronies.

#### 3.1. Effects of stimulus asynchrony on early audio-visual processing

Robust multisensory interactions on auditory and visual stimuli were found for simultaneously presented audio-visual stimuli. These interactions are reminiscent of similar effects on audio-visual stimuli that have been reported before in the superior colliculus using animal single cell recordings (Meredith et al., 1987). In that study, neuronal responses in SC were recorded from anaesthetized cats for different stimulus asynchronies of auditory and visual stimuli. The authors reported reliable response enhancements in SC when auditory and visual inputs are presented in exact or in near temporal synchrony, which parallels the present observation of robust cortical interactions for simultaneously presented audio-visual inputs in human subjects.

The effects elicited by simultaneously presented audio-visual stimuli were observed over both medial-frontal and occipital brain regions. The observation that visual GBR effects were focused over occipital regions could reflect that they include activity derived from visual cortical regions. In contrast, the auditory GBR effects were observed to be mainly over frontal and fronto-central scalp regions, which could reflect that they include activity from auditory cortical areas on the superior



temporal plane (Pantev et al., 1991). Future studies will be necessary to better specify the neural generators underlying these scalp-recorded effects.

The interactions triggered by auditory inputs were found between 30 and 80 ms after stimulus onset over medial-frontal brain regions, while the interactions triggered by visual inputs were observed over occipital regions in a time range between 60 and 120 ms. The early medial-frontal multisensory interactions in response to auditory inputs in the present study had a somewhat shorter latency than the frontally distributed audio-visual activations that have been reported previously using ERPs (Giard & Peronnet, 1999; Talsma & Woldorff, 2005), but are reminiscent of an anterior gamma-band modulation by spatial selective attention we have observed before (Senkowski et al., 2005). Such early multisensory interactions over medial-frontal brain regions are remarkable because the earliest visual ERP component (C1), which is likely to be generated in striate visual cortex, has an onset latency of about 50–60 ms (Foxe & Simpson, 2002; Gomez Gonzalez, Clark, Fan, Luck, & Hillyard, 1994; Murray, Foxe, Higgins, Javitt, & Schroeder, 2001). This suggests that multisensory audio-visual interactions can appear almost instantly after the initial cortical processing of visual inputs. Schroeder, Foxe, and colleagues have recently presented a model that could explain such early multisensory interactions in the brain (Fuxe & Schroeder, 2005; Schroeder & Foxe, 2002, 2005; Schroeder et al., 2003). The model proposes very rapid feed-back feed-forward processing mechanisms between different sensory modalities. Evidence for this model stems from investigations on the laminar profile and the timing of sensory inputs in several of the primate neocortical areas in which multisensory convergence occurs. The finding of early integration effects to simultaneously presented audio-visual stimuli is also in line with some recent reports of early multisensory interactions in ERPs (Fort, Delpuech, Pernier, & Giard, 2002; Giard & Peronnet, 1999; Molholm et al., 2002; Molholm, Ritter, Javitt, & Foxe, 2004; Talsma & Woldorff, 2005) and in high frequency oscillatory beta and gamma responses (Senkowski et al., 2005; Senkowski, Molholm, Gomez-Ramirez, & Foxe, *in press*).

In addition to the multisensory interactions on simultaneously presented audio-visual stimuli, we observed robust interactions over occipital brain areas when an auditory stimulus preceded a visual stimulus by  $100 \pm 25$  ms (i.e.,  $V|_{A(-100 \pm 25)}$ ). Interestingly, the results of the behavioral prestudy showed differences on the perceptual level for  $V|_{A(-100 \pm 25)}$  stimuli compared to the other SOA time windows. Subjects detected more asynchronies for  $V|_{A(-100 \pm 25)}$  stimuli than for the other four SOAs time windows that were used in the main experiment. This result suggests that the multisensory interactions on the GBRs for  $V|_{A(-100 \pm 25)}$  stimuli might be related to differences at the perceptual level. This interpretation is consistent with behavioral studies that have revealed lower scores for subjective synchrony when an auditory stimulus preceded a visual by 50–100 ms as compared to when a visual stimulus preceded an auditory by 50–100 ms (Lewald & Guski, 2003; Slutsky & Recanzone, 2001). Moreover, Meredith et al. (1987) have reported that multisensory interactions were often of greatest magnitude for onset disparities between auditory and visual inputs of 100 ms (including

stimuli in which auditory preceded visual inputs). However, we did not observe multisensory interactions when visual stimuli preceded auditory by 50 ms or more, as it has been described in some previous behavioral studies (Lewald & Guski, 2003; Slutsky & Recanzone, 2001). It might be that possible interaction effects for these stimulus asynchronies can be found in lower frequency ranges. The present study did not control for overlapping activity of slower frequency ranges. Future studies with the appropriate controls could address whether longer latency processing in lower frequency ranges or in broad-band ERPs may be linked to the previously reported effects on multisensory stimuli when a visual input precedes an auditory by about 100 ms.

### 3.2. *Effects of attention on early audio-visual processing*

We did not observe significant effects of our attentional manipulation on auditory or visual GBRs. This observation might seem to somewhat contradict our previous studies in which we found spatial selective attention effects on audio-visual GBRs (Senkowski et al., 2005) and on audio-visual ERPs (Talsma & Woldorff, 2005). However, in these other studies both modalities were attended in parallel, and comparisons were made between the multisensory interactions for stimuli occurring in an attended region of space versus those occurring in an unattended region of space. In the present study, the subjects were instructed to focus their attention to only one specific modality, and all stimuli were presented in an attended region of space. Some previous studies have implicated a supramodal spatial attention mechanism in which all stimuli in an attended region of space receive enhanced processing (relative to stimuli occurring elsewhere), regardless of which modality is attended (Driver & Spence, 1998; Eimer & Schroger, 1998; Talsma & Kok, 2002). Thus, the effects of modality-specific attention on the multisensory integration processes might have been mitigated in the present experiment because all the stimuli occurred in an attended region of space during both attention conditions, thereby automatically receiving enhanced processing regardless of which modality was attended. These results thus also differ from those recently reported by Busse, Roberts, Crist, Weissman, and Woldorff, 2005, in which spatial attention to visual stimuli occurring in one location in space can spread to encompass (at long latencies) synchronously occurring auditory stimuli arising from a different spatial location. In addition, there is also a debate as to whether non-spatial attention modulates early event-related gamma responses even to unisensory stimulation. Some studies have reported attention effects on auditory (Debener, Herrmann, Kranczioch, Gembris, & Engel, 2003; Yordanova et al., 2000) or visual (Fell, Fernandez, Klaver, Elger, & Fries, 2003; Herrmann et al., 1999) GBRs, whereas others have not (Karakas & Basar, 1998; Tallon-Baudry et al., 1996). The present data would be consistent with the latter observation that non-spatial attention does not have much influence on early GBRs.

A somewhat surprising finding in our study were longer RTs in the ‘attend auditory’ as compared to the ‘attend visual’ condition. Various studies have reported shorter RTs for auditory

as compared to visual stimuli (Fort et al., 2002; Molholm et al., 2002; Talsma & Woldorff, 2005), which can generally be attributed to a faster processing of sensory information in the auditory system than in the visual system. Although we controlled for factors such as arousal by keeping the error rate between the two conditions approximately equal, we found longer RTs in the ‘attend auditory’ condition than in the ‘attend visual’ condition. The longer RTs may indicate that the auditory discrimination task was more demanding than the visual discrimination task. Similarly, Miller (1991) found longer RTs to auditory targets as compared to visual targets of multisensory audio-visual stimuli without reporting differences in error rates between the auditory and the visual discrimination task.

#### 4. Conclusions

The present study demonstrates that early audio-visual multisensory processing is highly sensitive to the relative onset timing of the auditory and visual component inputs. One of the main findings is the observation that multisensory interactions are reflected in evoked gamma responses over medial-frontal (30–80 ms) and occipital (60–120 ms) brain areas for simultaneously presented auditory and visual inputs. A second effect of stimulus asynchrony, one which might reflect changes on the perceptual level of the detection of an asynchrony, was observed over occipital brain areas when auditory stimuli preceded visual by 100 ms. Our overarching conclusion is that the precision of the relative timing of auditory and visual components of a multisensory stimulus can affect early cross-modal processing interactions.

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