Attention is often illustrated by the metaphor of an internal spotlight, a mechanism that enables an organism to select and preferentially process behaviorally relevant input. Brain-imaging studies in humans (see Herrmann & Knight, 2001; Hillyard, Vogel, & Hillyard, 2007; Giard, Fort, Mouchetant-Rostaing, & Pernier, 2000; Hillyard, Xiang, Shamma, & Simon, 2009; Fritz, Elhilali, David, & Shamma, 2005) have demonstrated that attending to a stimulus, can cause a suppression of activity in other frontal and auditory-cortical channels to independently address attentional effects on low-level sensory input inhibition involves early selection. We identified a sequence of early (<200 ms post-onset) auditory cortical effects, comprised of onset response attenuation and the emergence of an inhibitory response, and provide new, direct evidence that listeners actively ignoring a sound can reduce their behavioral objectives.

Studies in all sensory modalities have demonstrated amplification of early brain responses to attended stimuli, but less is known about the processes by which listeners selectively ignore responses to non-attended stimuli, or both. A number of brain-imaging (e.g. Alain & Woods, 1994; Bidet-Caulet et al., 2007; Hillyard et al., 1993; Näätänen, 1992; Snyder, Alain, & Picton, 2006; Teder-Salejarvi, 1980, 1992) and psychophysical studies of auditory selective attention, brain responses to attended sounds usually show increased amplitudes relative to responses to the same sounds when they are not attended (e.g. Alain & Woods, 1994; Bidet-Caulet et al., 2007; Hillyard et al., 1993; Näätänen, 1992; Snyder, Alain, & Picton, 2006; Teder-Salejarvi, 1980, 1992). However, when the scene is busy (e.g.Lavie, 2005). Indeed, increased activity is attention-grabbing and hinders the organism's ability to concentrate on task-relevant features (e.g.Ipata, Gee, Gottlieb, Bisley, & Goldberg, 2006; Melara, Rao, & Tong, 2002).

Another aspect of attention is the ability to actively ignore irrelevant or distracting stimuli. Ignoring may be viewed as a direct side effect of attending, caused by limited immediate processing resources (e.g.Hink, Schwent, & Picton, 1973; Petkov et al., 2004; Woldorff & Family, 2008). Ignoring is frequently an active process—for instance, if the distracter is attention-grabbing and hinders the organism's ability to concentrate on task-relevant features (e.g.Ipata, Gee, Gottlieb, Bisley, & Goldberg, 2006; Melara, Rao, & Tong, 2002). In summary, attention and ignoring are correlated and involved in the detection of important features in the environment. However, the mechanisms underlying these processes are not well understood.

We used MEG (magnetoencephalography) with a new paradigm to dissociate the effects of selectively attending and ignoring in time. Two different tasks were performed successively on the same acoustic stimuli: triplets of tones (A, B, C) with different frequencies, and noise-bursts interspersed between the triplets. In the PASSIVE task subjects were instructed to respond as fast as possible to an auditory signal, ignoring unrelated noise. In the COMPARE task subjects were instructed to respond to a change in frequency of one of the tones, ignoring unrelated noise. These two tasks allow us to study the neural mechanisms underlying attention and ignoring in humans.

We observed the earliest attend/ignore effects as early as 100 ms post-stimulus onset in auditory cortex. These appear to be generated by modulation of exogenous (stimulus-driven) sensory evoked activity. Specifically related to ignoring, we demonstrate that listeners can selectively ignore auditory tones when they are not attended. This shows that the human auditory cortex can actively modulate sensory input. These findings provide new, direct evidence that listeners actively ignoring a sound can reduce their behavioral objectives.
1. Materials and methods

1.1. Subjects

All participants were right-handed (Oldfield, 1971), reported normal hearing, and had no history of neurological disorder. The data from one subject were discarded.

1.2. Stimuli

The stimuli consisted of pure tone pips presented at a comfortable listening level. Pure tone frequency discrimination thresholds were measured in a three-stimuli (PASSIVE) task. The conditions of the thresholds are as follows:

- A ≈ 800 Hz
- B ≈ 400 Hz
- C ≈ 800 Hz

These conditions resulted in a range of pure tone frequency discrimination thresholds from 200 Hz to 800 Hz. The stimulus presentation consisted of triplets presented at 100 ms inter-tone-interval (from offset to onset). The triplets were randomized, with the inter-stimulus interval (ISI; from offset to onset of a triplet) randomized between 1400 and 2100 ms.

Before the recording, individual discrimination thresholds were obtained for each participant.

1.3. Discrimination threshold estimation

The average thresholds measured for this group of non-trained individuals was 1.10 (2010) 3262–3271

1.4. Procedure

Two tasks were performed successively on the same stimuli in each task block. The tasks were interleaved. In the PASSIVE task, participants were instructed to disregard the noise bursts and respond when tones A and C were of the same frequency. In the COMPARE task, listeners were instructed to respond as fast as possible (by pressing a response button held in their dominant hand) to the noise bursts. The noise bursts were included in the task block, with 10 ms cosine-squared ramps, interspersed randomly between the triplets. A sampling rate of 44.1 kHz was used.

Hansen & Hillyard (1988) and Särkkä et al. (2008) demonstrated that the time course of inhibition is usually reported to emerge later—after 200 ms post-tone onset—at the time of the N1/M100 auditory onset potential.

Effects of distracter suppression are usually reported to emerge later—from about 200 ms (but never within a triplet).

In our study, we used tone-pips of three different frequencies presented in random bursts. Since the stimuli were identical in both tasks, differences in the effects are usually reported to occur substantially later than the enhancement of the deviant tones compared to neutral conditions suggesting that inhibition of processing non-attended signals contributed to the measured difference in the effects.
1.5. Neuromagnetic recording and data analysis

1.5.1. Channel selection

1.5.2. Evoked responses

Fig. 1. Frontal Channel Selection

10 channels in each hemisphere

(A) Frontal Channel Selection

(B) Auditory Channel Selection

5 channels in each hemisphere (5 in each sink or source)
1.6. Comparison across task conditions

Fig. 2. The COMPARE task was designed in such a way that the initial processing of A, B and C tones is the same for all triplets (targets and non-targets), diverging only after the subject in each hemisphere. Data were not spectrally filtered beyond the online average (average over all subjects for each of the 156 channels) or the group-RMS (RMS of RMSs; over 4 triplet conditions). Epochs with amplitudes larger than 3 pT in the PASSIVE (top) and COMPARE (bottom) tasks. Epochs with amplitudes larger than 3 pT in the PASSIVE (top) and COMPARE (bottom) tasks. Time was 340 ms (SD = 95 ms) post-noise onset. There was no effect of task order on any of these measures. There was no effect of task order on any of these measures.

2. Results

2.1. Behavior

2.2. Electrophysiological data

2.3. Task effects on brain responses to the triplet stimuli
Fig. 3. The RMS time course of composite (averaged across triplet conditions and hemispheres) COMPARE and PASSIVE amplitudes recorded from all auditory (top), posterior auditory (middle) and frontal (bottom) channels. Tone onsets are marked with green bars. Statistically significant differences between COMPARE (red) and PASSIVE (blue) amplitudes are marked with pink (COMPARE > PASSIVE) or light-blue (PASSIVE > COMPARE) shading. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

We therefore focus on the posterior auditory channels (see Fig. 1B) as indexes of auditory cortical activation. These will be referred to as “auditory channels” in the remainder of this report. The pre-triplet interval (baseline) did not differ between task conditions for the auditory channels. For the frontal channels it was somewhat higher for COMPARE than for PASSIVE (though not consistently across listeners). Because such differences are of potential interest, we did not apply baseline correction (subtraction from the response of mean pre-stimulus activity).

Peak M100 amplitudes in auditory channels did not differ between conditions for A tones. This may reflect the fact that both tasks require the subject to attend to the onset of each new triplet because it is relevant for both tasks (it must be distinguished from noise for PASSIVE, and its pitch recorded for the COMPARE task). However, the M100 responses for tones B and C exhibit small but significant task-related amplitude differences. Peak M100 amplitudes are significantly higher for COMPARE than PASSIVE for tone C (an average amplitude difference of about 7 fT or 10%), and lower for tone B (an average amplitude difference of about 7 fT or 9%). The sizes of these effects are comparable to those reported in other attention-related evoked response studies (e.g. Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Gutschalk et al., 2005; Lange et al., 2003; Sanders & Astheimer, 2008). Although it appears from the average that there is a difference in latency between tone B M100 responses in PASSIVE and COMPARE, this was not significant across subjects.

In Fig. 3 (auditory channels) the M100 response to tone B appears to be preceded by an ongoing difference between conditions (500–650 ms). One might speculate that the tone B M100 ‘rides’ upon this ongoing baseline, and that this explains the amplitude differences at the M100 response. To investigate this possibility we reanalyzed the data by baseline-correcting the responses according to the 100 ms interval preceding the onset of tone B (presented in Supplementary Fig. 1). The figure demonstrates that the difference at the M100 response survives this re-analysis and is therefore likely not due to an ongoing amplitude
The maximum amplitude in a
which underlie the M100 response. Indeed, a repeated measures
resized to result from refractory effects within the neural generators
RMS peak) with task-condition and tone (A, B or C) as factors
ANOVA on M100 peak-latencies, with task-condition and tone (A,
A and C. The lack of significance
between COMPARE and PASSIVE for tone B relative to tones
1900 ms post-triplet onset. The fact that the
strik ing effect of ignoring (or trying to ignore) tone B in the COM-
process to optimize the processing of tone C.

We found no significant effects of task.

When comparing response amplitudes between tasks, the most
difference preceding tone B, but rather reflects a genuine sensory
in case of PASSIVE (subjects know they
encoding tone A in memory, a process which has been shown to involve sen-
tory cortex (Gaab & Schlaug, 2003; Grimault et al., 2009; Luo et al.,
memory. In auditory cortex, in the
tains relatively constant amplitude. Higher sustained activity in the
post-triplet onset) drops sharply, whereas PASSIVE activity main-
forward looking of tone information in memory. In auditory cortex, in the
terms of the stimulus unrelated to attention. In order to identify
related to the anticipation of tone arrival and the subsequent encod-
progressively decline from tone A to tone B to tone C, this effect is
conditions only becomes significant at 650 ms post-triplet onset,
for C is greater than for B.

In addition to these main effects of interest which occur shortly
further.

The pattern of activation in frontal channels reveals an initial dif-
activity dominates C tone-related activity in the PASSIVE condi-
tion (left) relative to the PASSIVE condition (right). An inspection
of channels, the response to the onsets of B (green) and C (orange).
Another means of examining the effect of attending vs. ignoring
it is possible that additional aspects of the dynamics of slow
suggested by the artifact rejection routine (see Section 1) strongly supports a
brain source rather than eye movement artifacts. It is important
ment is sustained over time and, as the statistical analysis suggests,
3. Discussion

The present study focuses on the temporal dynamics of attentional processes in auditory cortex—the neural processes underlying the amplification of responses to attended stimuli and suppression of responses to distracters within an acoustic scene that unfolds over time. We demonstrated that priming listeners to selectively attend to certain moments in time while ignoring other moments can modulate early onset responses in auditory cortex by attenuating responses to signals which listeners are attempting to ignore and boosting responses to task-relevant sounds.

Several previous studies have tried to isolate effects of attending and ignoring by comparing selective attention conditions with a ‘baseline’ neutral condition, hypothesized to require neither attending nor ignoring. For instance, Michie et al. (1990) used a dichotic presentation task—signals were presented to left and right ears and listeners were instructed to attend to one ear while ignoring the other. As a control, subjects performed an unrelated visual task while passively listening to the auditory stimuli (Michie et al., 1990, 1993). Comparing brain responses to auditory signals when they were attended or unattended with responses to the same stimuli when subjects were focusing their attention on a visual task, revealed changes in both the attended and unattended ERPs relative to the control condition. Specifically, attended ERPs were enhanced over the interval from about 100 to 200 ms post-onset, while unattended ERPs were suppressed over the interval from 200 to 500 ms post-onset (see also Alho, Woods, et al., 1994; Bidet-Caulet et al., 2010).

Alain and Woods (1994) (see also, Alain et al., 1993) attempted to isolate effects specific to attending and ignoring by presenting listeners with sequences of tone-pips of three different frequencies presented in random order. Listeners were instructed to attend to one of the tones while ignoring the others. In different conditions the three tones were either evenly spaced (‘evenly spaced; ES condition), the attended tone was distinct, with the distracter tones clustered together (‘clustered easy; CE condition), or else the attended tone was grouped with one of the distracters (‘clustered hard; CH condition). The data indicated that distracter grouping enhanced the difference between the responses to task-relevant and task-irrelevant tones. Comparing the different conditions suggested that this effect was due both to increased negativity to attended tones from 150 to 170 ms post-onset (CE vs. ES conditions) and decreased responses to non-attended tones from 190 to 450 ms post-onset (CH vs. ES conditions).

While these previous studies examined attentional facilitation vs. suppression in the context of spatial attention or feature-based (pitch-based) attention, we investigated them from the perspective of attention in time. It has been shown that listeners can take...


3.1. Temporal dynamics of attending

Effects of attention in the present study were manifested as a stimulus results in decreased M100 response in auditory cortex. Indeed, Rif et al. (1991) reported to emerge around 200 ms after the M100 response for tone B. Based on its magnitude, this response is of particular interest as it has been suggested to reflect voluntary orienting of attention (Näätänen et al., 1978; Alho, Teder, Lavikainen, & Canavan, & Hillyard, 1991). We did not find an effect during the earlier, post-stimulus onset (Alain & Woods, 1994; Alho et al., 1987; Bidet-Caulet et al., 2010; Degerman et al., 2008; Melara et al., 2002; Caulet et al., 2010; Gazzaley et al., 2005). In the visual literature, a decrease in amplitude of the P1 (Näätänen, et al., 1978) has been reported (Luck et al., 1994; Luck & Hillyard, 1995). However Gazzaley et al. (2005), in a visual ERP study that more closely resembles our auditory task, did not observe any amplitude suppression effects. The difference may be due to the lack of an appropriate control (Giard et al., 2000; Giard, Perrin, Pernier, & Peronnet, 1988; Hillyard et al., 1998). Early task-related effects were observed exclusively in frontal channels. These effects have usually been interpreted as being mediated by bottom-up perceptual processes in sensory cortices, for example by modulating the excitability of the relevant sensory neuron. Nevertheless, a more detailed analysis of the time course of the attentional effects observed at stimulus onset result from bottom-up processing negativity is generated by a matching process between sensory processing of the to-be-ignored stimulus (Theeuwes & Chen, 2007). These responses are hypothesized to reflect voluntary orienting in a top-down ('goal directed') frontal cortex system which facilitates bottom-up processing of task-relevant signals (Lange et al., 2003; Ohgami et al., 2004; but see Engdahl, Bjerre, & Christoffersen, 2003). In the present study, we demonstrate similar effects in the post-stimulus onset) component has been documented in ERP studies (Brunia & van Boxtel, 2004; Lange et al., 2003; Van Boxtel & Böcker, 2004) which is due to the lack of an appropriate control (see, e.g. Hillyard et al., 1998; Lange et al., 2003 for review). However, in the auditory domain, these effects have not been studied in detail. Therefore, the aim of the present study was to investigate the effects of audiovisual attention on the ERP in the auditory domain.

3.2. Temporal dynamics of ignoring

In the auditory domain, the temporal dynamics of ignoring...
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Acknowlegements

Appendix A. Supplementary data

Evaluations

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