



Stimulus-focused attention speeds up auditory processing

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ABSTRACT

Stimulus-focused attention enhances the processing of auditory stimuli, which is indicated by enhanced neural activity. In situations where fast responses are required, attention may not only serve as a means to gain more information about the relevant stimulus, but it may provide a processing speed gain as well. In two experiments we investigated whether attentional focusing decreased the latency of the auditory N1 event related potential. In Experiment 1 slowly emerging, soft (20 dB sensation level) sounds were presented in two conditions, in which participants performed a sound-detection task or watched a silent movie and ignored the sounds. N1 latency was shorter in the sound-detection task in comparison to the ignore condition. In Experiment 2 we investigated whether the attentional N1 latency-decrease was caused by a frequency-specific attentional preparation or not. To this end, tone sequences were presented with a single tone frequency or with four different frequencies. N1 latency was shorter in the sound-detection task in comparison to the ignore condition regardless the number of frequencies. These results suggest that stimulus-focused attention increases stimulus processing speed by generally increasing sensory gain.

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1. Introduction

It is well-known that stimulus-focused attention improves auditory performance by enabling one to process relevant stimuli more efficiently. Using various paradigms, numerous studies confirmed that attention directed to the sounds enhances and sharpens neural activity already at the subcortical level of the auditory pathway (Frith and Friston, 1996; Giard et al., 1994; Maison et al., 2001; Rinne et al., 2008), as well as in the primary and secondary human auditory cortices (e. g., Giard et al., 1988; Grady et al., 1997; Jäncke et al., 1999; Okamoto et al., 2007; Rif et al., 1991; Rinne et al., 2007; Salmi et al., 2009; Woldorff et al., 1993). In everyday life there are many situations in which the role of attention is not to make a more detailed analysis of a sound possible, but rather to allow fast responses through fast detection of the relevant sounds. Therefore, attentional effects should not only be reflected in enhanced activity, but also in an increase of overall stimulus processing speed. In the psychological literature this notion is known as 'prior entry hypothesis' (Titchener, 1908); which originally states that attended stimuli come into consciousness more rapidly than unattended stimuli. The speeding-up

of perceptual, that is, sensory processing as an effect of attention was intensively investigated for more than a hundred years with various paradigms in different sensory modalities. However, evidence supporting the existence of the prior-entry effect, to date, is rather mixed (Di Russo and Spinelli, 1999; McDonald et al., 2005; Schneider and Bavelier, 2003; Schuller, and Rossion, 2001; Seibold et al., 2011; Shore et al., 2001; Spence et al., 2001; Vibell et al., 2007; Yates, and Nicholls, 2009; Zampini et al., 2005; for summary, see Spence, and Parise, 2010). Due to its superior temporal resolution, the method of event related brain potentials (ERPs) is a suitable choice for the investigation of changes in processing speed. In the first experiment we investigated whether auditory processing speed gains were reflected in the latency of the auditory N1 ERP, then in a further experiment we investigated whether the observed effect was due to a frequency-specific attentional preparation or not.

The auditory N1 waveform peaks between 80 and 120 ms after the onset of a tone or a transient auditory event. It is maximally negative on fronto-central leads and often shows a polarity inversion at the mastoids when the electroencephalogram (EEG) is recorded with nose-reference; which suggests that N1 at least in part originates from the auditory cortex (Vaughan and Ritter, 1970; Wolpaw and Penry, 1975; for summary, see Näätänen and Picton, 1987; Giard et al., 1994; and Herrmann and Knight, 2001). Beside this supratemporal, stimulus-specific subcomponent, the N1 waveform includes other (non-specific) subcomponents as well (Giard et al., 1994; Herrmann and Knight, 2001; Näätänen and Picton, 1987; Näätänen and Winkler, 1999; Vaughan and Ritter, 1970; Wolpaw and Penry, 1975). In functional terms, N1 is mainly referred to as an ERP

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correlate of stimulus onset detection (Parasuraman and Beatty, 1980). Moreover, it is usually described as an exogenous ERP component (Alho et al., 1994; Hansen and Hillyard, 1980; Woldorff and Hillyard, 1991; for a summary, see Herrmann and Knight, 2001), because it reacts sensitively to changes in physical stimulus- and stimulus presentation characteristics. For example, it has been demonstrated that the amplitude of the N1 response exhibits stimulus-specific refractoriness (Barry et al., 1992; Budd et al., 1998). Also, when stimulus intensity is increased, N1 amplitude increases while N1 latency decreases (Arlinger, 1976; Conolly, 1993; Pantev et al., 1989; Picton et al., 1977; Roberts et al., 2000; Stufflebeam et al., 1998). A number of studies demonstrated that the N1 wave is sensitive to tone frequency changes, which affects both its amplitude and latency (Crottaz-Herbette and Ragot, 2000; Dimitrijevic et al., 2008; Jacobson et al., 1992; Näätänen et al., 1988; Näätänen and Winkler, 1999; Pantev et al., 1988; Pantev et al., 1995; Roberts and Poeppel, 1996; Salajegheh et al., 2004; Stufflebeam et al., 1998; Tiitinen et al., 1993; Verkindt et al., 1994; Woods et al., 1993; for a review, see Roberts et al., 2000).

Whereas N1 reflects sensory processing which does not require voluntary activation, it is also affected by the participant's attentional state (Herrmann and Knight, 2001). A large number of studies have demonstrated attention-related ERP changes in the time window of the auditory N1 (e.g., Hillyard et al., 1973; Picton and Hillyard, 1974; Hansen and Hillyard, 1980; Näätänen, 1982; Woods et al., 1984; Näätänen and Picton, 1987). Selective attention studies mainly reported an ERP amplitude enhancement for the stimulus presented to the attended ear compared to the physically identical stimulus given to the unattended ear. It has been a highly debated topic whether this amplitude enhancement is genuine (i.e. brought about by the selective enhancement of the N1 generator process) or apparent (i.e. caused by the activation of functionally distinct, but temporally overlapping ERP components; see Alho et al., 1986, 1992, 1994; Giard et al., 1988; Hillyard et al., 1973; Näätänen, 1982; Näätänen et al., 1978; Näätänen and Michie, 1979; Näätänen and Picton, 1987; Rif et al., 1991; Woldorff and Hillyard, 1991; Woldorff et al., 1993).

It seems plausible that attention may lead to faster neural responses, particularly when sounds are difficult to detect. Consequently, attentional effects may be reflected not only in the enhancement of the N1 amplitude, but also in the decrease of the N1 latency. So far, attentional effects on N1 latency have been scarcely reported (e.g., Seibold et al., 2011 found that the latency of the N1 waveform decreased for target oddball sounds as the function of the preceding cue-target foreperiod in a cued oddball discrimination task), and only few studies addressed directly whether the latency of the magnetic counterpart of N1 (N1m) was affected by attention, with mixed results: Mäkinen et al. (2004) found no attention-related effect, while Okamoto et al., 2007 found an attention-related latency decrease for tones presented in band-eliminated noise. The scarcity of positive reports may be rooted in the generally used range of experimental settings, which might not be optimal for the observation of attention-related latency-effects. In most experiments clearly audible sounds are presented, typically at or above 50 dB sensation level (SL, above hearing threshold level). Moreover, sound onsets are sharp: rise times typically range from 2.5 to 20 ms. Whereas these settings make it possible to obtain ERPs with high signal-to-noise ratio, it seems reasonable to assume that such sounds already lead to a temporally highly focused processing response, which does not allow for substantial speed gains through the increased mobilization of attentional resources (see similar arguments by Schwent et al., 1976 for N1 amplitude effects). That is, these stimulus parameters lead to a ceiling-effect: there is virtually nothing to be gained in terms of stimulus detection efficiency by directing more attention to these sounds, because detection-related processes are already maximally engaged (saturated). The goal of the present study was to investigate whether a measurable attentional speed gain could be observed when soft, slowly emerging sound signals are to be detected. We hypothesized that these sounds do not lead to saturated sound-detection responses,

and therefore allow for the observation of an attentional processing speed gain. Whereas such sounds are highly atypical in ERP-based auditory research settings, they may often play an important role in everyday life (e.g. listening to whether the baby has woken up in the next room.)

A model describing how a sensory processing speed gain may be reflected by the reduction of N1 latency can be based on the assumption that on the level of individual sound-onset events the latency of N1 elicitation is probabilistic (jittered; Thornton et al., 2007), and the single-sweep N1 latency distribution accumulates the temporal variability of all neural processes which lead to the elicitation of N1. It has been suggested that attention increases the synchronization of neural responses (Friston et al., 1996; Tononi et al., 1998a; Tononi et al., 1998b), which, applied in the context of the auditory N1, suggests that the well-known attentional N1 amplitude enhancement effect is caused at least in part by a decrease in the latency jitter of single-sweep N1 responses, which results in a higher-amplitude N1 in the averaged ERP (Thornton et al., 2007). It should be noted, however, that the reduction of latency-jitter might not be the only cause of the average amplitude-difference between passive and active conditions: Tiitinen et al. (2005) found that the amplitude difference was present even at the single-trial level. In the present study, we assumed that attention changes the single-sweep N1 latency distribution by allowing an earlier triggering of single-sweep N1s, thereby not only narrowing the distribution, but also shifting its center (mode) closer to stimulus onset (Fig. 1). This should result not only in a higher-amplitude average waveform, but in earlier average peak latency as well.

Importantly, for stimuli with sharp onsets, the magnitude of the latency decrease may be too small, and go unnoticed in the average ERP. If attention synchronizes and speeds up processes which lead to the generation of N1, then the magnitude of the hypothetical latency effect may be increased if the single sweep N1 latency distribution is spread out over time. It is well-known that slow physical changes in sound parameters generally elicit temporally wider and lower-amplitude average N1s than those with fast changes (Kodera et al., 1979; Onishi and Davis, 1968). In Experiment 1 we presented soft tones, and manipulated sound fade-in speeds (rise time), to make potential attention-related decreases in N1 latency observable in the average N1 waveform. Moreover, as described in the model above, attention-related latency-reductions were hypothesized to be more substantial for sounds with longer rise times.

2. Experiment 1

2.1. Methods

Thirteen healthy volunteers reporting normal hearing status (six women, aged 18–26 years, mean 21 years; one left-handed) participated

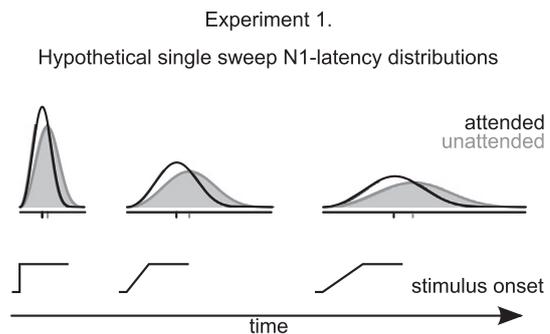


Fig. 1. Hypothetical single-sweep N1-latency distributions (probability density functions) for three rise times when tones are attended or unattended. Tick marks on the horizontal axes indicate the center (mode) of the latency distribution in the attended (black line, white filling) and unattended (gray line, gray filling) conditions. When rise time is short, the latency-distribution difference between the attended and unattended conditions may not be substantial, however, for longer rise times it may bring about larger differences in the N1 peak latencies, which may result in observable latency differences in the average ERP waveforms.

in the experiment for monetary compensation. Written informed consent was obtained from each of them after the nature of the experiment was explained to them. Data from one participant was discarded due to the absence of clearly observable N1 peaks.

Participants were comfortably seated in a sound-attenuated room during the experiment. Hearing thresholds were individually determined using a continuous, 1000 Hz sinusoid tone at the beginning of the experiment. In the following, this intensity level (0 dB SL) is used as a reference. Four sinusoid tones (1000 Hz) with different linear rise times (5, 200, 400 and 600 ms) were presented binaurally via headphones (HD-600, Sennheiser, Wedemark, Germany). After the linear rise, a constant intensity level of 20 dB (SL) was sustained, then tones faded out with a 5 ms linear fall time. Overall tone durations were 205, 300, 500 and 610 ms respectively, including rise and fall times. These tone durations enabled the assessment of the onset-related N1 waveform without interference from tone offset-related waveforms. The tones were presented in blocks of 68 tones (17 of each type) in random order, with a random stimulus onset asynchrony (SOA) of 2–5 s. Experimental blocks were separated by short breaks as needed.

The experiment was divided into two parts. In one part, the *active*, in the other part the *passive* condition was administered. The order of the parts was counterbalanced between participants. In the passive condition participants were watching a silent subtitled movie of their own choice and were instructed to ignore the auditory stimulation. In the active condition participants performed a simple reaction time task: they were instructed to press a response key held in their dominant hand to each sound as fast as possible, but without false alarms. After each block, a graph showing *each* of their correct response times (RTs) was presented, as well as average hit rate and RT. By visualizing the dispersion of the individual response times, this made it possible to monitor whether participants complied with the speed instruction, and to motivate participants to maintain a high level of performance throughout the experiment. Hit rate, and average reaction time in the 5–1000 ms interval following the onset of the stimuli were calculated for each participant. The effect of rise time on hit rates and reaction times was analyzed in one-way repeated measures analyses of variance (ANOVAs).

The EEG was recorded with 250 Hz sampling rate (with on-line 40 Hz low-pass filtering) with a Synamp 2 amplifier (Compumedics Neuroscan, Victoria, Australia) from 11 scalp locations (F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4 of the international 10–20 system and from the left and right mastoids, Lm and Rm, respectively) with the common reference electrode placed on the tip of the nose. Horizontal eye movements were monitored with a bipolar setup with electrodes placed lateral to the outer canthi of the two eyes; vertical eye movements were monitored with electrodes placed above and below the right eye. The continuous EEG was band-pass filtered offline (1–18 Hz). 600 ms long epochs including a 100 ms pre-stimulus interval were extracted. Amplitude calculations were referred to the average signal measured in the pre-stimulus interval. Epochs corresponding to the first three trials of each block and epochs with a signal range exceeding 100 μ V on any channel were discarded from the analyses. Epochs corresponding to tones with different rise times were averaged separately for each participant in both conditions.

The comparison of active and passive conditions may pose some difficulties to the interpretation of the ERP data, because they also differ in task- and motor requirements. Since motor-related ERP waveforms are spread over longer time-periods following the N1 response (Luck, 2005) the potential overlap of motor-related ERPs does not pose problems in the present setting; moreover, stimulus onset asynchrony (SOA) is long enough to prevent such overlaps from previous trials. But task-related differences may give rise to ERP differences which may not reflect differences in sensory processing per se. Indeed, in the active condition N1 peaks were overlapped by an additional negative ERP at frontal and central sites (see Fig. 2),

therefore, the N1 peaks were assessed at the mastoid leads in both the active and passive conditions (using the average signal of the left and right mastoids, referred to as common mastoid, CM, in the following). Measuring N1 at the mastoids provides an unbiased estimate of the supratemporal N1 subcomponent; because only this N1 subcomponent reverses its polarity at mastoid sites when a nose reference is used (Näätänen and Winkler, 1999; for detailed description, see Näätänen and Picton, 1987; Vaughan and Ritter, 1970; Wolpaw and Penry, 1975). As shown on Fig. 2 tones with longer rise times (200, 400 and 600 ms) elicited temporally wider and lower-amplitude group average N1s. For tones with 5 ms rise time N1 peaks were identified as the maximum positive peaks at CM lead in a time window of 50 to 150 ms from tone onset. Individual N1 amplitudes measured as the average signal in a 20 ms long window centered at the individual's N1 peaks for active and passive conditions were also calculated at CM. For tones with longer rise times, the unequivocal assessment of individual peak latencies was not possible at the mastoids, due to the unfavorable signal to noise ratios. Therefore only the ERPs elicited by the 5-ms-rise-time tone were submitted to latency and amplitude analysis. Two-tailed paired *t* tests were calculated to test whether N1 peak amplitude and latency differed between the two conditions.

2.2. Results

2.2.1. Behavioral performance

The one-way ANOVA of the RTs revealed a significant stimulus effect ($F[3, 33] = 231.53, p < .001, \epsilon = .40$), showing (Fig. 4) that RTs increased as the function of rise time (mean reaction times were 235.3, 283.8, 314.0 and 339.4 ms, respectively for the 5, 200, 400 and 600 ms rise time tone, calculated from the physical onset of the stimuli). For hit rate, no significant effect was found. The mean hit rate was 99.28%.

2.2.2. ERP data

N1 responses, which showed a polarity inversion at the mastoids, were clearly observable for all types of tones in each condition in the group average ERPs (Fig. 2). The N1 peaks elicited by the four tones followed the order of rise times on both fronto-central and mastoid leads (i.e. N1 peaked later for longer rise times). In the active condition, N1 was overlapped by an additional waveform at frontal and central sites. Whereas the group average (and most individual ERPs) show only a single fronto-central peak with increased latency (see Fig. 2, left and middle column), in the individual ERPs N1 was followed by a distinct second peak for some participants (see Fig. 2, right column for the ERP data of a representative participant). As described in the Methods, due to this overlap, and the low signal-to-noise ratio for the ERPs elicited by longer rise time tones (especially in the passive condition), the individual peak latencies could be assessed unequivocally only for the 5 ms rise time tone at the CM lead.

N1 peaked earlier in the active than in the passive condition for 5 ms rise time tone at the mastoids ($t[11] = -2.382, p < .05$; mean active-passive difference: -4.67 ms). Whereas no inferential statistics can be provided due to the poorer signal-to-noise ratios, for the longer rise time tones, the group average N1 peaked earlier in the active than in the passive condition (200 ms rise time tone: 144 vs. 152 ms; 400 ms: 168 vs. 212 ms; 600 ms: 188 vs. 200 ms) at the mastoids (see Fig. 3).

Whereas the unequivocal individual assessment of N1 peak latencies was not feasible, a condition (active, passive) \times rise time (5, 200, 400, 600 ms) repeated measures ANOVA of the amplitudes calculated as the mean signal in a 20 ms long window centered on the group average peak latencies could be calculated, which showed a significant condition main effect ($F[1, 11] = 7.81, p < .05$), indicating a higher N1 amplitude in the active condition; and a significant stimulus main effect ($F[3, 33] = 13.84, p < .001, \epsilon = .71$), due to tones with shorter rise times eliciting larger N1 responses (see Figs. 3 and 4).

Experiment 1.

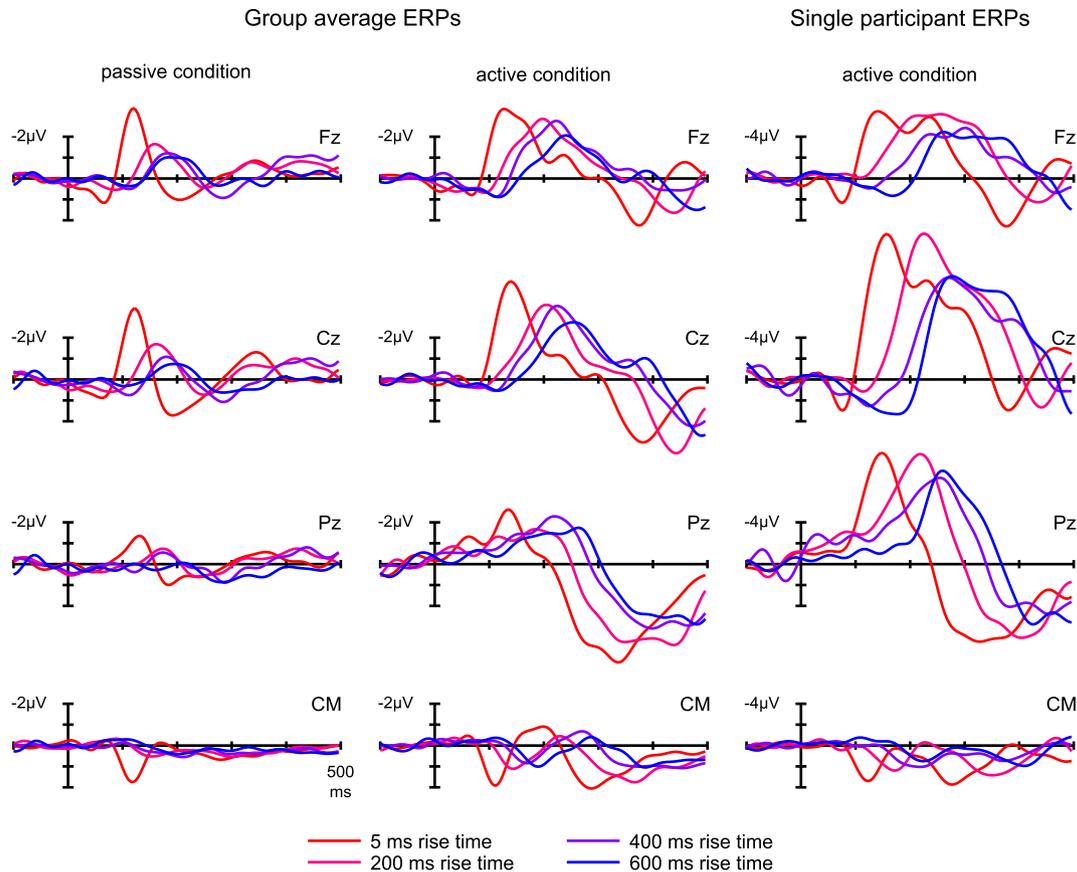


Fig. 2. Group-average ERP waveforms in Experiment 1 in the passive (left column) and active (middle column) conditions; as well as individual ERPs of one participant from the active condition (right column) on the Fz, Cz, Pz leads, and the average mastoids signal (CM). The physical onset of the sounds is at the crossing of the axes (0 ms). Note that the calibration of the vertical axes is different for the single participant ERPs (right column).

2.3. Discussion – Experiment 1

The experimental settings used in Experiment 1 proved to be suitable for the observation of attention-related processing speed gains. We found that N1 peaked earlier when participants performed a stimulus-detection task in contrast to when they were watching a subtitled movie and ignored the sounds. This indicates that stimulus-focused attention speeds up auditory processing. Whereas between-condition N1-latency differences observable in the group average responses were larger for tones with longer rise times except for the 600 ms rise time tone (active-passive difference in the *group average* responses, 5 ms: -4 ms; 200 ms: -8 ms; 400 ms: -44 ms; 600 ms: -12 ms), our second hypothesis that the magnitude of the attentional latency-effect increases with longer rise times could not be statistically investigated due to the low signal-to-noise ratio.

For the N1 amplitudes, the expected results were found: N1 amplitude was higher in the active than in the passive condition, which is on a par with the results of selective attentional studies (e. g. Picton and Hillyard, 1974; Hansen and Hillyard, 1980; Woods et al., 1984; for review, see Näätänen, 1982; Näätänen and Picton, 1987). In the active condition, an additional, slightly later component was observable at frontocentral leads which overlapped the N1 response (see the General Discussion), which made it necessary to use the signals from the mastoid leads.

The first experiment demonstrated that focusing on the incoming sounds can shorten the latency of the N1 response, which indicates that stimulus-focused attention speeds up auditory processing.

Because this result says little about the nature of this attentional processing speed-up, a further experiment was conducted.

3. Experiment 2

Experiment 2 was conducted to further specify the attention-related latency decrease found in Experiment 1. Contrasting Experiment 1 with that of Mäkinen et al. (2004) we proposed that the low overall intensity during stimulation may allow for a higher sensory gain setting, that is, a general non-stimulus-specific auditory processing enhancement (see e. g. Petkov et al., 2004; Woods et al., 2009), which results in a latency effect of measurable magnitude. This is, however, not the only mechanism that allows for enhanced auditory processing; there is also evidence that attention also results in selective tuning to the to-be-attended tones (e. g. Okamoto et al., 2007; Paltoglou et al., 2009). Therefore, in Experiment 2, we addressed the question whether the observed latency-effect results from stimulus-specific or unspecific processing enhancement.

Specifically, because all sounds had the same tone frequency in Experiment 1, the N1 latency-decrease may have resulted from a specific tuning to the given tone frequency, but also from a general processing enhancement. To separate these possibilities, in Experiment 2 we presented pure tones with different frequencies in mixed and homogenous experimental blocks. If the attention-related N1 latency decrease resulted from a frequency-specific enhancement, mixing various frequency tones would eliminate the latency-effect. On the

Experiment 1. Group average ERPs

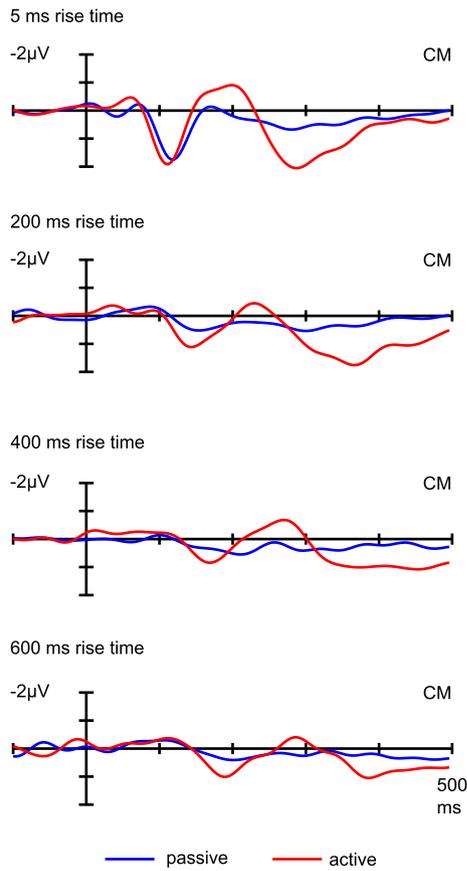


Fig. 3. Group-average ($N = 12$) ERP waveforms in Experiment 1 for each rise time separately in active and passive conditions on the average mastoid (CM) lead. Note that amplitude and latency analyses were carried out on individual data.

other hand, a general enhancement would result in an earlier N1 peak regardless the homogeneity of the presentation sequence.

3.1. Methods

Eighteen healthy volunteers reporting normal hearing status (eight women, aged 20–24 years, mean 21.8 years; two left-handed) participated in the experiment with written informed consent.

The experimental procedures used in the second experiment were identical to that of the first experiment except for the following changes. Because in Experiment 1 tones with longer rise times did not elicit ERPs which would allow the unequivocal assessment of individual N1 peaks at the mastoids, in Experiment 2, all tones were presented with 5 ms linear rise times. Overall tone duration was 205 ms, including rise and fall times. Four sinusoid tones with different frequencies (493.9 Hz, 659.3 Hz, 880 Hz and 1175 Hz; five semitones in between) were presented binaurally. The frequencies were selected so that the frequency-differences were much larger than the bandwidths of auditory filters centered at the four frequencies (which range from about 8 to 16% of the central frequency in the given frequency range, Moore, 1995). Tones were either presented in homogeneous or mixed experimental blocks. In the homogenous blocks one of the tones was delivered throughout the entire block, whereas, in the mixed condition the four types of tones were delivered in random order (17 of each type). Experiment 2 also consisted of two parts: in one part the active, in the other part the passive condition was administered. The order of the parts

was counterbalanced between participants. Both part consisted of four mixed and four homogeneous blocks presented in an interwoven order (HMMHHMMH–MHHMMHMM, where “H” and “M” stand for the homogeneous and mixed blocks, respectively) separated by short breaks as needed. The order of the homogenous blocks was random in both parts. The effect of block type on hit rates and reaction times was analyzed in two-tailed paired t tests.

The EEG was recorded as in Experiment 1, except for the sampling rate, which was 500 Hz. Filtering, rejection criteria and amplitude calculations were identical to that in Experiment 1. Epochs corresponding to tones in passive and active conditions and in homogeneous and mixed blocks were averaged separately for each participant (i.e. tones with different frequencies were pooled).

N1 peaks were identified in the four conditions for each participant as the maximal positive peaks in the time window of 50 to 150 ms from the CM (common mastoid), except for one person, whose RM (right mastoid) provided much better signal to noise ratio. Just as in Experiment 1, an additional component overlapping with the N1 at frontal and central sites appeared in the active condition; this made it necessary to use the mastoid leads. Individual N1 amplitudes were calculated as the average mastoid signal (CM), measured in a 20 ms long window centered at the individual's N1 peaks for each condition. N1 peak latencies and amplitudes were submitted to a condition (active, passive) \times block type (homogeneous, mixed) repeated measures ANOVA.

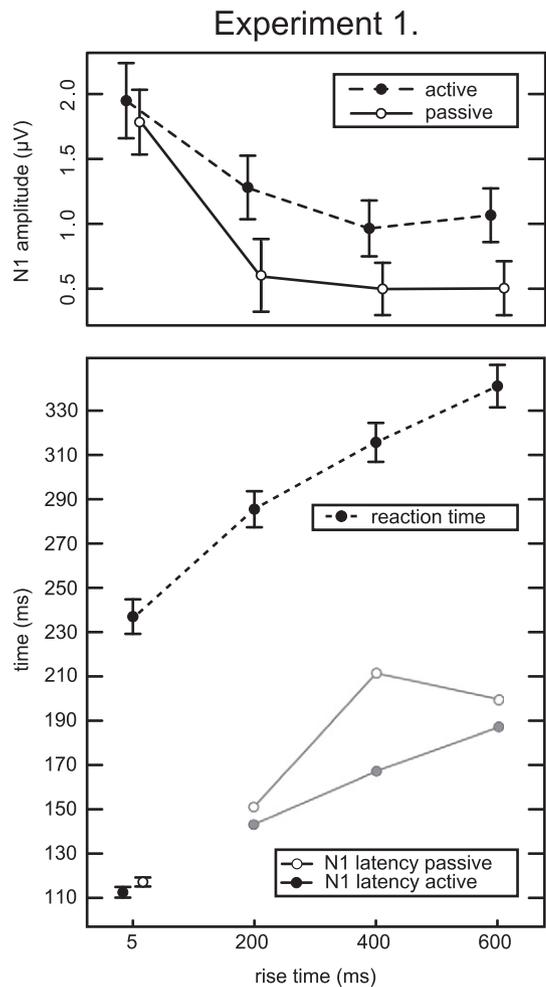


Fig. 4. Group-average ($N = 12$) reaction times, N1 amplitudes and -latencies (with standard errors) at the mastoids for the different rise times and conditions. N1 latencies represent the group-average of individually measured N1 latencies for the 5-ms rise time tone (with standard errors), and the group-average N1 latencies measured on the group mean ERP elicited by the 200; 400 and 600 ms rise time tones.

3.2. Results

3.2.1. Behavioral performance

Responses were faster in the homogeneous than in the mixed blocks ($t=2.67$, $p<.05$; mean RT was 243.04 ms in homogeneous, and 249.18 ms in mixed blocks). For hit rate, no significant effect was found. The mean hit rate was 99.65%.

3.2.2. ERP data

N1 responses, which showed a polarity inversion at the mastoids, were clearly observable for all tones in each condition (Fig. 5). As in Experiment 1, in the active condition the N1 waveform was overlapped by an additional waveform at frontal and central sites. The two-way ANOVA of peak latencies measured at the mastoids (see Fig. 6) showed a significant condition main effect only ($F[1, 17]=5.1$, $p<.05$), indicating shorter latency in the active condition (mean latency difference between active and passive conditions: -4.17 ms); however, no significant block type effect ($F[1, 17]=0.92$, $p=.35$), or interaction ($F[1, 17]=0.05$, $p=.83$) was found. The two-way ANOVA of the N1 peak amplitudes

(see Fig. 6) showed a significant condition main effect ($F[1, 17]=5.01$, $p<.05$), indicating a higher N1 amplitude in the active condition. No significant block type effect ($F[1, 17]=0.28$, $p=.61$) or interaction ($F[1, 17]=0.11$, $p=.75$) was found.

3.3. Discussion – Experiment 2

The results show that stimulus-focused attention results in earlier N1 latency, replicating the finding in Experiment 1. Moreover, no significant effect related to frequency-specificity was found; the results are consistent with the hypothesis that the observed N1 latency reduction stems from a general attentional increase in the sensory gain of the auditory system.

4. General discussion

The results of our experiments indicate that sound-focused attention can speed up auditory processing. This is in line with previous studies reporting sensory acceleration as an effect of attention in a

Experiment 2.

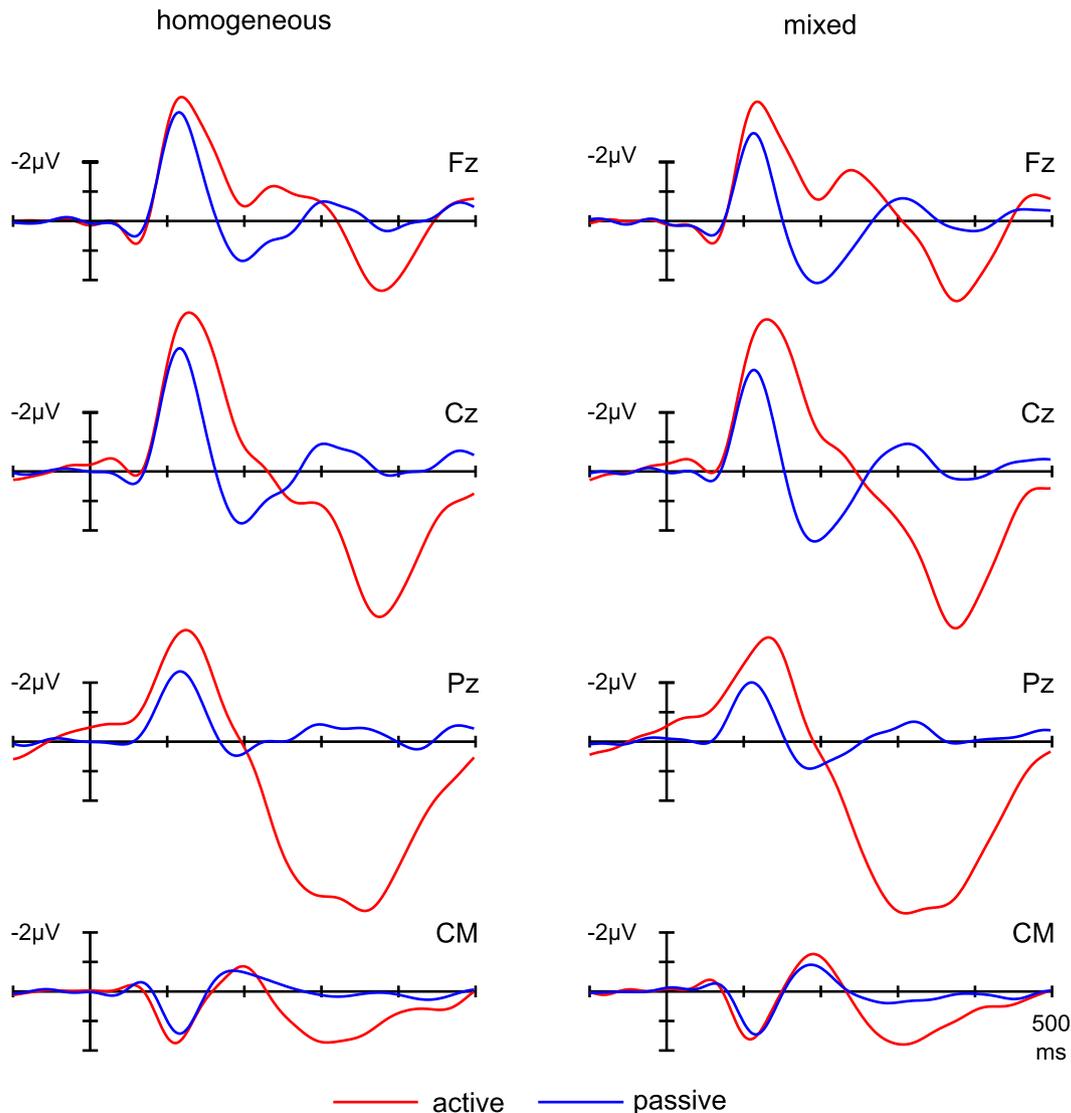


Fig. 5. Group-average ERP waveforms in Experiment 2 in the homogeneous (left column) and mixed (right column) conditions on the Fz, Cz, Pz leads, and the average mastoids signal (CM); red line showing active, blue line showing passive conditions. The physical onset of the sounds is at the crossing of the axes (0 ms).

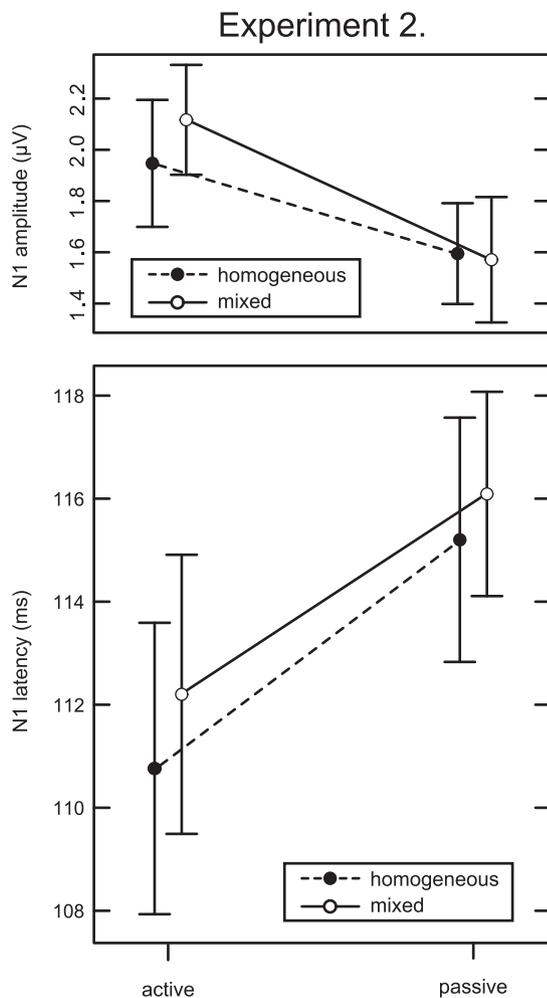


Fig. 6. Group-average N1 amplitudes and latencies (with standard errors) at the mastoids in Experiment 2 in the active and passive conditions in the mixed (continuous line) and homogeneous (dashed line) experimental blocks.

tone detection task in noise (Okamoto et al., 2007) and in temporal perceptual judgment and (crossmodal) selective attention paradigms (e.g. Seibold et al., 2011; Vibell et al., 2007; for summary, see Spence, and Parise, 2010).

In contrast with the results of a highly similar previous study (Mäkinen et al., 2004), we did find an attention-related N1 latency-decrease. The cause of this between-study difference may be rooted in the overall stimulus intensity levels used in the two paradigms. That high stimulus intensity may render attentional effects on the amplitude of the auditory N1 unobservable, was suggested by Schwent et al. (1976). In the Mäkinen et al. (2004) study, the top intensity level of each sound was 60 dB (sound pressure level), whereas in the present study it was 20 dB (sensation level). Whereas both studies featured stimulation intervals in which tone intensities slowly rose above detection threshold level, the presence of relatively high intensity periods in the Mäkinen et al. study might have led to a lower sensory gain (Woldorff et al., 1993; Hillyard et al., 1998; Okamoto et al., 2007; see also Robinson, and McAlpine, 2009) setting than in the present study. That is, one may hypothesize that for lower overall sound levels, the sustained attention necessary for the detection task may produce a higher sensory gain than for a louder overall sound level. That is, the optimal gain setting may partly be based on the maximal overall level of intensity during the whole period of stimulation: though the task relevant parts of the stimulation may be of low intensity, the recurrent loud periods may lead to a lower overall sensory gain setting. This notion extends the interpretation

of decreased auditory ERP amplitudes elicited in paired click paradigms, in which the amplitude decrease from the first to the second tone within the tone-pair is interpreted as the reflection of a sensory gating mechanism providing an optimal level of sensory stimulation (see e.g. Boutros, et al., 2009).

For the N1 amplitudes, we replicated the well-documented attentional enhancement effect: N1 amplitude was higher in the active than in the passive condition, which is on a par with the results of selective attentional studies (e.g. Picton and Hillyard, 1974; Hansen and Hillyard, 1980; Woods et al., 1984; for review, see Näätänen, 1982; Näätänen and Picton, 1987). It is to be noted that the comparison between the active and passive conditions showed ERP differences which might not be related to differences in sensory processing per se, but rather to the evaluation of the stimuli in task-related terms: In the active condition, an additional, slightly later component was observable at frontocentral leads which overlapped the N1 response, which is similar to the negative ERP enhancement elicited by attended compared to unattended stimuli in selective attentional studies (Nd [negative difference waveform] and PN [processing negativity]; for a review, see Näätänen and Picton, 1987). This additional component did not appear at the mastoids. Because the positive aspect of the N1 at the mastoids was enhanced by attention (i.e. it was more positive), it is reasonable to assume that typically observed N1 amplitude increases may include both a “genuine” N1-increase resulting from the attentional modulation of the supratemporal N1 subcomponent, and the overlap from a different, slightly later fronto-centrally negative ERP.

Though the attention-related N1 latency effect was found in Experiment 2, there was no significant difference in this effect between the homogeneous and mixed conditions. In contrast, responses were faster in the homogeneous than in the mixed condition, which suggests, that the between condition response-time difference may not be related to a sensory processing difference. The lack of N1-latency difference between the two conditions is compatible with the findings of Okamoto et al. (2007), who found an attentional N1-latency decrease to tones presented in band-eliminated noise, which was not modulated by the width of the noise-free band within which the tone was presented. These results hint at the possibility that a general attentional enhancement may bring about a sensory processing speed increase, but a stimulus-specific attentional sharpening may be based not on the enhancement of the processing of the given frequency, but on the suppression of spectrally close frequency bands.

In summary, we found in two experiments that the latency of the auditory N1 elicited by tones in a detection task decreased, and its amplitude increased in comparison to when the same sounds were task-irrelevant. It seems possible that a potential factor in revealing the attentional effect on N1 latency was the relative low intensity (20 dB SL) of the presented tones, but further research is needed to investigate this assumption. The results suggest that stimulus-focused attention enhances and speeds up sensory processing by increasing the general sensory gain in comparison to that in a passive attentional state.

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