

Auditory attention causes gain enhancement and frequency sharpening at successive stages of cortical processing – evidence from human EEG

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Keywords:	Human auditory cortex, attentional modulation, repetition suppression, stimulus-specific adaptation, cortical auditory-evoked potentials (CAEPs)

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3 1 Title: **Auditory attention causes gain enhancement and frequency sharpening at successive**
4 2 **stages of cortical processing – evidence from human EEG**

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8 4 Running head: Successive gain enhancement and sharpening effects
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23 15 Keywords: Human auditory cortex, attentional modulation, repetition suppression, stimulus-
24 16 specific adaptation, cortical auditory-evoked potentials (CAEPs).
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26 18 ABSTRACT

27 19 Previous findings have suggested that auditory attention causes not only enhancement in
28 20 neural processing gain, but also sharpening in neural frequency tuning in human auditory
29 21 cortex. The current study was aimed to reexamine these findings, and investigate whether
30 22 attentional gain enhancement and frequency sharpening emerge at the same or different
31 23 processing levels, and whether they represent independent or cooperative effects. For that,
32 24 we examined the pattern of attentional modulation effects on early, sensory-driven cortical
33 25 auditory-evoked potentials (CAEPs) occurring at different latencies. Attention was
34 26 manipulated using a dichotic listening task and was thus not selectively directed to specific
35 27 frequency values. Possible attention-related changes in frequency tuning selectivity were
36 28 measured with an EEG adaptation paradigm. Our results show marked disparities in
37 29 attention effects between the earlier N1 CAEP deflection and the subsequent P2 deflection,
38 30 with the N1 showing a strong gain enhancement effect, but no sharpening, and the P2
39 31 showing clear evidence of sharpening, but no independent gain effect. They suggest that
40 32 gain enhancement and frequency sharpening represent successive stages of a cooperative

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3 33 attentional modulation mechanism, which appears to increase the representational
4 34 bandwidth of attended versus unattended sounds.
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8 36 INTRODUCTION

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10 37 There is manifold evidence that attention causes top-down modulation of sensory-driven, or
11 38 “exogenous”, cortical responses (e.g., Fritz, Shamma, Elhilali, & Klein, 2003; Hillyard, Hink,
12 39 Schwent, & Picton, 1973; Spitzer, Desimone, & Moran, 1988; reviewed in: Fritz, Elhilali,
13 40 David, & Shamma, 2007; Mangun & Hillyard, 1995), but the mechanisms underlying this
14 41 modulation still remain unclear. Two alternative models have been proposed: the “gain
15 42 enhancement” model assumes that attention increases neuronal responsiveness to the
16 43 attended stimulus (Hillyard, Vogel, & Luck, 1998; McAdams & Maunsell, 1999), and the
17 44 “sharpening” model, that attention increases neuronal tuning selectivity (Atiani, Elhilali,
18 45 David, Fritz, & Shamma, 2009; Fritz et al., 2003; Spitzer et al., 1988). The current study
19 46 aimed to test whether or how these models apply to the auditory domain. In particular, we
20 47 wanted to test (i) whether exogenous auditory responses are really affected by attentional
21 48 sharpening, and, if so, (ii) how gain enhancement and sharpening relate within the context
22 49 of the auditory processing hierarchy: do they occur at the same or different processing
23 50 levels, and do they operate cooperatively or independently of one another?
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34 51 Numerous earlier studies have found non-invasively recorded auditory cortical
35 52 responses to be larger when the evoking sound is attended, rather than unattended
36 53 (EEG/MEG: Fujiwara, Nagamine, Imai, Tanaka, & Shibasaki, 1998; Hillyard et al., 1973;
37 54 Hillyard et al., 1998; Woldorff et al., 1993; Woldorff & Hillyard, 1991; fMRI: Jäncke,
38 55 Mirzazade, & Shah, 1999), and have generally interpreted this finding within the context of a
39 56 gain enhancement mechanism. More recently, however, it has been suggested that auditory
40 57 attentional modulation also involves sharpening (Ahveninen et al., 2011; Kauramaki,
41 58 Jääskeläinen, & Sams, 2007; Okamoto, Stracke, Wolters, Schmael, & Pantev, 2007). To
42 59 demonstrate sharpening, the previous studies have used paradigms involving “notched
43 60 noise” (NN) masking, a technique that has been used extensively in behavioral
44 61 measurements of auditory frequency selectivity (e.g., Glasberg & Moore, 1990). NN masking
45 62 requires the subject to attend to a fixed-frequency tone, whilst trying to ignore a
46 63 concurrently presented broadband noise with a spectral notch centered on the tone
47 64 frequency. When the notch is narrow enough so that the tone response is partially
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3 65 obscured, or “masked”, by the noise response, the size of the unobscured portion of the
4 66 tone response (over and above the noise response) should depend on the tuning selectivity
5 67 of the tone-responsive neurons (Sams & Salmelin, 1994), and should thus be sensitive to any
6 68 sharpening in tuning selectivity induced by attention. Consistent with this expectation, the
7 69 previous studies have found greater attentional enhancement of the tone response size
8 70 when the notch was narrower than when it was wider (Kauramaki et al., 2007; Okamoto et
9 71 al., 2007), or when the masking noise was omitted altogether (Ahveninen et al., 2011).
10 72 Arguably, however, this finding could also be explained in terms of gain enhancement. This
11 73 is, because the tone was presented at a fixed intensity and would thus have been less
12 74 audible when presented in a narrow-notched noise. As a result, the unattended tone
13 75 response size would have been smaller, and the attentional task would have been more
14 76 difficult to perform. Earlier findings (Alho, Woods, Algazi, & Näätänen, 1992; Boudreau,
15 77 Williford, & Maunsell, 2006; Schwent, Hillyard, & Galambos, 1976a, 1976b) suggest that
16 78 both factors should have led to greater attentional gain enhancement, thus mimicking the
17 79 effect of attentional sharpening.

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29 80 To avoid these confounds, the current study manipulated attention and measured
30 81 tuning selectivity independently using dichotic listening and adaptation, respectively. Tone
31 82 or noise sequences were presented concurrently to opposite ears (“Ipsi” and “Contra” in Fig.
32 83 1A) and subjects were asked to alternately attend to one or other sequence. Cortical
33 84 auditory-evoked potentials (CAEPs) were recorded in response to the tone sequences, and
34 85 the tone frequency was varied randomly from trial to trial to vary the degree of adaptation
35 86 between successive tones. Adaptation refers to the suppression in neuronal response when
36 87 the same or similar stimulus is presented repeatedly (hence also referred to as “repetition
37 88 suppression”; Grill-Spector, Henson, & Martin, 2006). Adaptation is ubiquitous across many
38 89 sensory domains and has become a popular tool for probing functional properties of
39 90 neuronal populations, particularly in the visual domain (reviewed in Snow, Coen-Cagli, &
40 91 Schwartz, 2017; Webster, 2015), but to a lesser degree also in the auditory domain (e.g.,
41 92 Briley, Breakey, & Krumbholz, 2013; Edmonds & Krumbholz, 2014; Hewson-Stoate,
42 93 Schonwiesner, & Krumbholz, 2006; Magezi & Krumbholz, 2010; Salminen, May, Alku, &
43 94 Tiitinen, 2009). Under the assumption that adaptation is caused by neuronal fatigue
44 95 (mediated by synaptic depression or somatic after-hyperpolarization; Briley & Krumbholz,
45 96 2013; Lanting, Briley, Sumner, & Krumbholz, 2013), the degree of adaptation between two

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3 97 successive tones should depend on the degree of overlap between the neuron populations
4 98 responsive to the tones, and this, in turn, should depend on the neurons' frequency tuning
5 99 selectivity. Figure 1B shows predictions of how the adapted tone response sizes might be
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8 100 affected by attentional gain enhancement and sharpening effects. The predictions are based
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10 101 on a simple neuron population model, with model neurons tuned for frequency and subject
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12 102 to activity-dependent adaptation, or fatigue (see Methods for model details). Due to
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14 103 adaptation, the aggregate population response size to the current tone is predicted to
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16 104 increase with increasing frequency separation of the preceding tone, regardless of attention
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18 105 condition (right panels in Fig. 1B). Under the assumption of a pure gain enhancement
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20 106 mechanism (with multiplicative gain; top row in Fig. 1B), attention is predicted to increase
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22 107 the population response size equally across all frequency separations (if response size is
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24 108 expressed in logarithmic units), leaving the shape of the response size function unchanged.
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26 109 In contrast, a pure sharpening mechanism (middle row in Fig. 1B) is predicted to increase
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28 110 the initial slope of the response size function (at small frequency separations), but also, to
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30 111 cause an overall suppression in response size across all frequency separations. The
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32 112 suppression arises, because, as the neurons' tuning selectivity increases, fewer neurons are
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34 113 activated and thus the aggregate population response size decreases. In order to avoid
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36 114 suppression, the sharpening has to be combined with a gain enhancement such that the
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38 115 aggregate response size remains constant (Fig. 1B, bottom row). As a result, the initial slope
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40 116 of the response size function is again predicted to steepen, but the response size now
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42 117 remains unchanged at zero and large frequency separations (when the responses to the
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44 118 successive tones overlap either completely or not at all; see left and middle panels in Fig.
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46 119 1B).

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48 120 ***insert Fig 1 about here***

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50 121 The previous studies that have used NN masking to investigate auditory attentional
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52 122 modulation mechanisms (Ahveninen et al., 2011; Kauramaki et al., 2007; Okamoto et al.,
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54 123 2007) have focused exclusively on the prominent N1 deflection of the CAEPs (Näätänen &
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56 124 Picton, 1987). Here, we also examined the preceding and following P1 and P2 deflections,
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58 125 which, like the N1, are exogenous, and thus presumably represent earlier and later stages of
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60 126 sensory-driven auditory processing. Our results suggest that gain enhancement and
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128 127 sharpening represent cooperative components of a hierarchically distributed auditory
attentional modulation mechanism, affecting different sensory-driven processing levels: the

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3 129 earliest observed attention effects (in the N1) appeared to be pure gain enhancement
4 130 effects, whilst sharpening effects appeared to emerge only at later processing levels (in the
5 131 P2). Our results suggest that gain enhancement and sharpening might work together to
6 132 increase the representational bandwidth, or “data rate”, of attended over unattended
7 133 auditory information.
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12 135 MATERIALS AND METHODS

13 136 **Participants**

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16 137 23 subjects (7 male; mean age = 23.1, SD = 3.8 years) participated after having given written
17 138 informed consent. All subjects had hearing thresholds at or below 20 dB HL at all
18 139 audiometric frequencies (250-8000 Hz), and had no history of audiological or neurological
19 140 disease. The experimental procedures accorded with the Declaration of Helsinki (Version 6,
20 141 2008) and were approved by the Ethics Committee of the University of Nottingham School
21 142 of Psychology, but were not formally pre-registered online in accordance with the 2014
22 143 amendment to the declaration.
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28 144 **Stimuli and procedure**

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30 145 During the EEG experiment, subjects were comfortably seated in an electrically shielded,
31 146 sound-attenuating booth (IAC Acoustics, Winchester, United Kingdom). The experiment
32 147 consisted of four runs with short breaks in between. In three runs, referred to as “active
33 148 runs”, subjects were required to alternately attend to tone or noise sequences, presented to
34 149 opposite ears, and detect infrequent targets within the attended ear. The to-be-attended
35 150 ear was indicated by visual instruction and was switched every ~2 min. The ear of
36 151 presentation of the tone and noise sequences was counterbalanced across subjects. The
37 152 active runs lasted about 12 min each. In the remaining run, referred to as “passive run”, the
38 153 stimuli were presented passively whilst the subjects watched a silent sub-titled movie of
39 154 their own choice to remain alert. The duration of the passive run was matched to the total
40 155 duration for which subjects attended to each ear over the three active runs (i.e., $3 \times 6 \text{ min} =$
41 156 18 min). The active and passive runs were played consecutively, in counterbalanced order
42 157 across subjects.
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53 158 The tones (“Ipsi” in Fig. 1A) had a duration of 100 ms, including 20-ms cosine-
54 159 squared onset and offset ramps, and were presented at a fixed stimulus onset interval (SOI)
55 160 of 500 ms. A fixed SOI was used, because varying it would have varied the degree of
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3 161 adaptation between successive tones (Lanting et al., 2013) and thus confounded the tuning
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5 162 selectivity measurement. The tone frequencies were distributed equally between four
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7 163 different values, which were by 0, 75, 150 and 300 cents higher than 1000 Hz (1000, 1044,
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9 164 1091, 1189 Hz). The tone sequences were pseudo-random de Bruijn sequences consisting of
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11 165 256 items each (lasting ~2 min). They were designed such that not only each frequency
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13 166 individually, but also each possible combination of two, three or four consecutive
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15 167 frequencies occurred an exactly equal number of times (64, 16, 4 and 1, respectively;
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17 168 Brimijoin & O'Neill, 2010).

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19 169 The noise stimuli ("Contra" in Fig. 1A) were generated from equally exciting noise
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21 170 (with equal energy falling in each auditory filter; Glasberg & Moore, 2000), which was box-
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23 171 car filtered between 2000 and 3000 Hz. They had a duration of 200 ms, and were amplitude-
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25 172 modulated with a waxing amplitude envelope consisting of linear onset and offset ramps
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27 173 lasting 150 and 50 ms, respectively. The SOI of the noises was randomized between 666 and
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29 174 966 ms (mean: 816 ms) to decorrelate the onset times of the tones and noises across the
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31 175 two ears.

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33 176 The tone targets were distinguished from the non-target tones by a linearly rising
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35 177 frequency ramp (the non-target tones had a steady frequency; right panel in Fig. 1A). They
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37 178 were presented randomly with a probability of 7.5%, with the constraint that every two
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39 179 successive target tones were separated by at least four non-target tones. The noise targets
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41 180 were time-reversed versions of the non-target noises (non-targets were waxing, and targets
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43 181 were waning noises; Fig. 1A; idea taken from Cusack, Deeks, Aikman, & Carlyon, 2004). They
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45 182 were presented with a probability of 10% and separated by at least two non-target noises.
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47 183 On average, both the tone and noise targets occurred about 20 times within each ~2-min
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49 184 period (targets were presented within both the attended and unattended sequences).

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51 185 All stimuli were generated digitally using Matlab (The Mathworks, Natick, MA, USA)
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53 186 and digital-to-analogue converted with a 24.414-kHz sampling rate and 24-bit amplitude
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55 187 resolution using TDT System 3 (Tucker Davis Technologies, Alachua, FL, USA) consisting of an
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57 188 RP2.1 real-time processor and an HB7 headphone buffer. Both the tone and noise stimuli
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59 189 were presented at a sound pressure level (SPL) of 65 dB using Sennheiser HD-280 Pro
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61 190 circumaural headphones (Sennheiser, Wedemark, Germany).

191 **EEG recordings**

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3 192 CAEPs were recorded with 33 Ag/AgCl ring electrodes (EASYCAP, Herrsching, Germany),
4 193 placed according to the standard 10-20 layout, and a BrainAmp DC EEG amplifier (Brain
5 194 Products, Gilching, Germany). Skin-to-electrode impedances were maintained below 5 k Ω
6 195 throughout the recordings. The recording reference was the vertex (Cz) channel and the
7 196 ground was placed on the central forehead (AFz). The electrode signals were sampled at 500
8 197 Hz and bandpass-filtered online between 0.1 and 250 Hz using BrainVision Recorder (Brain
9 198 Products). Only the responses to the non-target tones were analyzed further.

199 **EEG data analysis**

16 200 The EEG data were first pre-processed using the EEGLAB toolbox (Delorme & Makeig, 2004),
17 201 which runs under Matlab. First, they were lowpass filtered at 35 Hz using a -48-dB/oct zero-
18 202 phase IIR filter, and then they were re-referenced to average reference and segmented into
19 203 500-ms epochs ranging from 100 ms before, to 400 ms after the onsets of the non-target
20 204 tones. Epochs containing unusually large amplitudes across electrodes (joint probability
21 205 larger or equal to three standard deviations) were rejected automatically. The remaining
22 206 epochs were submitted to an independent component analysis (extended infomax
23 207 algorithm). Components representing eye blinks, lateral eye movements and electro-cardiac
24 208 activity were removed by manual inspection of the components' temporal traces and scalp
25 209 topographies.

26 210 Activity during the baseline period of the tone responses (before the tone onset) was
27 211 both highly non-stationary and also considerably larger for attended than unattended trials
28 212 (Fig. 2A), suggesting the presence of longer-lasting endogenous activity from preceding trials
29 213 (Woldorff, 1993). To minimize the effect of this activity on the analysis of the discernible
30 214 exogenous deflections (P1, N1 and P2; Fig. 2A), we baseline-corrected each deflection
31 215 separately, using a different baseline window (referred to as "deflection-specific" baseline
32 216 correction). All windows were given a minimal duration of only 8 ms. The windows for the
33 217 N1 and P2 were centered at the peaks of the respective preceding, opposite-polarity
34 218 deflections (P1 and N1, respectively), thus effectively creating a peak-to-peak difference.
35 219 This would be expected to minimize any unipolar activity associated with endogenous
36 220 attentional processing, such as the so-called "processing negativity" (Näätänen, 1990),
37 221 which would affect opposite-polarity deflections in opposite directions, and thus cancel in
38 222 the peak-to-peak difference. The window for the P1 was located at the tone onset (around 0
39 223 ms), close to the P1 deflection start. The baseline correction was performed separately for

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3 224 each subject and analyzed condition. The baseline-corrected deflections will be referred to
4 225 as $P1_0$, $N1_{P1}$ and $P2_{N1}$ to indicate the differences in baseline window (see Fig. 2B).

6 226 The $P1_0$, $N1_{P1}$ and $P2_{N1}$ peak amplitudes were measured both from the original
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8 227 sensor data, and also from source waveforms derived from source models fitted to each
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10 228 deflection peak. The sensor data were evaluated at the sensors that showed the largest
11 229 unattended deflection peaks on average (Fz for the $P1_0$ and $N1_{P1}$, and Cz for the $P2_{N1}$) and
12 230 referenced to the linked mastoids (average of TP9 and TP10). The source models were fitted
13 231 to the unattended conditions only (when subjects attended to the noise sequences in the
14 232 opposite ear or watched a silent movie) to create a spatial filter for exogenous auditory
15 233 cortical activity. They were implemented in the Brain Electrical Source Analysis software,
16 234 version 5.3 (BESA, Gräfelfing, Germany), and each consisted of two hemispherically
17 235 symmetric regional equivalent current dipoles (ECDs; Scherg & Ebersole, 1993), with a four-
18 236 shell ellipsoidal volume conductor as head model. First, the ECD locations were fitted to a
19 237 30-ms window centered at the relevant deflection peak in the grand-average response
20 238 across all subjects and unattended conditions. Then, the ECDs were then re-oriented
21 239 individually for each subject to maximize the peak source strength along their first dipole
22 240 direction, and the resulting reoriented first dipole directions were used to extract source
23 241 waveforms for each individual and condition. The source waveforms showed no significant
24 242 hemispheric differences, and were thus averaged across hemispheres.

25 243 The $P1_0$, $N1_{P1}$ and $P2_{N1}$ peak amplitudes were either averaged across all tone
26 244 frequencies, or evaluated separately for each absolute frequency separation, ΔF , between
27 245 the current and preceding tones, which could take one of four values (0, 75, 150 or 300
28 246 cents). On average, the number of trials available for each absolute frequency separation
29 247 and each subject was 391 (range: 347-414), 479 (409-517), 481 (428-507) and 241 (208-258)
30 248 when subjects attended to the tone sequences, 397 (374-419), 490 (463-512), 491 (465-508)
31 249 and 245 (231-260) when they attended to the noise sequences, and 380 (330-406), 469
32 250 (421-499), 467 (412-506) and 236 (212-248) when they watched a silent movie (passive
33 251 run).

51 252 **Statistical analyses**

52 253 Statistical analyses were conducted using *R* (R Core Team, 2013). Both the behavioral
53 254 (hit/false-alarm rates and reaction times for target detection) and CAEP data (deflection
54 255 peak amplitudes) were evaluated with linear mixed-effects models (nlme package; Pinheiro,

256 Bates, DebRoy, Sarkar, & Team, 2017). The CAEP peak amplitudes were first converted to
 257 logarithmic units.

258 Homogeneity of variance was tested using Levene's test (car package; Fox &
 259 Weisberg, 2011), and normality using quantile-quantile plots of the model residuals. Where
 260 variance homogeneity was violated (i.e., the residuals were significantly different across
 261 factor levels), each observation was weighted by the inverse of the variance for the
 262 respective factor level. This reduces the influence of noisier data points on the model fit.
 263 Normality was achieved by log-transformation (applied to the false-alarm rates and reaction
 264 times). Any overly influential data points were identified using Cook's distance and
 265 excluded.

266 In the models of the CAEP peak amplitudes, the linear frequency separation
 267 covariate (ΔF) was shifted downwards by 150 cents ($\Delta F \rightarrow \Delta F - 150$ cents) to reduce
 268 collinearity with the quadratic covariate (ΔF^2). Next to the fixed effects, all models also
 269 contained by-subjects random intercepts and fixed-factor slopes. The fixed effects were
 270 fitted using maximum likelihood (ML) estimation, and the random effects using restricted
 271 ML (REML) estimation. Random effects were tested using log-likelihood ratio tests. Random
 272 effects that failed to produce a significant improvement in model fit were omitted. Fixed
 273 effects were evaluated using conditional F-tests following the strategy described in Pinheiro
 274 and Bates (2000). Despite some missing data points, the number of data points were
 275 sufficiently similar across the various combinations of factor levels to allow type-III
 276 (marginal) tests to be evaluated for all included fixed effects. Significant fixed effects were
 277 post-hoc tested using Tukey's honestly significant difference (multcomp package; Hothorn,
 278 Bretz, & Westfall, 2008).

279 **Neuron population model of attentional modulation effects**

280 Predicted effects of gain enhancement and sharpening were derived with a neuron
 281 population model, where each neuron was tuned to a different characteristic frequency, f_c ,
 282 and subject to activity-dependent adaptation or fatigue, A . The shape of the frequency
 283 tuning was defined by a rounded-exponential (roex)

284 function, $W(f) = \left(1 - p \frac{|f_c - f|}{f_c}\right) e^{-p \frac{|f_c - f|}{f_c}}$ (Eq. 1), where f is the frequency of the tone
 285 stimulus, $|f_c - f|$ is its absolute separation from the neuron's characteristic frequency (f_c),
 286 and p is a parameter that determines the tuning sharpness. p was set such that tuning curve

widths corresponded to the equivalent rectangular bandwidths (ERBs) of the auditory frequency filters as determined by behavioral NN masking: $p = \frac{4f_c}{ERB(f_c)}$, where $ERB(f_c) = 24.7(4.37f_c + 1)$ (Glasberg & Moore, 1990). The characteristic frequencies (f_c) varied from 50 to 16000 Hz and were distributed evenly on a cochlear frequency (ERB-rate; Moore & Glasberg, 1983) scale.

Adaptation was modelled by multiplying the unadapted response to the current tone frequency, f_0 [given by $W(f_0)$; Eq. 1] with a factor $1-A$, where A was proportional to the response to the preceding tone frequency, f_{-1} [given by $W(f_{-1})$]. The degree of adaptation (A) was assumed to decay exponentially over time (t): $A(t) = A(t = 0)e^{-t/\tau}$. The decay time constant, τ , was set to 721.34 ms (compare Briley & Krumbholz, 2013; Roth et al., 1976), which meant that, between successive tone onsets, adaptation decayed by 50% (because $e^{-500/721.34} = 0.5$). The aggregate response size was derived by summing the adapted single-neuron responses across neurons.

Attentional gain enhancement was modelled by multiplying the single-neuron tuning functions W (Eq. 1) with a gain factor, $G > 1$. In the simulation shown in Fig. 1B (upper row), G was set to 2 – doubling the attended compared to unattended response size. Attentional sharpening was modelled by dividing the tuning sharpness parameter, p , by a sharpening factor, $S < 1$. In the simulations shown in Fig 1B (middle and bottom rows), S was set to 0.5 – halving the ERBs of the attended compared to unattended tuning functions. If no gain is applied ($G = 1$), halving the ERBs halves the aggregate response sizes (middle row). In order to preserve the aggregate response size (bottom row), G was concurrently raised to 2.

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309 RESULTS

310 Behavioral results

311 During the EEG recordings, subjects either ignored the experimental sounds and watched a
 312 silent subtitled movie, or alternately monitored the tone or noise sequences in the different
 313 ears for occasional target sounds (frequency-modulated tones and waning noises,
 314 respectively; Fig. 1A). In order to match the difficulty in detecting the tone and noise targets,
 315 each subject first attended a short pilot session, where the target salience (determined by
 316 the frequency or amplitude modulation depth, respectively) was adjusted to yield a ~75%
 317 hit rate. Across subjects, the adjusted frequency modulation depth of the tone targets

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3 318 ranged between 100-200 cents, and the amplitude modulation depth of the noise targets
4 319 ranged between 50-100%.

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6 320 During the experiment proper, the tone targets yielded an actual hit rate close to the
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8 321 adjusted rate (mean \pm standard error: $76.0 \pm 3.1\%$), and a false alarm rate of $10.0 \pm 2.8\%$. In
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10 322 contrast, the actual hit rate for the noise targets was significantly higher [$85.0 \pm 2.8\%$;
11 323 $F(1,105) = 11.3$, $p = 0.0011$; here and onwards, statistical tests are based on linear mixed-
12 324 effects models (LMMs), with F and p values based on conditional F-tests; see Methods], and
13 325 the false-alarm rate significantly lower [$4.4 \pm 1.3\%$; $F(1,105) = 5.8$ $p = 0.0180$]. At the same
14 326 time, however, the noise targets also yielded a longer reaction time [613.6 ± 26.3 ms vs
15 327 566.0 ± 18.0 ms for the tone targets; $F(1,104) = 5.7$ $p = 0.0185$], suggesting that subjects
16 328 traded response speed with response accuracy. In the case of the tone sequences, the scope
17 329 for such speed-accuracy trade-off was limited by the shorter SOI (500 ms vs 816 ± 150 ms
18 330 for the noise sequences; see Methods), which limited the reaction time. The presence of
19 331 speed-accuracy trade-off is supported by the inverse efficiency score (IES), which combines
20 332 response speed and accuracy measures into a single, overall measure of task performance
21 333 [$IES = RT/(1-PE)$, where RT is the reaction time and PE is the proportion of errors, i.e., false
22 334 alarms and missed targets; Townsend & Ashby, 1978], and which was not significantly
23 335 different between the tone and noise sequences [tones vs noises: 814.4 ± 124.1 ms vs 829.5
24 336 ± 72.2 ms; $F(1,103) = 0.12$ $p = 0.7159$]. The IES was also not significantly different across the
25 337 three successive ~ 12 -min measurement runs ["active runs"; main effect of run: $F(1,103) =$
26 338 0.63 , $p = 0.4274$; interaction between run and sequence type: $F(1,103) = 0.28$, $p = 0.5949$].

339 **Average CAEPs**

340 The average CAEPs to the non-target tones (averaged across all frequency separations
341 between successive tones; Fig. 2A) exhibited three successive transient deflections, P1, N1
342 and P2, which were clearly discernible, and peaked at similar latencies (around 60, 105 and
343 150 ms), both when the tones were attended (top panel in Fig. 2A), and when they were
344 unattended (i.e., when subjects attended to the noise sequences in the other ear or
345 watched a silent movie; bottom panel in Fig. 2A). Due to the relatively short SOI used (500
346 ms), the CAEPs failed to return to a steady baseline before the subsequent tone onset. As a
347 result, the transient deflections were riding on a background of slowly-varying non-
348 stationary EEG activity from previous trials, which appeared to be particularly evident in the

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3 349 attended condition (Fig. 2A, top). The non-stationarity of this background activity meant
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5 350 that it could not be eliminated by conventional baseline correction, and the use of a fixed
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7 351 SOI (required to control the degree of adaptation between successive tones) meant that it
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9 352 could also not be eliminated by deconvolution-based methods (Lütkenhöner, 2010;
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11 353 Woldorff, 1993). To address this problem, we here opted to baseline-correct each deflection
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13 354 separately, using a baseline window that was both minimal in duration and located close to
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15 355 the respective deflection start (deflection-specific baselining; see Methods). The N1 and P2
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17 356 were baseline-corrected to the respective preceding, opposite-polarity peak – effectively
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19 357 creating a peak-to-peak difference. This would have minimized both the slowly-varying
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21 358 previous-trial baseline, as well as any unipolar endogenous attention-related activity elicited
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23 359 within the current trial (such as the processing negativity; Näätänen, 1990). The baseline-
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25 360 corrected deflections are shown in Fig. 2B (separately for each attention condition) and will
26
27 361 be referred to as P1₀, N1_{P1} and P2_{N1}. Figure 3A shows that they exhibited scalp voltage
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29 362 distributions typical of sources in supratemporal auditory cortex (characterized by a voltage
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31 363 inversion over the temporal bone; Scherg, Vajsar, & Picton, 1989; Vaughan & Ritter, 1970).

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364 ***insert Fig 2 about here***

365 CAEPs measured at individual sensors may reflect a mixture of contributions from
366 both exogenous and endogenous sources, but only the exogenous contributions represent
367 the *modulatory* attention effects that we aim to investigate. Thus, to maximize these
368 contributions, we analyzed the CAEPs not only in the original sensor space (using the
369 sensors that showed the largest unattended peak amplitude for the respective analyzed
370 deflection; see Methods and Fig. 2B), but also in a source space representing exogenous
371 sources. A different source model was used for each subject and analyzed deflection, based
372 on equivalent dipoles fitted to the respective deflection peak in the individual *unattended*
373 responses (where endogenous contributions should have been minimal; see Methods).
374 Figure 3B shows that the best-fitting sources for all three unattended deflections (P1₀, N1_{P1}
375 and P2_{N1}) localized to the approximate auditory cortex region, and that their average
376 orientations were roughly perpendicular to the supratemporal plane. The goodness of fit
377 ranged between 89.4 and 98.5% for the P1 [mean \pm standard deviation: 96.4 ± 2.4],
378 between 93.7 and 98.5% for the N1 (97.1 ± 1.4), and between 88.3 and 98.3% for the P2
379 (95.6 ± 2.2). The sources were used as spatial filters to extract source waveforms for each
380 individual and condition (see Fig. 3C for the grand-average source waveforms for each

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3 381 attention condition), and the source waveforms were averaged across hemispheres,
4 382 because no significant hemisphere-specific condition effects were found.

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6 383 ***insert Fig 3 about here***
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8 384 **Attention effects on average CAEPs**

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10 385 Comparison of the average CAEP waveforms between attention conditions (see Figs 2B & 3C
11 386 for the sensor and source waveforms, respectively) suggests that the $N1_{P1}$, and, to a lesser
12 387 degree, also the $P2_{N1}$, were enhanced when the tones were attended than when they were
13 388 unattended, whereas the $P1_0$ seemed to be largely unaffected by attention. The waveforms
14 389 also suggest that there was little difference between the two unattended conditions (i.e.,
15 390 when subjects attended to the noise sequences or watched a silent movie, labelled
16 391 "ignored" and "passive" in Figs 2B & 3C) – for any of the three deflections.

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18 392 These results were confirmed by submitting the average deflection peak amplitudes
19 393 (in logarithmic units; Fig. 4A) to linear mixed-effects statistical models (LMMs), with
20 394 attention condition and deflection (if appropriate) as fixed factors. The models were
21 395 calculated either for successive deflection pairs [$P1_0/N1_{P1}$ and $N1_{P1}/P2_{N1}$], or for each
22 396 deflection separately (henceforth referred to as "combined" or "separate LMMs"). Effects
23 397 that were significant in the current, but not the preceding deflection were interpreted as
24 398 "emerging" at the level of the current deflection. Both for the sensor, and for the source
25 399 data, the combined LMM of the $P1_0/N1_{P1}$ peak amplitudes revealed a significant overall
26 400 (main) effect of attention condition [sensor: $F(2,107) = 3.8$, $p = 0.0254$; source: $F(2,105) =$
27 401 6.3 , $p = 0.0026$], but also showed a significant deflection by attention condition interaction
28 402 [sensor: $F(2,107) = 15.5$, $p < 0.0001$; source: $F(2,105) = 11.1$, $p < 0.0001$]. The interaction
29 403 arose, because the attention condition effect was significant only for the $N1_{P1}$ [shown by the
30 404 respective separate LMMs; sensor: $F(2,42) = 33.0$, $p < 0.001$; source: $F(2,42) = 28.7$, $p <$
31 405 0.0001], but non-significant for the $P1_0$ [sensor: $F(2,43) = 0.8$, $p = 0.4717$; source: $F(2,41) =$
32 406 0.4 , $p = 0.6672$]. This suggests that the attention condition effect first emerged at the level
33 407 of the $N1$. In the combined LMM of the $N1_{P1}/P2_{N1}$ peak amplitudes, the main effect of
34 408 attention condition was again significant for both the sensor and the source data [sensor:
35 409 $F(2,107) = 13.3$, $p < 0.001$; source: $F(2,105) = 11.5$, $p < 0.0001$]. In this case, the deflection by
36 410 attention condition interaction was significant for the source data [$F(2,105) = 5.7$, $p =$
37 411 0.0045], but non-significant for the sensor data [$F(2,107) = 0.7$, $p = 0.5079$]. Consistent with
38 412 this, the separate LMM for the $P2_{N1}$ showed a significant attention condition effect for the

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3 413 sensor data [$F(2,42) = 4.1, p = 0.0233$], but not for the source data [$F(2,41) = 2.12, p =$
4 414 0.1274]. This suggests that the attention condition effect on the average $P2_{N1}$ peak
5 415 amplitudes was more labile than for the $N1_{P1}$. For the $N1_{P1}$, the attention condition effect
6 416 was due to larger peak amplitudes in the attended compared to both unattended (ignored
7 417 and passive) conditions. This was true for both the sensor (both $p \leq 0.0001$) and source data
8 418 (both $p < 0.0001$). For the $P2_{N1}$ sensor amplitudes, the difference between the attended and
9 419 ignored conditions was significant ($p = 0.00971$), but the difference between the attended
10 420 and the passive conditions was non-significant ($p = 0.22429$; see stars in Fig. 4A). The
11 421 ignored and passive conditions showed little or no differences between one another – for
12 422 any deflection and in either the sensor or source data (all $p > 0.4$).

423 **Attention effects on frequency-specific adaptation**

424 To test whether the observed attention effects on the average deflection peak amplitudes
425 were generated by gain enhancement or sharpening, we evaluated the peak amplitudes
426 separately for the different frequency separations, ΔF , from the preceding tone, which were
427 expected to cause different degrees of adaptation (Fig. 1B). In the statistical models (LMMs)
428 frequency separation was included both as a linear (ΔF) and quadratic (ΔF^2) fixed covariate,
429 because, based on the neuron population model predictions (Fig. 1B), the linear covariate
430 alone was not expected to be able to capture the effect of sharpening. For gain
431 enhancement, the model predicted a constant increase in the response size across all
432 frequency separations from the preceding tone. Statistically, this should create a main effect
433 of attention condition, with no interaction with either frequency separation covariate (ΔF or
434 ΔF^2). In contrast, the sharpening mechanism was predicted to cause the response size
435 function to become steeper at small frequency separations, thus making the function more
436 non-linear. Statistically, this should give rise to a significant interaction between ΔF^2 and
437 attention condition. The average peak amplitudes had shown no significant differences
438 between the ignored and passive conditions for any deflection (see Fig. 4A) and the same
439 was also true for the peak amplitudes as a function of frequency separation (Fig. 4B&C).
440 Therefore, the ignored and passive conditions were now merged to a form a single
441 “unattended” condition.

442 ***insert Fig 4 about here***

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3 443 The $N1_{P1}$ and $P2_{N1}$ peak amplitudes increased with increasing frequency separation (Fig.
4 444 4B&C), as predicted by the neuron population model (compare Fig. 1B). The corresponding
5 445 (separate) LMMs revealed that this increase was significant for both the sensor [main effect
6 446 of ΔF ; $N1_{P1}$: $F(1,241) = 13.8$, $p = 0.003$; $P2_{N1}$: $F(1,243) = 15.2$, $p = 0.0001$] and source data
7 447 [$N1_{P1}$: $F(1,241) = 5.3$, $p = 0.0221$; $P2_{N1}$: $F(1,243) = 17.9$, $p < 0.0001$]. These results indicate
8 448 that the N1 and P2 were affected by frequency-specific adaptation. In contrast, the peak
9 449 amplitudes for the $P1_0$ showed little or no change with frequency separation, for either the
10 450 sensor [main effects of ΔF and ΔF^2 ; both $F(1,235) \leq 0.5$, $p \geq 0.4788$] or source data [both
11 451 $F(1,236) \leq 0.8$, $p \geq 0.3751$], suggesting that the P1 was either not adapted, or that
12 452 adaptation in the P1 was non-specific to frequency.

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20 453 Figure 4B&C (middle panels) suggests that attention increased the $N1_{P1}$ peak amplitudes
21 454 about equally across all frequency separations. This finding was statistically confirmed by
22 455 the non-significance of the interactions between attention condition and both ΔF and ΔF^2 in
23 456 the separate LMM for the $N1_{P1}$, which applied to both the sensor [both $F(1,241) \leq 1.3$, $p \geq$
24 457 0.2558] and source data [both $F(1,241) \leq 2.5$, $p \geq 0.1164$], and is consistent with the neuron
25 458 population model predictions for gain enhancement (compare upper right panel in Fig. 1B).
26 459 In contrast, the attention effect on the $P2_{N1}$ peak amplitudes depended strongly on
27 460 frequency separation, with little or no increase at the zero and largest frequency
28 461 separations (0 and 300 cents; 100 cents correspond to 1 semitone), but large increases at
29 462 the intervening frequency separations (75 and 150 cents; rightmost panels in Fig. 4B&C).
30 463 This pattern is consistent with the neuron population model predictions for sharpening
31 464 combined with a commensurate gain enhancement to preserve the aggregate response size
32 465 (compare bottom right panel in Fig. 1B). Statistically, it was confirmed by the significance of
33 466 the interaction between attention condition and ΔF^2 in the separate LMM for the $P2_{N1}$,
34 467 which, again, applied to both the sensor [$F(1,243) = 11.0$, $p = 0.001$] and source data
35 468 [$F(1,243) = 5.0$, $p = 0.0264$]. The interaction between attention condition and ΔF was non-
36 469 significant [sensor: $F(1,243) = 0.4$, $p = 0.5292$; source: $F(1,243) = 0.2$, $p = 0.6822$].

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41 470 The difference in the pattern of frequency separation-dependent attention effects
42 471 between the $N1_{P1}$ and $P2_{N1}$ was statistically confirmed by the three-way interaction
43 472 between deflection, attention condition and ΔF^2 in the corresponding combined LMM
44 473 ($N1_{P1}/P2_{N1}$). This interaction, which was significant in the sensor data [$F(1,506) = 8.2$, $p =$

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3 474 0.0045] and approached significance in the source data [$F(1,506) = 3.2, p = 0.0764$],
4 475 suggesting that sharpening emerges only at the level of the P2. In contrast to the $N1_{P1}$ and
5 476 $P2_{N1}$, the $P1_0$ peak amplitudes showed no significant attention effects, at any frequency
6 477 separation, as confirmed by the lack of significant interactions between attention condition
7 478 and both ΔF or ΔF^2 in the separate LLMs for the $P1_0$ [sensor: both $F(1,235) \leq 0.1, p \geq 0.7699$;
8 479 source: both $F(1,236) \leq 1.4, p \geq 0.2427$].
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481 DISCUSSION

16 482 The current results suggest that the earliest effects of auditory attentional modulation
17 483 are mediated by a pure gain enhancement mechanism, and that sharpening emerges only at
18 484 later processing stages. In the current results, the earliest measured deflection, the P1 –
19 485 presumed to be generated in primary auditory cortex (Liégeois-Chauvel, Musolino, Badier,
20 486 Marquis, & Chauvel, 1994; Mäkelä, Hämäläinen, Hari, & McEvoy, 1994; Yvert, Crouzeix,
21 487 Bertrand, Seither-Preisler, & Pantev, 2001) – was little or not affected by attention. The
22 488 subsequent N1 showed a strong attention-related enhancement in average peak amplitude,
23 489 but no differential effects on frequency-specific adaptation, suggesting that the N1 was
24 490 affected by a pure gain enhancement mechanism. In contrast, the latest measured
25 491 deflection, the P2, showed a lesser enhancement in average peak amplitude, but a marked
26 492 increase in the degree of adaptation specificity. Predictions from a neuron population model
27 493 showed that the pattern of the effects in the P2 was consistent with a sharpening in neural
28 494 tuning selectivity, combined with a commensurate gain enhancement so that the overall
29 495 response size remained unchanged.
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41 496 These results are consistent with previous studies that have also found large attentional
42 497 enhancements in N1 peak amplitude (Hillyard et al., 1973; Neelon, Williams, & Garell,
43 498 2006a, 2006b), but contradict the conclusion of the previous NN masking studies
44 499 (Ahveninen et al., 2011; Kauramaki et al., 2007; Okamoto et al., 2007) that attentional
45 500 enhancement of the N1 is caused by neuronal sharpening. In the NN studies, attention was
46 501 directed to a specific frequency value and the audibility of the attended stimulus was
47 502 allowed to vary across conditions. As explained above (Introduction) this would likely have
48 503 led to variation in the amount of attentional gain enhancement, in a way that would have
49 504 mimicked the expected effect of sharpening (Alho et al., 1992; Boudreau et al., 2006;
50 505 Schwent et al., 1976a, 1976b). In the current study, attention was directed to one or other
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3 506 ear, and stimulus audibility was fixed across conditions. Our results thus suggest that
4 507 attention can sharpen selectivity for a feature (here, frequency) even when attention is not
5 508 selectively focused on a specific feature value. A similar conclusion was reached by Murray
6 509 and Wojciulik (2004), who used an adaptation paradigm to demonstrate attentional
7 510 sharpening for visual orientation. In both our and Murray and Wojciulik's studies, the
8 511 feature in which sharpening was observed (frequency and visual orientation, respectively)
9 512 was task-relevant (in Murray and Wojciulik's study, subjects had to detect a change in image
10 513 orientation; in our study, they had to detect a small frequency modulation). It is thus
11 514 possible that task relevance is a prerequisite for sharpening to occur.

12 515 The absence of significant attention effects in the earliest, P1, deflection in the current
13 516 study is consistent with several previous studies (Hillyard et al., 1973; Neelon, Williams, &
14 517 Garell, 2006a, 2006b) that have also found no significant P1 attention effects. Other studies,
15 518 however, that have used shorter SOIs, did find significant attention effects in the P1, and
16 519 even earlier, deflections (Woldorff et al., 1993; Woldorff & Hillyard, 1991), suggesting that
17 520 the first emergence of attention effects is graded with attentional load.

18 521 The current finding of a small but significant (in the sensor data) attentional
19 522 enhancement in the average P2 peak amplitude contrasts with some previous CAEP studies
20 523 that have found either no significant change (Hillyard et al., 1973) or even a reduction
21 524 (Hansen & Hillyard, 1980) in the P2 amplitude as a result of attention. The reduction has
22 525 been attributed to a separate unipolar deflection, termed the "processing negativity" or
23 526 "Nd", thought to reflect endogenous attention-related processes (Näätänen, 1990). Due to
24 527 its negative polarity, the Nd would be expected to add to any modulatory enhancement of
25 528 the N1, but diminish any enhancement of the P2. In the current study, this effect would
26 529 have been minimized by the deflection-specific baselining procedure used (see Methods).
27 530 Significant attentional enhancement of the P2 has also been found in intracranial recordings
28 531 from the auditory temporal region (Neelon et al., 2006a, 2006b), where any influence of the
29 532 Nd may also have been minimal. The Nd can be demonstrated by calculating the difference
30 533 wave between attended and unattended responses. In the current study, this was precluded
31 534 by the experimental design: Difference waves can only be meaningfully calculated when the
32 535 previous-trial baseline activity in the attended and unattended responses is either the same
33 536 on average (e.g., Hansen & Hillyard, 1983; Hillyard & Münte, 1984), or can be effectively
34 537 corrected for (e.g., Woldorff & Hillyard, 1991; Woldorff, 1993). In the current study,

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3 538 attended and unattended trials were temporally separated into different blocks, and so,
4 539 attended trials were always preceded by attended trials, and unattended trials were always
5 540 preceded by unattended trials. As a result, the attended responses exhibited a substantially
6 541 larger previous-trial baseline, on average, than the unattended responses. Correcting for the
7 542 baseline was also not possible, as this requires a sufficiently variable SOI (Lütkenhöner,
8 543 2010; Woldorff, 1993). In the current study, the SOI had to be fixed to control the degree of
9 544 adaptation between successive trials.

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15 545 The N1 and P2 have often been viewed as part of the same component process (the so-
16 546 called “N1-P2 complex”). However, the marked differences in the pattern of their observed
17 547 attention effects suggests that, rather than representing a unitary complex, the N1 and P2
18 548 represent different hierarchical levels of exogenous auditory processing that play distinct
19 549 functional roles in conscious sound perception. This is supported by previous findings
20 550 showing that the N1 and P2 differ not only in source structure (Godey, Schwartz, de Graaf,
21 551 Chauvel, & Liégeois-Chauvel, 2001; Hari, Kaila, Katila, Tuomisto, & Varpula, 1982; Hari et al.,
22 552 1987; Lütkenhöner & Steinsträter, 1998), but also in functional properties, such as
23 553 dependence on prior stimulation, general arousal, aging and auditory training (Crowley &
24 554 Colrain, 2004; Herrmann, Henry, Johnsrude, & Obleser, 2016; Ross, Jamali, & Tremblay,
25 555 2013; Ross & Tremblay, 2009; Roth et al., 1976; Tremblay, Ross, Inoue, McClannahan, &
26 556 Collet, 2014).

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35 557 The effect of attention on adaptation, or “repetition suppression”, has been investigated
36 558 by several previous studies – particularly in the visual domain and using fMRI (see Henson &
37 559 Mouchlianitis, 2007, for review). The results from these studies, however, have been mixed,
38 560 with some studies finding similar repetition suppression in both attended and unattended
39 561 conditions (Bentley, Vuilleumier, Thiel, Driver, & Dolan, 2003; Vuilleumier, Schwartz,
40 562 Duhoux, Dolan, & Driver, 2005), but others finding repetition suppression to be either
41 563 reduced (Murray & Wojciulik, 2004) or absent in unattended conditions (Eger, Henson,
42 564 Driver, & Dolan, 2004; Henson & Mouchlianitis, 2007; Yi, Kelley, Marois, & Chun, 2006; Yi,
43 565 Woodman, Widders, Marois, & Chun, 2004). The previous studies compared responses to
44 566 repeated versus different stimuli, but, unlike the current study, did not vary the degree of
45 567 stimulus difference. The current results suggest that the amount of unattended repetition
46 568 suppression should depend on the relation between the degree of stimulus difference and
47 569 neuronal tuning selectivity: if we had compared repeated versus different tones with only a

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3 570 single frequency separation, we would have observed similar attended and unattended
4 571 repetition suppression, if the frequency separation had been greater than 150 cents, but
5 572 reduced or absent unattended repetition suppression if the frequency separation had been
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7 573 equal to or smaller than 150 cents (see Fig. 4B&C).

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9 574 Previous studies from the visual (Summerfield, Trittschuh, Monti, Mesulam, & Egner,
10 575 2008; Summerfield, Wyart, Johnen, & de Gardelle, 2011) and auditory (Todorovic, van Ede,
11 576 Maris, & de Lange, 2011; Wacongne et al., 2011) domains have demonstrated that
12 577 repetition suppression is not only determined by the local stimulus context (locally
13 578 preceding stimuli), but is also modulated by prior expectation, such that the amount of
14 579 repetition suppression is reduced when stimulus repetition is unexpected. This is contrary to
15 580 the idea of bottom-up neuronal fatigue, and has been taken to suggest that repetition
16 581 suppression may instead reflect the action of a hierarchical predictive coding mechanism,
17 582 which combines bottom-up stimulus representations with prior, top-down stimulus
18 583 expectations (e.g., Friston, 2005; Knill & Pouget, 2004). Within this predictive coding
19 584 framework, it has been hypothesized that attention may modulate the top-down stimulus
20 585 expectations – increasing expectation for attended over unattended stimuli (Friston, 2009;
21 586 Rao, 2005). Several recent studies have interpreted their findings within the context of this
22 587 hypothesis (Chennu et al., 2013; Hsu, Hämäläinen, & Waszak, 2014; Kok, Rahnev, Jehee,
23 588 Lau, & de Lange, 2012). The current study, however, suggests an alternative, or at least
24 589 complementary, explanation. This is, because all stimuli and all stimulus transitions
25 590 (including higher-order transitions between non-consecutive stimuli) were perfectly
26 591 balanced (see Methods), and thus presumably equally expected – and attention was also
27 592 distributed equally across all stimuli. This excludes an explanation in terms of top-down
28 593 expectation, and instead suggests that attention modulates bottom-up representational
29 594 properties.

30 595 The P2 amplitude showed little or no attention-related change when the frequency
31 596 separation from the preceding tone was either zero or larger. According to the neuron
32 597 population model predictions, this suggest that the P2 was affected by a combination of
33 598 sharpening and gain enhancement, and that the amount of gain enhancement matched the
34 599 degree of sharpening, such that the overall response size remained unchanged. This
35 600 suggests that gain enhancement and sharpening are distinct but cooperative components of
36 601 a hierarchically distributed attentional modulation mechanism, which adaptively adjusts the

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3 602 representational bandwidth of auditory cortical processing in accordance with attentional
4 603 demand. Sharpening increases representational resolution, but, without a commensurate
5 604 enhancement in gain, this would lead to decrease in representational accuracy (because
6 605 fewer channels would be activated, or each channel would be activated less strongly). By
7 606 combining and matching gain enhancement and sharpening effects, the auditory system can
8 607 increase representational resolution whilst, at the same time, maintaining representational
9 608 accuracy. And by cascading the gain enhancement and sharpening effects across different
10 609 processing levels – presumably with different limitations on representational resources
11 610 (Ahissar & Hochstein, 2004), the system retains the ability to quickly switch attention to
12 611 new, or currently unattended, sounds.
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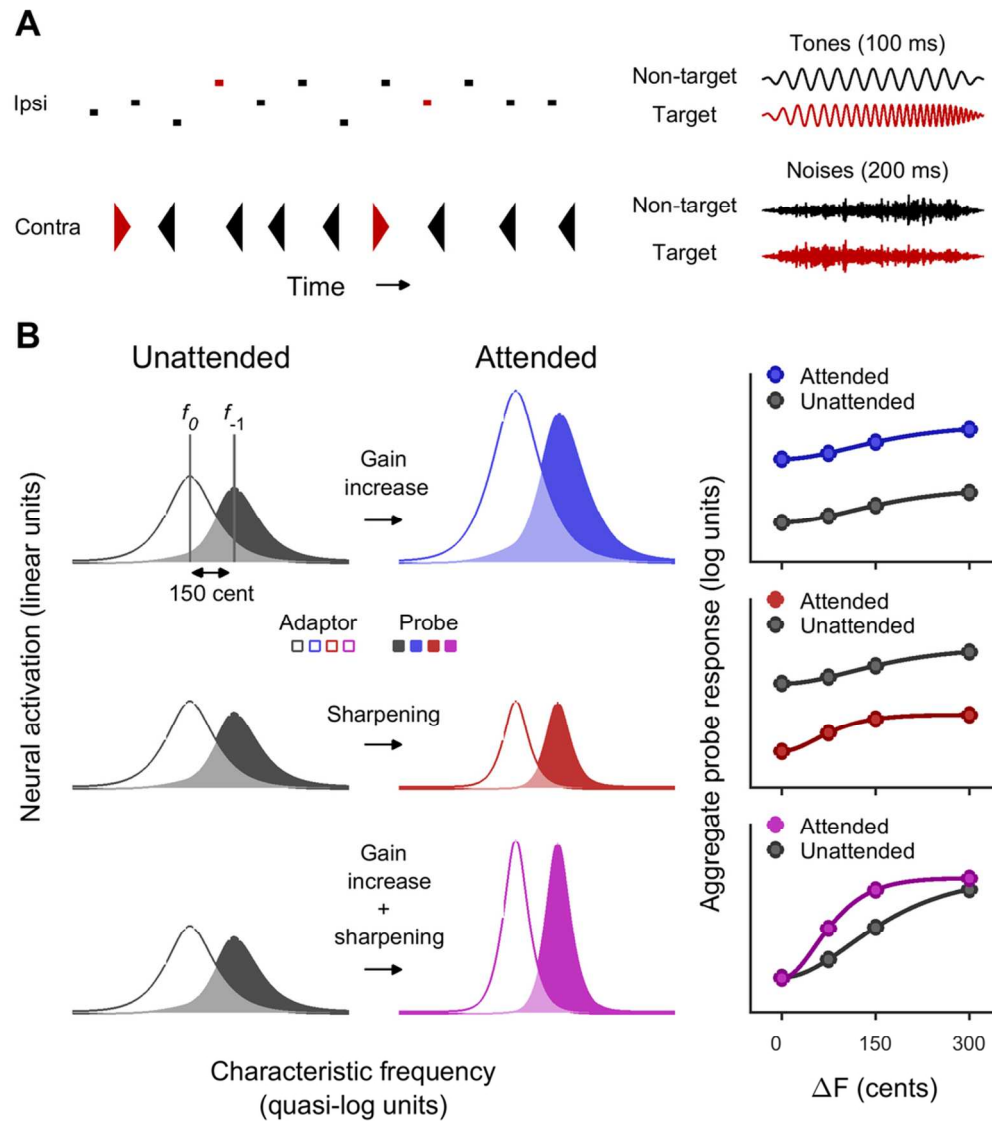


Figure 1: Experimental design and neuron population model predictions. (A) Dichotic attention task: one ear received rapid sequences of sine tones varying pseudo-randomly between four different frequencies ("Ipsi"), and the other received sequences of waxing noises ("Contra"). Subjects were instructed to attend to either sequence alternately (~ 2 min cycle) and detect rare target sounds (shown in red; non-targets are shown in black) in the attended sequence. The tone targets were distinguished by an upward-sweeping frequency trajectory, and the noise targets by a time-reversed (waning) amplitude envelope (see sound examples on the right; tone frequencies and stimulus durations not to scale). (B) Neuron population model predictions of attentional gain enhancement and sharpening (see Methods). The top and middle rows show the predicted effects of gain enhancement and sharpening separately, and the bottom row shows the effect of sharpening combined with a gain increase to counteract suppression in the aggregate response size. The left and middle columns show simulated population activity distributions to the adapting and adapted tones (open and filled outlines), plotted as a function of neuron characteristic frequency in quasi-logarithmic (cochlear frequency) units. The right column shows the aggregate sizes of the adapted responses as a function of the adaptor-probe frequency separation. The unattended responses are shown in gray (replotted across rows), and the attended responses in color.

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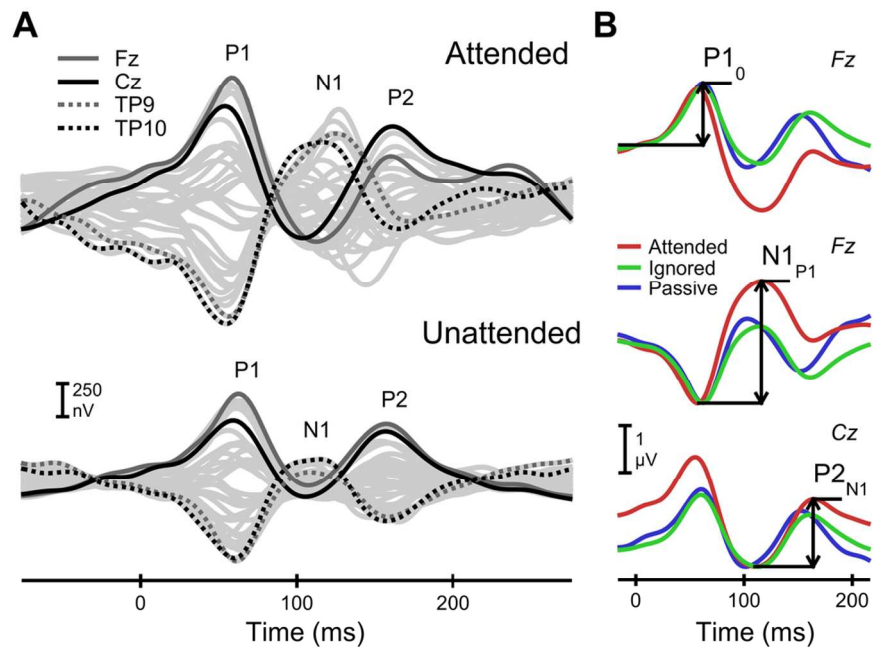


Figure 2: Cortical auditory-evoked potentials (CAEPs). (A) Grand-average CAEPs across subjects and tone frequencies in the attended (top) and unattended (bottom) conditions, shown as a butterfly plot of all 33 sensors (gray lines). The colored lines highlight the sensors with the largest positive (fronto-central and central; Fz and Cz) and negative (left and right mastoids; TP9 and TP10) deflection amplitudes. No baseline correction was applied to these responses. (B) Baseline-corrected grand-average CAEPs for the P1 (P1₀; top), N1 (N1_{P1}; middle) and P2 (P2_{N1}; bottom) and each attention condition (attended, ignored and passive; see legend). The waveforms shows the sensors with the largest positive amplitude for each deflection (Fz for P1₀ and N1_{P1}, Cz for the P2_{N1}), referenced to the average of the mastoid sensors (TP9 and TP10). The vertical arrows show the baseline-corrected peak amplitudes for the attended condition.

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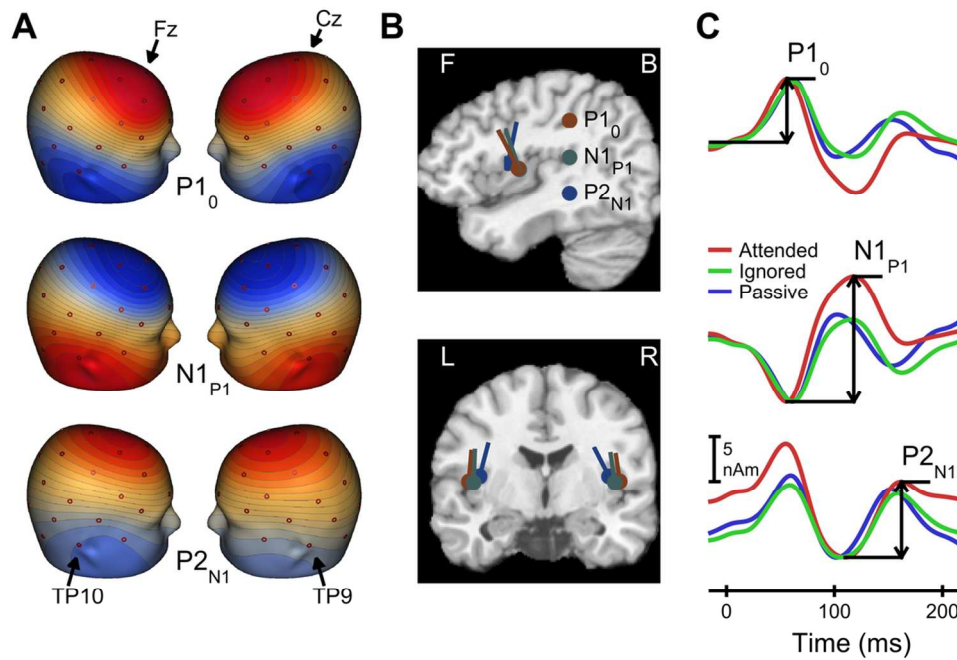


Figure 3: CAEP source analysis. (A) Scalp voltage distributions at the peak latencies of the baseline-corrected P10, N1P1 and P2N1 deflections, averaged over all unattended trials (ignored and passive conditions). (B) Source locations of symmetric equivalent current dipole (ECD) pairs, fitted to each deflection peak (see Methods). The dipole locations (dots) and orientations (short lines) are shown on sagittal (top) and coronal (bottom) slices of the single-subject MNI template brain. (C) Grand-average source waveforms for the P10 (top), N1P1 (middle) and P2N1 (bottom) deflections in each attention condition. The vertical arrows show the baseline-corrected peak amplitudes for the attended condition.

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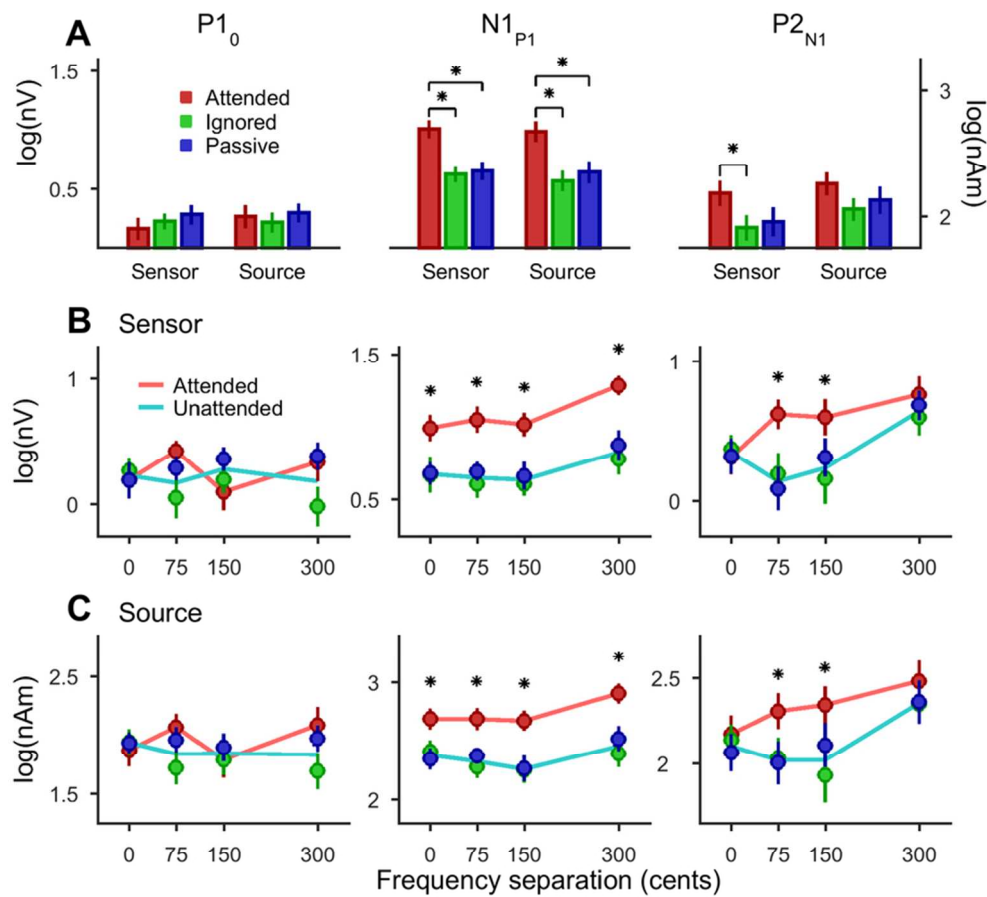


Figure 4: Attention effects on CAEP peak amplitudes. (A) Attention effect of the average deflection peak amplitudes. Different attention conditions are indicated by different colors (see legend), and different deflections are shown in different panels. In each panel, the left set of bars shows the results for the sensor data, and the right set of bars shows the results for the source data. (B) Attention effect on the sensor-based deflection peak amplitudes as a function of the frequency separation from the preceding tone (expressed as absolute value in cents, where 100 cents = 1 semitone). The different attention conditions are shown by different colors as in A. (C) Same as in (B), but for the source-based deflection peak amplitudes. In all panels, the mean deflection peak amplitudes are expressed in logarithmic units, and the error bars show the logarithmic standard error of the mean.

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