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BEHAVIORAL AND NEURAL PECULIARITIES OF AUDITORY LOOMING PERCEPTION IN HUMANS

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ABSTRACT

Our auditory system constantly monitors the environment to protect us from harmful events such as collisions with approaching objects. The auditory looming bias is an astoundingly fast perceptual bias favoring approaching compared to receding sonic motion and was demonstrated behaviorally even in infants of four months in age. Previous studies targeting behavioral and neural correlates of said bias exclusively manipulated overall sound intensity. In our earlier work we demonstrated that spectrally manipulated stimuli, maintaining their overall sound intensity, can also induce the looming effect. Very recent neural investigations based on intensity ramps suggest that the prefrontal cortex plays an important role in eliciting looming bias, by causing a functional override in the auditory cortex. Here, we show results of testing the generalisability of that neural mechanism to spectrally induced biases. We further explore the involvement of inferior parietal areas known to be important for the processing of auditory motion.

1. INTRODUCTION

As encountered in nature, approaching objects pose a greater threat than receding ones. The phenomenon, that approaching - or looming - sounds are perceived as more salient to listeners than receding ones, is termed the "auditory looming bias". As such it manifests in various forms and across ages: animal studies demonstrate faster learning [1] and increased attention [2], while human studies have shown its presence in loudness changes [3, 4], alertness to perceived speed [5] and relative distance [6], and overall faster reaction times [7]. Interestingly, behavioral indications for auditory looming bias were demonstrated even in infants of four months in age who most presumably are not yet aware of the hazardous nature of approaching objects [8].

Despite its behavioral salience, though, the precise cortical mechanisms underlying this bias are not yet clearly understood. Inferior parietal areas of the cortex (Inferior Parietal Lobule - IPL) have been found crucial in spatial hearing, thus making them an important part in sound motion processing [9]. Functional investigations have specifically highlighted the involvement of frontal, parietal and

temporal regions in the preferential processing of looming sounds [4]. Additionally, recent connectivity analyses argue for a frontal-to-temporal top-down overriding of information, aiming to prioritize the processing of looming versus receding sounds [7]. Regarding the timing of the looming responses, our prior investigations of Event-Related Potentials (ERPs) yielded significantly increased activity, centered around the vertex electrodes, within the 120 - 200 ms interval after motion onset [10].

So far, studies have been examining the looming bias largely using intensity-based stimuli. Approaching sound sources come with increasing sound intensity, hence it is an effective parameter with which to simulate motion in distance. Yet when examining the neural substrate, increases in intensity are potential confounders of observed changes [11].

In previous work we have demonstrated that prompting of the looming sensation is possible while maintaining the overall stimulus intensity constant [10]. To this end, we used spectral cues that are naturally induced via acoustic filtering by the human morphology and give us the sensation of externalisation of sound sources [12]. Due to the shape of the human pinna, they are mostly pronounced in the high frequencies. By manipulating the spectral cues in a sound stimulus, one can create the percept of motion in distance.

In the present work we use those spectrally manipulated stimuli to investigate the potential top-down modulation, originating in the Prefrontal Cortex (PFC) and targeting the Primary Auditory Cortex (PAC), following a looming stimulus presentation. We further look into the circuitry involving the IPL and investigate its projections to the functionally connected frontal (PFC) and temporal (PAC) regions.

2. MATERIALS & METHODS

2.1 Subjects

For the present study we reanalysed previously collected data [10] of 15 paid volunteers (age 20-29 y, M=24, SD=3.7; 10 females). All subjects were individuals with no hearing loss greater than 20 dB relative to the normal-hearing population (audiometric thresholds 500 Hz-8 kHz).

2.2 Stimuli

Stimuli consisted of two consecutively presented Gaussian white noises, with limited bandwidth from 1-16 kHz and filtered with the listener-specific Head-Related Transfer Functions (HRTFs). The spectral contrast factor C was varied among three positions, $C \in \{0, 0.5, 1\}$, while the overall sound intensity remained unchanged. $C = 1$ represents the original spectral HRTF profile creating an external sound source sensation, while $C = 0$ corresponds to a flat spectral profile creating an internal sensation within the listener's head. $C = 0.5$ simulates a position between the aforementioned two. The event of interest for the present study is the onset of spectral contrast change, taking place at $t = 0$. The overall duration of the trial comprises 1200 ms, followed by an open response period (Fig. 1).

2.3 Procedure.

The experimental paradigm consisted of a motion direction discrimination task (Fig. 1). By varying factor C , looming ($C_1 > C_2$), receding ($C_1 < C_2$) or static ($C_1 = C_2$) stimuli were created among external ($C = 1$), intermediate ($C = 0.5$) and internal ($C = 0$) positions. Listeners were asked to judge the motion direction while no feedback was provided to them regarding the accuracy of their responses.

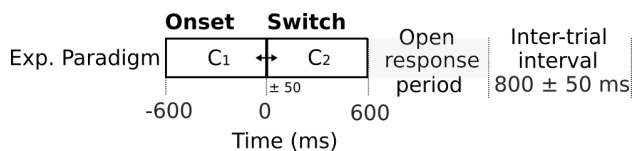


Figure 1: The spectral contrast factor C was manipulated to create looming and receding sounds. Noise filtered with factor C_1 was cross-faded to C_2 with a time jitter of ± 50 ms. Listeners were asked to report whether the sound was approaching, receding or static during an open response period. Adapted from [10].

2.4 Recordings & Analysis.

EEG recordings were collected using a 32-channel scalp EEG at a sampling rate of 512 Hz. After filtering (1-30 Hz) and applying Individual Component Analysis (ICA) for artifact removal, the source localization was done using sLORETA [13]. For the connectivity analysis we used the directed functional connectivity measure of Phase Transfer Entropy (PTE) [14].

We applied the normalised PTE metric on the trial averages as well as single trials in order to consider both synchronized and desynchronized activity, respectively. Values were calculated with a sliding window of 250 ms duration and a step size of 10 ms. Demonstrated in the abscissa of the corresponding plots is the center of said window. Values for the looming bias were calculated as the difference between the looming and the receding directed connectivity values, between each pair of cortical regions considered. Significance was deemed based on cluster-based permutation tests of looming versus receding

contrasts [15]. The analysis pipeline was implemented in EEGLab [16] (preprocessing) and Brainstorm [17] (post-processing).

Based on previous literature [4, 7, 9], we focused our search on three Regions Of Interest (ROIs): PAC, PFC, and IPL.

3. RESULTS

3.1 Parietal Activation

The cortical activation maps during the timing of previously observed looming biases in channel space (120 ms - 200 ms) [10] reveal mostly temporal and parietal activity for both the looming as well as the receding conditions (Fig. 2). The involvement of the parietal cortical regions is in line with literature highlighting their crucial role in spatial processing. Here, we find that such an activation also takes place in the case of spectrally modulated noise stimuli simulating motion in distance.

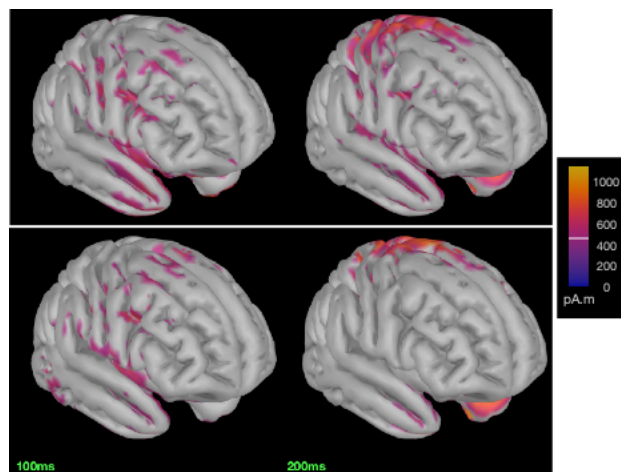
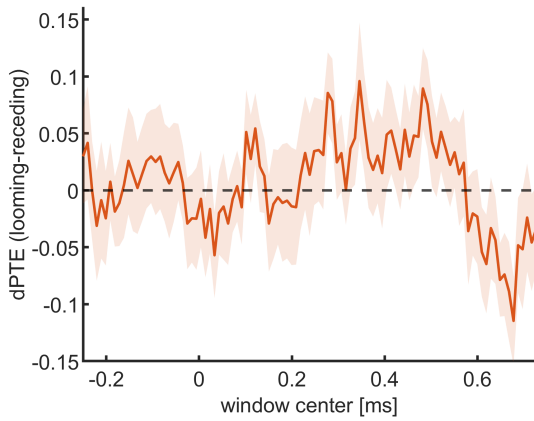


Figure 2: Connectivity maps for looming (upper panel) and receding (lower panel) stimuli.

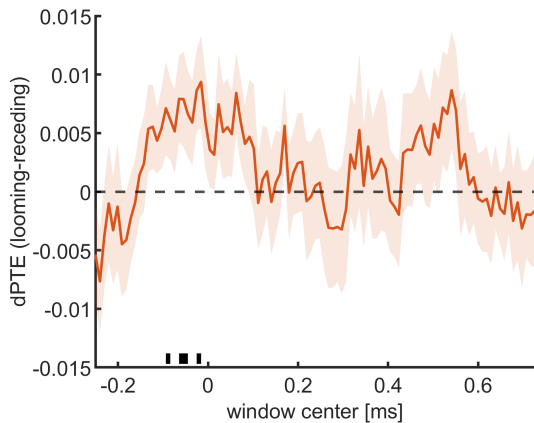
3.2 Parietal Network Involvement

As a next step we investigated the potential neural circuitry involving those parietal cortical regions, shown to be activated during the task. Following the averaged trial analysis, connectivity values did not yield any significant instances in the connections between the IPL and PFC (Fig. 3a) or IPL and PAC (Fig. 4a). Yet significant instances arise in the single-trial analysis in both of those cases (Fig. 3b and Fig. 4b). Since these occurrences appear in the case of single, but not averaged trial analysis, they resemble induced activity among the IPL, PFC and PAC. More precisely, connectivity values reveal a directed connectivity from IPL to PFC, as well as a bottom-up projection from PAC to IPL.

Based on our analysis, the timings of these projections seem to be interlaced and appearing before as well as during the stimulus change ($t = 0$).

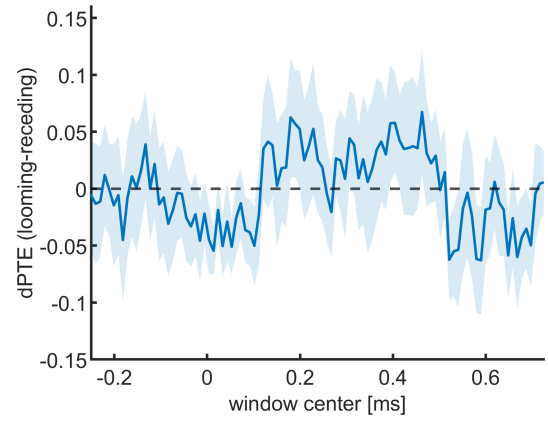


(a) averaged trials

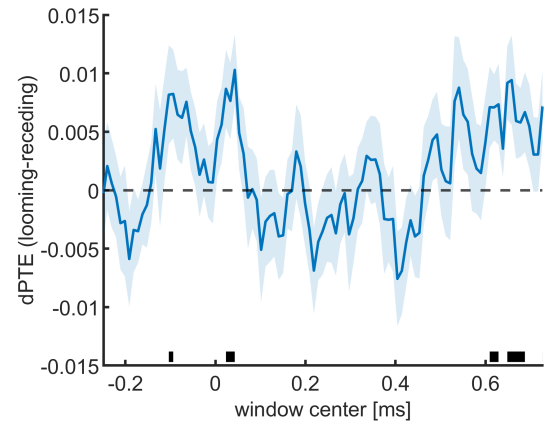


(b) single trials

Figure 3: IPL to PFC connectivity values (dPTE, \pm SEM, $n=15$) plotted against the center of the sliding time window (duration 250 ms). For averaged trial connectivity, no significant looming bias appears. In the case of the single trial analysis, significant occurrences of the looming bias are apparent at times before as well as around the stimulus change (black bars, $p < 0.05$). Positive dPTE values represent connectivity in the targeted direction (IPL to PFC), negative values in the opposite direction (PFC to IPL).



(a) averaged trials



(b) single trials

Figure 4: PAC to IPL connectivity values (dPTE, \pm SEM, $n=15$) plotted against the center of the sliding time window (duration 250 ms). For averaged trials, no significant looming bias appears. In the case of the single trials, significant occurrences of the looming bias are apparent at times before and at the stimulus change, while the looming bias is also prevalent at the offset of the sound stimulus (black bars, $p < 0.05$). Positive dPTE values represent connectivity in the targeted direction (PAC to IPL), negative values in the opposite direction (IPL to PAC).

3.3 Frontotemporal Circuitry

To investigate the proposed top-down modulation from PFC to PAC, figure 5 demonstrates the connectivity values for the looming bias between those areas. Directed connectivity from PAC to PFC for averaged trial analysis (Fig. 5a) shows significant instances at time points before as well as around the stimulus change. Such significances do not arise in the case of single-trial analysis (Fig. 5b), indicating a rather synchronised bottom-up activity evoked by the stimulus change in the case of looming stimuli.

Our results indicate a process, in which the PAC activity signals towards the PFC. Hence, our findings do not support the hypothesized top-down cortical modulation for prioritising the processing of looming against that of receding sounds.

4. DISCUSSION

Based on our previous work, demonstrating that the looming bias can be elicited with the use of spectral auditory cues at constant intensity, we here performed an exploratory connectivity analysis on the underlying network.

In contrast to recent findings, illustrating a top-down modulation favoring the processing of looming sounds [7], we do not find such an increased information transfer from the frontal to the parietal regions of interest. We observe the involvement of parietal regions in the processing of our stimuli; a result consistent with literature on the engagement of cortical regions in spatial auditory processing [4, 9]. When investigating the projections to frontal and temporal regions, parietal activity yields correlates in both directions: bottom-up connections are found from the temporal parts, while lateral activity is found towards the frontal cortical regions.

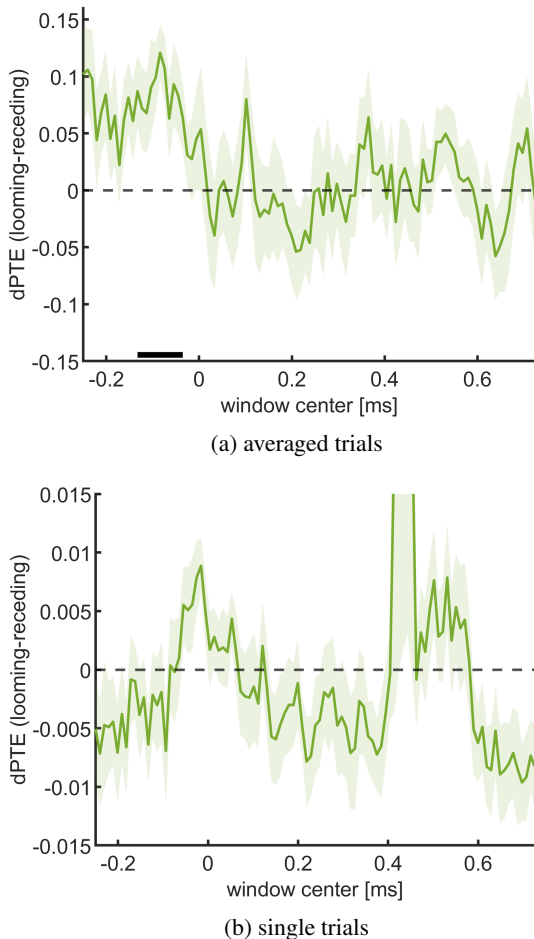


Figure 5: PAC to PFC connectivity values (dPTE, \pm SEM, $n=15$) plotted against the center of the sliding time window (duration 250 ms). For averaged trials, significant occurrences of the looming bias appear at times before as well as around the stimulus change (black bar, $p < 0.05$). No significant instances of the looming bias are apparent in the single-trial analysis. Positive dPTE values represent connectivity in the targeted direction (PAC to PFC), negative values in the opposite direction (PFC to PAC).

We observe the timing of significant instances of the looming bias around the stimulus change, or even preceding it, and mostly not extending after it. Given that we aim to study the brain responses at the stimulus change itself, we are puzzled by this finding. Considering the stimulus construction, we assume it to be attributed to expectation and prediction correlates on the side of the listener. In ongoing work, we are performing separate analyses only based on stimulus conditions that do not allow anticipation or deviate from it, as is the case for static sounds.

The choice of PTE as the connectivity measure largely relies on our target to test previous connectivity findings for our own stimuli. In the process of its implementation we came across several questions regarding its application (time windows, trial configuration, delay estimates etc.). We have investigated most of these aspects, but are still reserved regarding our results. For reasons of completion and robustness, we are presently analysing our data with

different connectivity methods. We thus aspire to get a better grasp on the differences of the metrics, and how they are reflected in our results.

For the purpose of the present study we reanalysed archived data, previously collected for an ERP study. Having used a 32-channel scalp EEG, the source localization accuracy is highly restricted. The ROIs themselves are locally separated enough to avoid smearing, yet there might be a higher amount of noise introduced. Especially in the case of the PAC, a very narrow region in the temporal lobe, the attributed results might actually be originating more broadly from the Superior Temporal Gyrus (STG). To remedy the limitation of the source localisation accuracy, we are currently in the process of collecting high-density EEG data. We are planning to use those for a more precise connectivity analysis, aiming to get a more detailed picture of the local activations.

5. ACKNOWLEDGEMENTS

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