

Research report

Frontal cortex selectively overrides auditory processing to bias perception for looming sonic motion

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HIGHLIGHTS

- Listeners showed perceptual bias (faster decisions) for looming vs. receding sounds.
- Neural (EEG) data mirrored perceptual anisotropy for looming events.
- Prefrontal regions and connectivity to auditory cortex overrides sensory processing.
- Brain prioritizes processing of approaching sounds via top-down control.

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ABSTRACT

Rising intensity sounds signal approaching objects traveling toward an observer. A variety of species preferentially respond to looming over receding auditory motion, reflecting an evolutionary perceptual bias for recognizing approaching threats. We probed the neural origins of this stark perceptual anisotropy to reveal how the brain creates privilege for auditory looming events. While recording neural activity via electroencephalography (EEG), human listeners rapidly judged whether dynamic (intensity varying) tones were looming or receding in percept. Behaviorally, listeners responded faster to auditory looms confirming a perceptual bias for approaching signals. EEG source analysis revealed sensory activation localized to primary auditory cortex (PAC) and decision-related activity in prefrontal cortex (PFC) within 200 ms after sound onset followed by additional expansive PFC activation by 500 ms. Notably, early PFC (but not PAC) activity rapidly differentiated looming and receding stimuli and this effect roughly co-occurred with sound arrival in auditory cortex. Brain-behavior correlations revealed an association between PFC neural latencies and listeners' speed of sonic motion judgments. Directed functional connectivity revealed stronger information flow from PFC → PAC during looming vs. receding sounds. Our electrophysiological data reveal a critical, previously undocumented role of prefrontal cortex in judging dynamic sonic motion. Both faster neural bias and a functional override of obligatory sensory processing via selective, directional PFC signaling toward auditory system establish the perceptual privilege for approaching looming sounds.

1. Introduction

Sensory cues signal biological motion that an organism can exploit to determine direction, speed, and perceived threat of an external source (Neuhoff and McBeath, 1996; Neuhoff, 1998; Vagnoni et al., 2012). In the visual domain, approaching objects create optical cues that symmetrically expand on the retina (Schiff et al., 1962). In audition, approaching sources usually produce a rising intensity gradient (e.g., soft → loud) (Baumgartner et al., 2017; Neuhoff, 1998) whereas

sounds with diminishing amplitude convey the sense of receding motion. Behavioral responses to these stimuli reveal a seemingly universal phenomenon in their perception: a stark perceptual bias for approaching sounds (Bach et al., 2008, 2009; Cappe et al., 2009; Neuhoff, 1998, 2016). Human listeners attend (von Muhlenen and Lleras, 2007) and respond faster to audiovisual looms (Bach et al., 2009; Neuhoff, 2016). Looms are also perceived to be longer (Grassi and Pavan, 2012), louder (Neuhoff, 1998; Stecker and Hafter, 2000), more tonal (Patterson, 1994), and are heard as having faster time-to-arrival

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(Neuhoff et al., 2009; Neuhoff, 2016) suggesting stronger perceptual salience than their retreating sonic counterparts. It has been argued that such perceptual overestimations for looming signals might be beneficial as they would increase the margin of safety for an observer when hearing approaching sound objects (Grassi and Pavan, 2012; Neuhoff, 1998, 2001).

Behavioral anisotropy toward increasing intensity tones (vs. equivalent falls in intensity) has been noted even in infant primates (Ghazanfar et al., 2002; Schiff et al., 1962). The fact both infant humans and rhesus monkeys show stereotyped avoidance to looming but not receding stimuli (Freiberg et al., 2001; Schiff et al., 1962) suggests the bias emerges early in life. Generalization across species further implies the privileged status of looming signals likely has a common phylogenetic (neural) origin that may reflect a selective advantage due to evolutionary pressures (Neuhoff, 1998, 2001). While looming cues sometimes signal success in acquiring sought-after objects during goal-directed behaviors (Schiff et al., 1962), they are overwhelmingly perceived as threatening (Schiff et al., 1962; Vagnoni et al., 2012) and anxiety/fear-inducing (Riskind et al., 2014) as approaching objects pose greater risk to an organism than receding objects. Given the clear survival importance of decoding sonic motion, a foundational question to address relates to the neural origins of this perceptual anisotropy and how the brain creates privilege for looming auditory motion.

Neural recordings from animal primary auditory cortex (PAC) show preferential firing to ramped compared to damped tones (Maier and Ghazanfar, 2007; Maier et al., 2008), an asymmetry independent of other intrinsic neuronal properties (e.g., characteristic frequency, response latency) (Lu et al., 2001). While PAC is highly sensitive to dynamic vs. static auditory motion (Warren et al., 2002), it remains unclear whether looming biases in auditory cortical regions are caused by native (*de novo*) properties in low-level sensory cortex or instead reflect top-down influences that modulate auditory encoding, perhaps selectively for looming sounds. To address these questions, we measured brain activity via electroencephalography (EEG) while human listeners made rapid judgments on whether tones varying dynamically in intensity were perceived as approaching or retreating. We hypothesized that brain responses would show an asymmetry in neural coding of looming vs. receding intensity sweeps (Neuhoff, 1998), mirroring the behavioral anisotropy. Given emerging views that higher-order brain areas selectively sculpt initial stages of auditory processing (Du et al., 2014; Fritz et al., 2010), we further expected that looming vs. receding judgments would strongly depend on functional coupling between frontal and auditory brain regions (Sheikhhattar et al., 2018; Winkowski et al., 2018). Through a combined neural source imaging and functional connectivity approach, our results demonstrate that while receding

signals are more strongly represented in auditory system, prefrontal cortex rapidly overrides this sensory processing to instead preferentially respond to looming sound objects.

2. Results

During EEG recording, participants ($n = 13$) completed a speeded identification task in which they decided whether complex tones either loomed or receded in percept (Cappe et al., 2012; Myers et al., 2017) (see *Methods and Materials*). Auditory motion was achieved by fading intensity in (looming) or out (receding) over the 1000 ms duration of the tones (Fig. 1a). Stimuli were otherwise identical except for their dynamics. Behavioral accuracy (%) in judging auditory motion was equally good (~80%) for both looming and receding tokens (paired *t*-test, two-tailed: $t_{12} = -0.26$, $P = 0.80$) (Fig. 1b). However, RTs were considerably faster for looming judgments (Fig. 1c; $t_{12} = -4.55$, $P < 0.0001$), confirming a perceptual speed bias for approaching sounds (Bach et al., 2008, 2009; Cappe et al., 2009; Neuhoff, 2016).

Source analysis of EEG responses to looming and receding sounds revealed auditory activation localized to primary auditory cortex (PAC), middle temporal gyrus, and decision-related activity in prefrontal cortex (PFC) within 200 ms after sound onset. This was followed by additional expansive PFC activation by 465 ms (Fig. 2). Notably, early PFC activity (~200 ms) rapidly differentiated looming and receding stimuli (Fig. 2b). We extracted source waveform time courses within PAC and PFC (pooling hemispheres) to quantify these neural effects (Fig. 3a, b; see Fig. S1 for individual subject traces). We used a running *t*-test to contrast looming and receding neural waveforms, requiring significant segments persist for > 15 ms to be considered reliable and minimize false positives (Guthrie and Buchwald, 1991). This analysis confirmed auditory motion direction was distinguished in early (0–200 ms) and late time windows (400–600 ms) within both PAC and PFC. The PAC component showed an obligatory “P1-N1-P2” wavelet characteristic of the “textbook” auditory cortical response that develops within ~200 ms of sound onset (Picton et al., 1999). However, the early modulation in PFC was especially notable given that it roughly co-occurred with sound arrival in PAC within the temporal lobe (Picton et al., 1999; Woldorff et al., 1993) (cf. see “●” peaks, Fig. 3a, b).

A mixed-model ANOVA (subjects = random effect) on peak amplitudes in the early time window showed neural activity was larger in magnitude (i.e., stronger negativity) within auditory PAC than PFC across the board (main effect of ROI: $F_{1,12} = 10.55$, $P = 0.007$) (Fig. 3c), an expected effect given auditory stimulation. In light of a marginal ROI \times stimulus interaction ($F_{1,12} = 3.80$, $P = 0.07$), we conducted follow-up Tukey-Kramer contrasts to assess stimulus effects

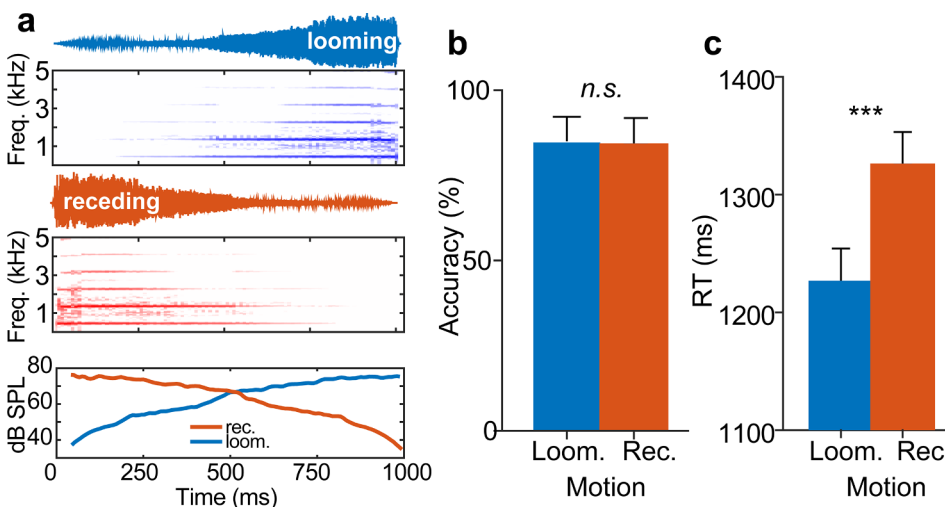


Fig. 1. Acoustic stimuli and behavioral responses to dynamic auditory motion. (a) Signal time waveforms (top) and spectrograms (middle). Looming stimuli were complex tones that faded in from 35 → 80 dB SPL; receding stimuli faded out from 80 → 35 dB SPL. The bottom most panel illustrates the stimulus amplitude contours. (b) Accuracy was equally good when identifying looming vs. receding sound motion. (c) Reaction times were ~100 ms faster identifying looms, suggesting a perceptual bias in processing speed when hearing approaching sounds. errorbars = ± 1 s.e.m., *** $P < 0.001$.

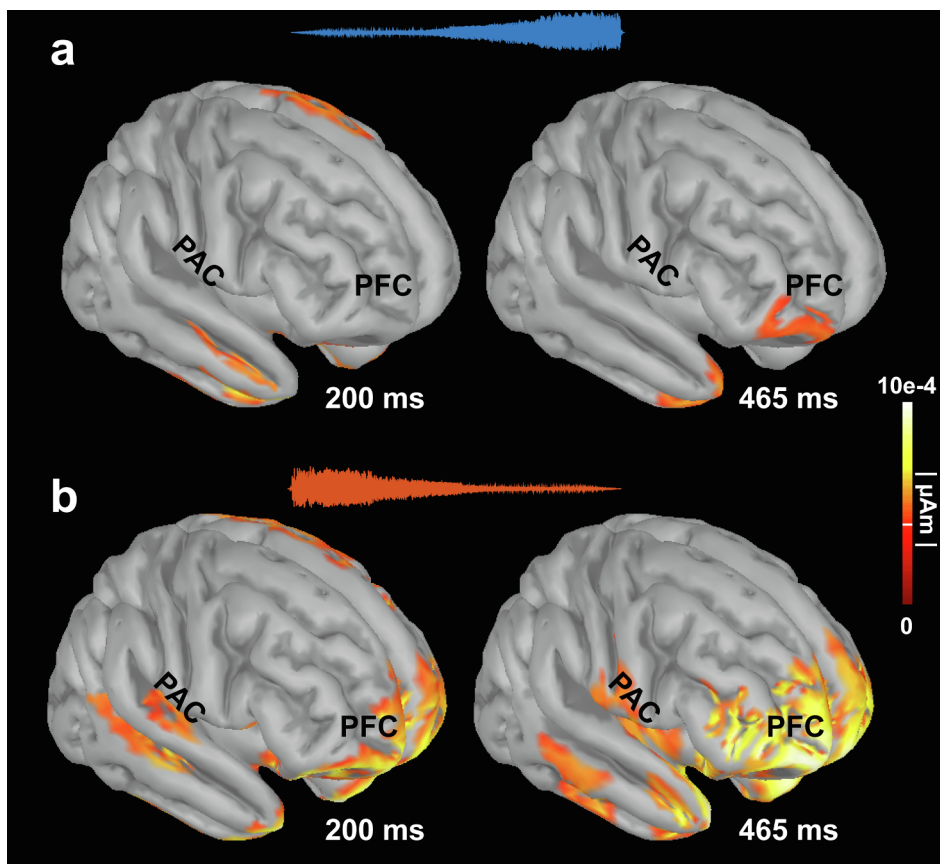


Fig. 2. Neural responses reveal a dynamic interplay between frontotemporal brain areas when judging the direction of sonic motion. Functional sLORETA maps for (a) looming and (b) receding sounds projected onto a semi-inflated brain (only right hemisphere is shown). Maps are thresholded at 40% of the max global magnitude. Dynamic sounds elicit very early (200 ms) and late (465 ms) neural activation localized to both PAC and PFC. PAC, primary auditory cortex; PFC, prefrontal cortex.

within each ROI. We found PFC amplitudes differentiated looming vs. receding sounds ($P = 0.027$) whereas the auditory PAC source did not ($P = 0.99$). Interestingly, response latencies showed a ROI \times stimulus interaction ($F_{1,12} = 40.65$, $P < 0.0001$) (Fig. 3d). Pairwise contrasts revealed neural timing was invariant to the direction of stimulus motion within auditory PAC ($P = 0.55$) but PFC activations were considerably earlier for looming compared to receding tones ($P < 0.0001$). In fact, the latency of frontal PFC activity was similar to PAC for looming stimuli ($P = 0.66$). These findings indicate a stark asymmetry in the speed of neural processing for looming compared to receding (retreating) auditory motion, with faster neural bias toward approaching sounds.

To evaluate the behavioral relevance of these differential neural responses to auditory motion, we conducted correlations between brain (PAC/PFC amplitudes and latencies) and behavioral (% RTs) measures. We found PFC latencies were strongly associated with the speed of behavioral decisions ($r = 0.65$, $P < 0.001$) (Fig. 4). Earlier engagement of PFC was linked with faster behavioral judgments of auditory motion. Contrastively, PFC amplitudes were not associated with accuracy ($r = 0.19$, $P = 0.37$) nor RTs ($r = 0.14$, $P = 0.51$), nor were any property of auditory PAC responses and behavior ($P_s > 0.11$; data not shown). The lack of brain-behavior correspondence with accuracy measures might however be expected given the similarity in perceptual reports for looming and receding stimuli (e.g., Fig. 1b). Nevertheless, the latency data reveal a critical role of PFC timing in mediating behaviors related to the perceptual-cognitive processing of auditory motion.

The PFC latency vs. RT correlation could reflect differences between conditions and/or subjects rather than brain-behavior associations within each listener. To further test this relation, we used repeated measures correlation (rmCorr) (Bakdash and Marusich, 2017) to account for non-independence among observations, adjust for between subject variability, and measure within-subjects correlations. rmCorr

evaluates the common intra-individual association between two measures. We used the *rmCorr* package (Bakdash and Marusich, 2017) in the R software environment (R Core team, 2018). This revealed the link between PFC latencies and RTs (cf. Fig. 4) remained strong even at the single-subject level ($r_m = 0.85$, $P < 0.0001$).

Increased involvement of PFC could reflect “top-down” processing that overrides auditory sensory processing selectively for looming sounds that convey the sense of an approaching source. We tested this possibility by measuring directed functional connectivity between PFC and PAC using phase transfer entropy (PTE), an information-theoretic measure of causal signal interactions (Bidelman et al., 2018; Lobier et al., 2014) (Fig. 5). We found that the strength of signaling in this frontotemporal pathway depended on both the direction of neural flow within this circuit and perceived motion of the auditory stimulus (direction \times stimulus interaction: $F_{1,12} = 15.81$, $P = 0.0003$). For looming sounds, neural signaling was stronger in the feedback than feedforward direction [i.e., (PFC \rightarrow PAC) > (PAC \rightarrow PFC); $P = 0.0295$]. In contrast, the connectivity pattern was bidirectional for receding sounds [i.e., (PFC \rightarrow PAC) = (PAC \rightarrow PFC); $P = 0.11$]. Overall, “top-down” (PFC \rightarrow PAC) propagation was also stronger than the reverse “bottom up” (PAC \rightarrow PFC) signaling ($F_{1,12} = 8.24$, $P = 0.014$).

3. Discussion

By recording neuroelectric brain activity to dynamic looming and receding sounds, we provide strong evidence of both a behavioral and neurobiological bias for approaching auditory signals. Our findings reveal a stark asymmetry in the neural processing of looming vs. receding sounds whereby approaching signals are evaluated more rapidly than those conveying the perception of retreating motion. This neuro-behavioral bias is driven by differential changes in prefrontal brain regions (PFC) rather than modulations in auditory-sensory cortex (PAC). Our results demonstrate that higher-order brain regions

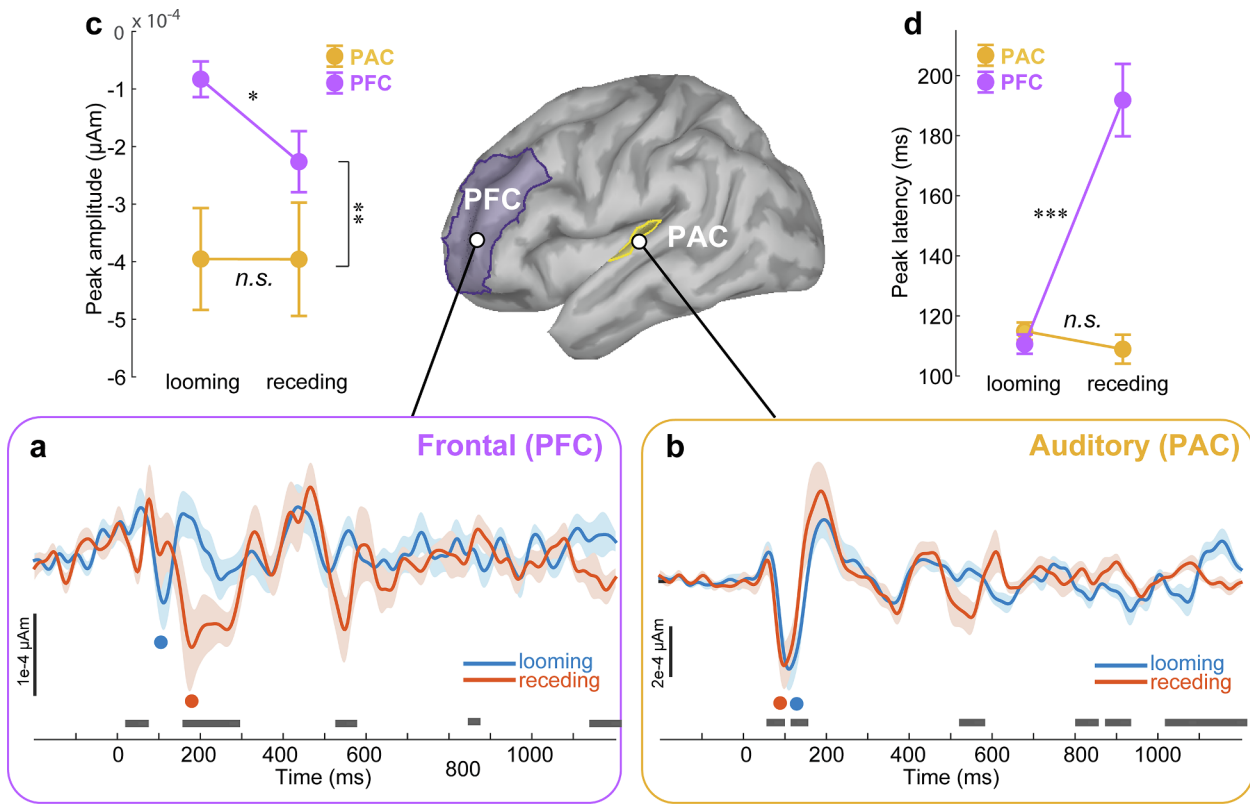


Fig. 3. Neuroelectric brain activity reveals preferential bias toward processing looming (approaching) sounds. Time waveforms extracted from the (a) PFC and (b) PAC source (see Fig. 2) for looming and receding sounds (collapsed across hemispheres). ■ = significant stimulus effect [running *t*-test, $P < 0.05$; > 15 ms contiguous significant segments (Guthrie and Buchwald, 1991)]. Auditory motion is distinguished in early (0–200 ms) and later time windows (400–600 ms) within both PAC and PFC. (c) PAC response peak magnitudes (●) were larger than in PFC across the board (**) as expected from the auditory stimulation. (d) Neural timing of frontal PFC activity (but not auditory PAC) was considerably faster for looming vs. receding tones revealing a processing bias for sounds approaching the listener. errorbars/shading = ± 1 s.e.m., * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

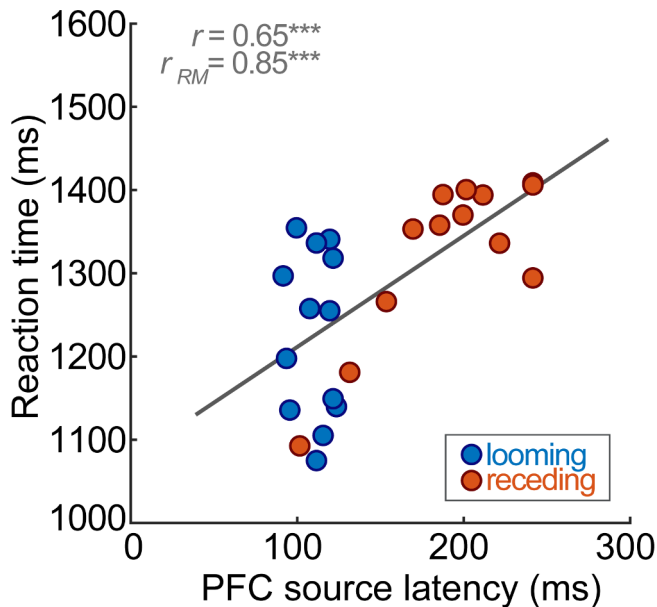


Fig. 4. Brain-behavior correlations reveal an association between frontal (PFC) neural timing and speed of auditory motion decisions. PFC source latencies predict listeners' behavioral RTs when identifying looming vs. receding sounds (aggregated across stimuli). r = Pearson's correlations; r_{RM} = repeated-measures correlations (rmCorr) accounting for within-subject dependencies between stimulus conditions (Bakdash and Marusch, 2017). *** $P < 0.001$.

(prefrontal cortex) directly interact with sensory regions (temporal cortex) to selectively “override” initial stages of auditory cortical processing and prioritize the brain’s response to approaching sound sources.

Behaviorally, we found listeners responded faster in judging looming vs. receding events, confirming a perceptual bias for approaching auditory signals (Bach et al., 2008, 2009; Baumgartner et al., 2017; Neuhoff, 1998; Neuhoff, 2016; Stecker and Hafter, 2000). Human listeners attend (von Muhlenen and Lleras, 2007) and respond faster to audiovisual looms (Bach et al., 2009; Neuhoff, 2016) and they are generally perceived as having faster time-to-arrival than their receding counterparts (Neuhoff et al., 2009; Neuhoff, 2016). Though a perceptual error, underestimating approaching source distance (a false positive error) is far less costly to an organism than overestimating source distance (false negative error) (Haselton and Nettle, 2006). Consequently, from an evolutionary standpoint, the seemingly universal propensity to respond faster to looming sounds and neurobehavioral biases observed here could have been shaped by natural selection (Neuhoff et al., 2009).

Our neural data converge with recent auditory neurophysiological studies suggesting electrical signatures of looming sound bias emerge in the human brain within ~200 ms (Baumgartner et al., 2017; Myers et al., 2017). However, our source-resolved EEG data help adjudicate the underlying neurobiological mechanisms of this auditory perceptual anisotropy. Notably, we found early frontal (PFC) but not auditory-sensory (PAC) brain activity rapidly differentiated looming and receding tokens. Similarly, prefrontal rather than auditory regions predicted listeners' speed of sonic motion judgments. Still, PAC did show

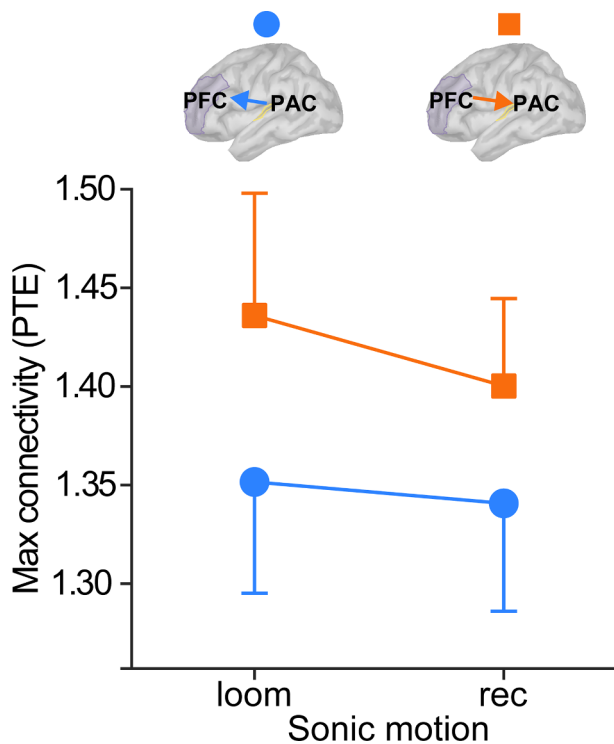


Fig. 5. Functional connectivity between frontal and temporal cortex drives auditory motion processing. Neural signaling directed between PFC and PAC in the feedforward (PAC → PFC) and feedback (PFC → PAC) directions computed via phase transfer entropy (PTE) (Lobier et al., 2014). “Top-down” PFC → PAC flow is stronger than the reverse flow for looming sounds. “Bottom-up” PAC → PFC signaling is invariant to the direction of sonic motion. errorbars = ± 1 s.e.m.

weak selectivity (larger and earlier responses) to receding tones, consistent with the stronger initial amplitude of those stimuli and well-known intensity dependence of the auditory ERPs (Cone and Whitaker, 2013; Davis and Zerlin, 1966; Müller, 1973)—which scale with intensity. Contrastively, and opposing these natural sensory propensities (which are actually biased toward receding sounds), we find prefrontal areas respond earlier and more robustly to *looming* events. The striking early generation of frontal PFC activity almost jointly with sound registration in PAC agrees with notions that behavioral choice signals evolve concurrently in frontoparietal networks concurrent with ongoing sensory processing (Siegel et al., 2015). In visual categorical learning tasks, for example, choice signals generated in PFC have been shown to precede those generated in visual sensory cortex (Siegel et al., 2015), similar to the effects observed here in the auditory domain.

Previous human neuroimaging studies have revealed a distributed neural network in processing sonic motion including brain regions related to processing auditory spatial motion, attention, and motor planning (Seifritz et al., 2002) as well as a bilateral posterior temporal-parietal network (Warren et al., 2002). Amygdala activation has also been noted (Bach et al., 2008), likely reflecting the warning function these sounds. However, in examining neural processing of sonic motion, most PET and fMRI studies have compared activations to moving and stationary stimuli (reviewed by Warren et al., 2002). Our finding that PAC fails to strongly differentiate auditory motion also contrasts with reports suggesting preferential coding of rising vs. falling sounds in early superior temporal areas (Seifritz et al., 2002). However, the slow integration time of fMRI/PET (order of seconds) renders it difficult to determine whether preferential coding of looms is *de novo* to primary auditory regions (e.g., Seifritz et al., 2002), or rather reflects modulatory influences inherited from elsewhere in the brain. Fueling this concern, increased fMRI sensitivity to looms develops over more than

10–20 s, long after the cessation of the actual stimulus motion (Seifritz et al., 2002). “Intrinsic” motor activity observed for looming vs. receding sounds (Seifritz et al., 2002) might be related to the longer integration windows of fMRI which can blur pre- and post-perceptual stages of processing. Indeed, at early pre-perceptual stages, we do not find strong motor activation for looms, but rather, strong interplay between frontal and temporal cortex (see Fig. 2). The fine temporal resolution provided by EEG (milliseconds) helps extend and resolve previous neuroimaging studies. While our findings do not diminish the contribution of other network hubs in processing sonic motion (Seifritz et al., 2002; Warren et al., 2002), we demonstrate a critical and previously undocumented role of prefrontal cortex in establishing the perceptual privilege for looming sound objects through rapid (< 200 ms) frontal modulatory control of auditory processing.

Functional connectivity corroborates these data by revealing information flow between frontal and auditory cortex is not only stronger but preferentially operates in a “top-down” state during auditory looming perception. Flow from PFC → PAC was stronger for looming auditory objects whereas the reverse (“bottom-up”) signaling from PAC → PFC was invariant to auditory motion direction. Collectively, these local and inter-regional neural effects suggest “top-down” processing overrides obligatory auditory coding when judging whether dynamic sounds are approaching or receding. Direct connections between (pre)frontal cortex and PAC have been identified in tracing studies (Hackett et al., 1999; Plakke and Romanski, 2014; Winkowski et al., 2018). Such projections could provide an anatomical basis to realize the PFC-induced modulations of auditory responses observed here.

More broadly, human and nonhuman studies have shown that strong frontotemporal coupling is necessary for complex perception including dynamic pattern recognition (Griffiths et al., 2000), audio-visual associative learning (Gaffan and Harrison, 1991), auditory categorization (Bidelman and Walker, 2019), and sound recognition memory (Fritz et al., 2005). Prefrontal areas are thought to lie at the apex of perceptual-cognitive processing hierarchy (Bagur et al., 2018; de Lafuente and Romo, 2006; Rahnev et al., 2016; Siegel et al., 2015). Human lesion data support the notion that these higher-order brain regions are critical for accurate cognition of perceptual events as evidenced by the fact that frontal lesions impair spatial orientation (du Boisgueheneuc et al., 2006), perceptual decision making (Rahnev et al., 2016), and auditory pattern recognition (Griffiths et al., 2000)—faculties which are presumably required to decode looming vs. receding sonic motion. Thus, our results confirm that PFC acts as a buffer to voluntary behaviors by decoupling perception from directed action (du Boisgueheneuc et al., 2006; Rahnev et al., 2016), based on sonic stimuli.

Alternatively, the differential engagement of PFC for looms may reflect biases in predictive coding. Indeed, temporal and frontal cortex are differentially sensitive to local and global regularities in the sensory environment (Dürschmid et al., 2016). Under this notion, the threatening (anxiety-provoking) nature of looms (Bach et al., 2008; Vagnoni et al., 2012) might cause them to be processed as somewhat “novel” auditory events, invoking increased PFC activity that is more sensitive to the “big picture” of an organism’s surrounding soundscape (Dürschmid et al., 2016). Frontal sites also integrate information over longer timescales than auditory-temporal areas (Dürschmid et al., 2016), which may account for the dominate PFC activity in the current study. Still, our data suggest this integration is rapid, occurring within several hundred milliseconds and in a similar time window as sound arrival in PAC.

Our stimuli were limited to sounds where sonic motion was manipulated via onset (and offset) intensity. While such amplitude gradients likely reflect the most naturalistic form of looming vs. receding auditory motion (Neuhoff, 1998, 2001), a question arises whether our findings are specific to motion in depth or whether the effects depend solely on sound onset energy. Indeed, our larger than expected RTs (cf.

Fig. 1c vs. Simon, 1967) suggest participants may have used the final intensity to make their judgements, which is also in line with the finding that RT speeds usually increase (get slower) with decreasing SPL (akin to our receding tokens). That said, recent EEG studies have demonstrated similar behavioral and neural biases for looms as observed here using spectrally contrasting stimuli with fixed intensity (Baumgartner et al., 2017). This suggests neural effects which are attributable to the *percept* of sonic motion rather than idiosyncratic to stimulus acoustics, *per se*. While we have no reason to believe our results would not generalize to other sonic motion stimuli, future studies could test this possibility, e.g., using sounds with similar onset level which then proceed to rise or fall.

Our data also cannot fully adjudicate whether observed neural bias for looming events reflect automatic or controlled processes. For example, attention to sonic motion via our active task may account for the strong PFC influence we find in our EEG data. On the contrary, in anesthetized cat, PAC responses show preferential coding of rising vs. falling tones (Stumpf et al., 1992), suggesting that bias for looming events may be partially reflected in low-level, automatic sensory processing that does not require attentional deployment. In future neuroimaging studies, it would be interesting to test the role of attention—and perhaps differential engagement of PFC and PAC—in sonic motion processing through comparison of active vs. passive listening paradigms.

In sum, our results show that auditory and frontal cortex are dynamically coupled from a functional perspective (Assaneo et al., 2019; Fritz et al., 2010) and that behavioral decisions help shape the flow of sensory information (Fritz et al., 2010; Siegel et al., 2015) to prioritize processing for looming over receding sound events.

4. Methods and materials

Participants. Thirteen young, normal-hearing adults (2 male, 11 females; age: $M = 23.7$, $SD = 2.4$ years) were recruited from the University of Memphis (UofM) and University of Tennessee Health Sciences Center (UTHSC) student bodies. Participants reported minimal formal music training (average 3.6 ± 3.5 years). All but three were right-handed and none reported a history of neuropsychiatric illness. They were paid for their time and gave informed consent in compliance with dual protocols approved by the Institutional Review Boards at UofM (#2370) and UTHSC (IRB#: 13-02782-XP).

Auditory stimuli. The task involved identifying complex sounds that were either looming or receding in percept (Cappe et al., 2012; Myers et al., 2017). Stimuli were otherwise identical except for their intensity dynamics. To induce the perception of sonic motion, auditory stimuli were faded in or out over their 1000 ms duration (10 ms ramping) to give the impression of “looming” (i.e., approaching; 35 → 80 dB SPL) or “receding” (80 → 35 dB SPL) movement (Fig. 1a). The amplitude contours followed roughly an equal power cross fade, which results in a symmetry between ramped and damped stimuli (Fig. 1a, bottom). Stimuli were 1000 Hz complex tones (triangle waveform; 48 kHz sampling rate) generated in Adobe Audition (Adobe Systems Inc.). Tone complexes were chosen given their strong salience for inducing looming/receding percepts (Neuhoff, 1998). Stimuli were presented bilaterally via shielded ER-2 insert earphones (Etymotic Research). Looming and receding tones were matched in RMS amplitude such that their average level was equated (i.e., they differed only in the direction of dynamic level change). Stimulus level was calibrated using a Larson–Davis SPL meter (Model LxT) measured in a 2-cc coupler (IEC 60126). Left and right ear channels were calibrated separately.

Task procedure. Participants sat comfortably in an electro-acoustically shielded booth to facilitate neural data collection. During EEG recordings (described below), listeners heard 150 presentations of each stimulus (randomly ordered) and were asked to judge each trial as either “looming” or “receding” via a computer button press. They were encouraged to respond as accurately and quickly as possible.

Participants used their dominant hand to ensure speeded responses. The interstimulus interval varied from 800 to 1400 ms (rectangular distribution) to avoid anticipating the next trial. Stimulus delivery and response collection were controlled by custom routines coded in MATLAB® 2013 (The MathWorks, Inc).

Both response identification accuracy (%) and reaction times (RTs) were logged separately for looming and receding trials. RTs were computed as the mean response speed across trials per condition. The RT clock started after stimulus cessation. RTs outside 250–8500 ms were deemed outliers (e.g., fast guesses, attentional lapses) and were excluded from analysis.

4.1. EEG recordings and analysis

Recording and preprocessing. EEG was recorded from 64 sintered Ag/AgCl electrodes at standard 10–10 scalp locations (Oostenveld and Praamstra, 2001). Continuous data were digitized at 1000 Hz (SynAmps RT amplifiers; Compumedics Neuroscan) with an online passband of 0.1–500 Hz. Electrodes placed on the outer canthi of the eyes and the superior and inferior orbit monitored ocular movements. Electrode impedances were < 10 kΩ. During acquisition, electrodes were referenced to an additional sensor placed ~1 cm posterior to the Cz channel. Preprocessing was conducted in the Curry 7 Neuroimaging Suite (Compumedics Neuroscan) and the MATLAB package Brainstorm (Tadel et al., 2011). Ocular artifacts (saccades and blinks) were first corrected in the continuous EEG using a principal component analysis (PCA) (Picton et al., 2000). Cleaned EEGs were then average referenced, filtered (1–30 Hz), epoched (–200–1100 ms), baseline corrected, and ensemble averaged across trials to derive ERPs for each stimulus per participant.

ERP source analysis. We performed distributed source analysis to more directly assess the underlying neural dynamics of auditory motion processing. We used a realistic, boundary element model (BEM) volume conductor (Fuchs et al., 1998, 2002) standardized to the MNI brain (Mazziotta et al., 1995) which are less prone to spatial errors than other head models (e.g., concentric spherical conductor) (Fuchs et al., 2002). The BEM head model was created using the built-in OpenMEEG (Gramfort et al., 2010) plugin in Brainstorm (Tadel et al., 2011). Locations of the 10–10 electrode array were warped to the template anatomy in Brainstorm. For the 64-ch electrode array used here, best case estimates of localization error for sLORETA is < 1.40 mm (Song et al., 2015). We did not collect individual subjects' MRIs though subject-specific anatomies and electrode digitization can improve source localization accuracy (Acar and Makeig, 2013). Our inverse methods were applied identically across listeners so while overall localization precision might be underestimated using template anatomies, this noise would manifest uniformly across our source reconstitution estimates. More critically, our approach easily resolves the macroscopic structures of interest from sensor data (i.e., PAC vs. PFC; Fig. 2).

We used the well-established sLORETA inverse solution (Pascual-Marqui, 2002) to estimate the distributed neuronal current density underlying the recorded sensor data. This algorithm models the inverse solution as many elementary dipoles distributed over a nodal mesh representing the cortical volume (15,000 vertices). sLORETA provides a smoothness constraint that ensures the estimated current changes little between neighboring neural populations within the volume conductor (Michel et al., 2004; Picton et al., 1999). Resulting activation maps represent the transcranial current source density underlying the scalp-recorded potentials as seen from the cortical surface. We used Brainstorm's default sLORETA settings for source reconstitution (Tadel et al., 2011).

From each sLORETA map, we extracted the time-course of bilateral source activity within two predefined ROIs: (1) primary auditory cortex of the superior temporal gyrus (“PAC” throughout the text) and (2) rostral middle frontal gyrus of prefrontal cortex (“PFC”). Source waveforms reflect neural activity (units μAm) as seen *within* each ROI. ROI

parcellation was based on anatomical segmentations of the Desikan-Killany atlas (Desikan et al., 2006). These ROIs correspond roughly with Brodmann areas BA 41 (PAC) and BA 46 (PFC). Anatomical tracing studies confirm direct projections between these regions (Hackett et al., 1999; Plakke and Romanski, 2014). While by no means exhaustive, these ROIs allowed us to (i) test specific hypotheses on our data and (ii) measure functional connectivity between auditory and frontal brain regions as listeners decided whether sounds were looming or receding. A similar frontotemporal circuit has been documented in previous neuroimaging studies on auditory identification (Binder et al., 2004) and individual differences in language learning (Assaneo et al., 2019). We then measured the latency and magnitude at the peak negativity in each time course, which in most cases fell between 0 and 250 ms. This window covered the two most prominent negative deflections of the PFC and PAC responses (see Fig. 3). Given the stark difference in morphology between source time courses, similar data-driven approaches have been used as a more unbiased way to quantify and directly compare ROI activity without having to define *a priori* peaks for analysis, particularly when their functional role is unknown (Bidelman and Walker, 2019; Murray et al., 2008).

Functional connectivity. To test whether auditory or frontal brain regions drive auditory motion processing, we measured *directed* functional connectivity between PAC and PFC using phase transfer entropy (PTE) (Bidelman et al., 2018; Lobier et al., 2014). PTE is a non-linear, information theoretic metric of directed signal interaction that is robust to noise and volume conducted cross-talk in EEG (Hillebrand et al., 2016; Vicente et al., 2011). PTE is *asymmetric* and can be computed bidirectionally ($X \rightarrow Y$ and $Y \rightarrow X$) to identify causal information flow between interacting brain regions. Higher PTE values indicate stronger connectivity; PTE = 0 reflects no directed flow. We measured PTE between PAC and PFC via the *PhaseTE_MF* (v2.5) function in Brainstorm (Tadel et al., 2011). PTE is estimated by building probability density functions of phase estimates across epochs between pairwise signals—here the two ROI time series (Lobier et al., 2014). We used the ‘scott’ binning approach for estimating the multivariate density histograms (Scott, 1992). To test whether the amount of information (e.g., number of samples) contributed to connectivity estimates, we varied the prediction delay (τ) of this algorithm from 50 to 1000 ms (50 steps). We report connectivity values as the maximum PTE across the epoch window computed in both the feedforward (PAC \rightarrow PFC) and feedback (PFC \rightarrow PAC) directions.

Author contributions

G.M.B. and M.M. designed and performed the research; G.M.B. analyzed the data; and G.M.B. and M.M. wrote the paper. The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.brainres.2019.146507>.

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