

## Research report

## Auditory perceptual restoration and illusory continuity correlates in the human brainstem

Gavin M. Bidelman<sup>a,b,\*</sup>, Chhayakanta Patro<sup>b</sup><sup>a</sup> Institute for Intelligent Systems, University of Memphis, Memphis, TN, USA<sup>b</sup> School of Communication Sciences & Disorders, University of Memphis, Memphis, TN, USA

## ARTICLE INFO

## Article history:

Received 11 December 2015

Received in revised form

20 May 2016

Accepted 26 May 2016

Available online 27 May 2016

## Keywords:

Frequency-following response (FFR)

Phonemic restoration

Brainstem response

Auditory perceptual illusion

## ABSTRACT

When noise obstructs portions of target sounds the auditory system fills in missing information, a phenomenon known as auditory restoration or induction. Previous work in animal models demonstrates that neurons in primary auditory cortex (A1) are capable of restoring occluded target signals suggesting that early auditory cortex is capable of inducing continuity in discontinuous signals (i.e., endogenous restoration). Current consensus is that the neural correlates of auditory induction and perceptual restoration emerge no earlier than A1. Moreover, the neural mechanisms supporting induction in humans are poorly understood. Here, we show that in human listeners, auditory brainstem nuclei support illusory auditory continuity well before engagement of cerebral cortex. We recorded brainstem responses to modulated target tones that did or did not promote illusory auditory percepts. Auditory continuity was manipulated by introducing masking noise or brief temporal interruptions in otherwise continuous tones. We found that auditory brainstem responses paralleled illusory continuity by tagging target sounds even when they were occluded by the auditory scene. Our results reveal (i) a pre-attentive, subcortical origin to a presumed cortical function and (ii) that brainstem signal processing helps partially cancel the negative effects of masking by restoring missing portions of auditory objects that are fragmented in the soundscape.

© 2016 Elsevier B.V. All rights reserved.

## 1. Introduction

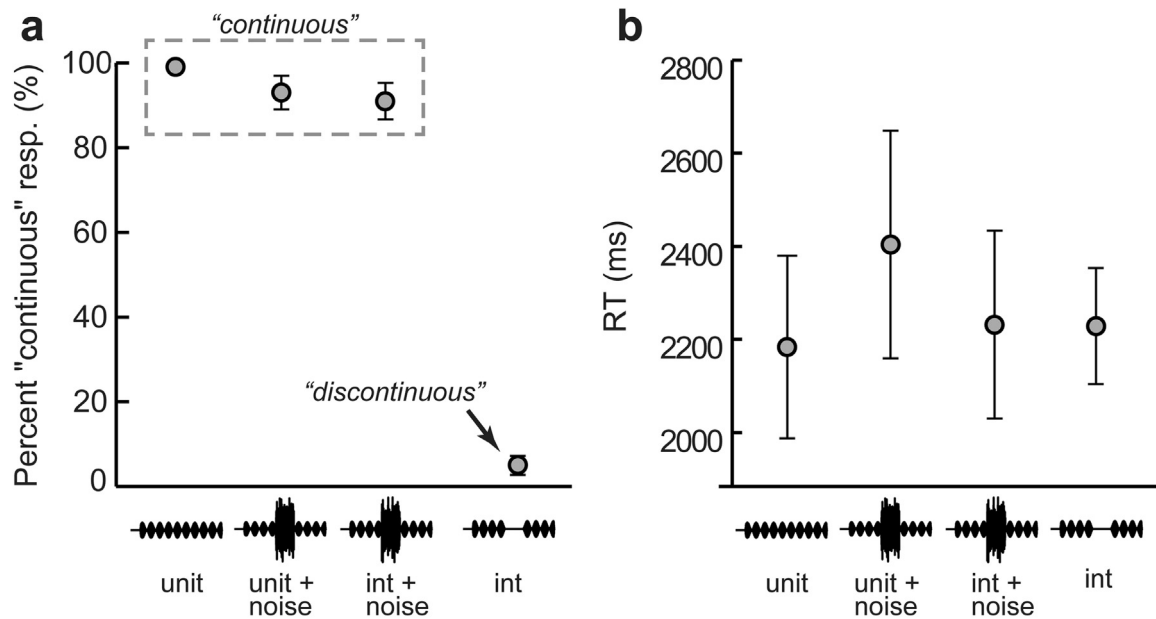
Sensory systems maintain stable representations of the world by filling in gaps when target information is obscured by competing signals, a process known as “auditory restoration” or “induction” (Petkov et al., 2007; Riecke et al., 2007; Riecke et al., 2009). This illusory continuity is best demonstrated by phonemic restoration (Warren, 1970; Warren et al., 1972) when listeners correctly perceive target speech that is momentarily interrupted by extraneous foreground noise. Remarkably, perceptual continuity is maintained even when the signal is physically absent (i.e., silent) during noise (Riecke et al., 2007, 2009; Warren, 1970) suggesting that the auditory system restores (i.e., perceptually completes) missing segments occluded from the auditory scene. Presumably, perceptual restoration represents an essential neurobiological mechanism of sensory processing that enables the brain to resolve imperfections in the soundscape and arrive at an accurate prediction of fragmented auditory signals.

The fundamental nature of sensory restoration is evident by the fact that analogous continuity illusion phenomena have been observed in the visual domain (Sugita, 1999), for nonspeech sounds (Micheyl et al., 2003; Riecke et al., 2009), and in nonhuman species, e.g., primates (Petkov et al., 2003) and birds (Braaten and Leary, 1999). Moreover, focused attention does not override induction (Micheyl et al., 2003; Petkov et al., 2003, 2007) implying that perceptual restoration might reflect the output of primitive, pre-attentive stages of brain processing. Yet, current consensus is that perceptual restoration/induction does not manifest along the neuroaxis prior to primary auditory cortex (King, 2007). A cortical origin is well-supported by electrophysiological recordings in animal models (Petkov et al., 2003, 2007), human neuroimaging (Micheyl et al., 2003; Riecke et al., 2007, 2009), and computational modeling (Husain et al., 2005) which demonstrate that receptive characteristics of auditory cortical neurons are compatible with continuity illusions (Petkov et al., 2007). Similarly, analogous studies show that visual continuity illusions occur in early visual brain regions, i.e., striate and peristriate cortex (Sugita, 1999). While a cortical underpinning is well-established, a key issue that remains to be resolved is whether correlates of perceptual induction emerge peripheral to cerebral cortex.

To this end, we investigated subcortical origins of auditory

\* Corresponding author at: School of Communication Sciences & Disorders, University of Memphis, 4055 North Park Loop, Memphis, TN 38152, USA.

E-mail address: [g.bidelman@memphis.edu](mailto:g.bidelman@memphis.edu) (G.M. Bidelman).



**Fig. 1.** Perceptual continuity of illusory auditory stimuli. (A) Percentage of trials listeners perceived uninterrupted (*unit*) or interrupted (*int*) modulated tones as “continuous” (i.e., no perceptible breaks). Despite stimuli with physical temporal discontinuities, occluding noise produced illusory percepts where listeners hear a continuous fluctuating tone. (B) Reaction times (RTs) for behavioral judgments. No differences were observed in the speed of listeners’ behavioral responses. errorbars =  $\pm$  s.e.m.

induction/restoration. We recorded brainstem frequency-following responses (FFRs) (Bidelman, 2015b) in human listeners elicited by modulated tones that did or did not promote illusory percepts (Riecke et al., 2007). FFRs reflect sustained neural ensemble activity from the upper brainstem that closely mirrors spectro-temporal properties of acoustic stimuli (Bidelman, 2015b). FFRs provide a neural “fingerprint” of complex acoustic signals within the human EEG. Their remarkable fidelity is evident by the fact that when replayed as auditory stimuli, (neural) FFR waveforms are actually intelligible to human listeners (Weiss and Bidelman, 2015). We selected tone frequencies well above the phase-locking capacity of cortical neurons (100–200 i.e.,  $\gg$  100–200 Hz) (Joris et al., 2004) to guarantee FFRs were of brainstem origin. Auditory continuity was manipulated by introducing masking noise or brief temporal interruptions in otherwise continuous fluctuating tones. To satisfy a brainstem correlate of auditory induction, we predicted FFRs would respond to target stimuli perceived as continuous, even during occluding noise and when the signal was physically silent in the auditory background. This finding would demonstrate that neural substrates supporting auditory restoration (Micheyl et al., 2003; Petkov et al., 2007), heretofore observed only cortically, might actually be inherited from lower, subcortical stages of the auditory system.

## 2. Results

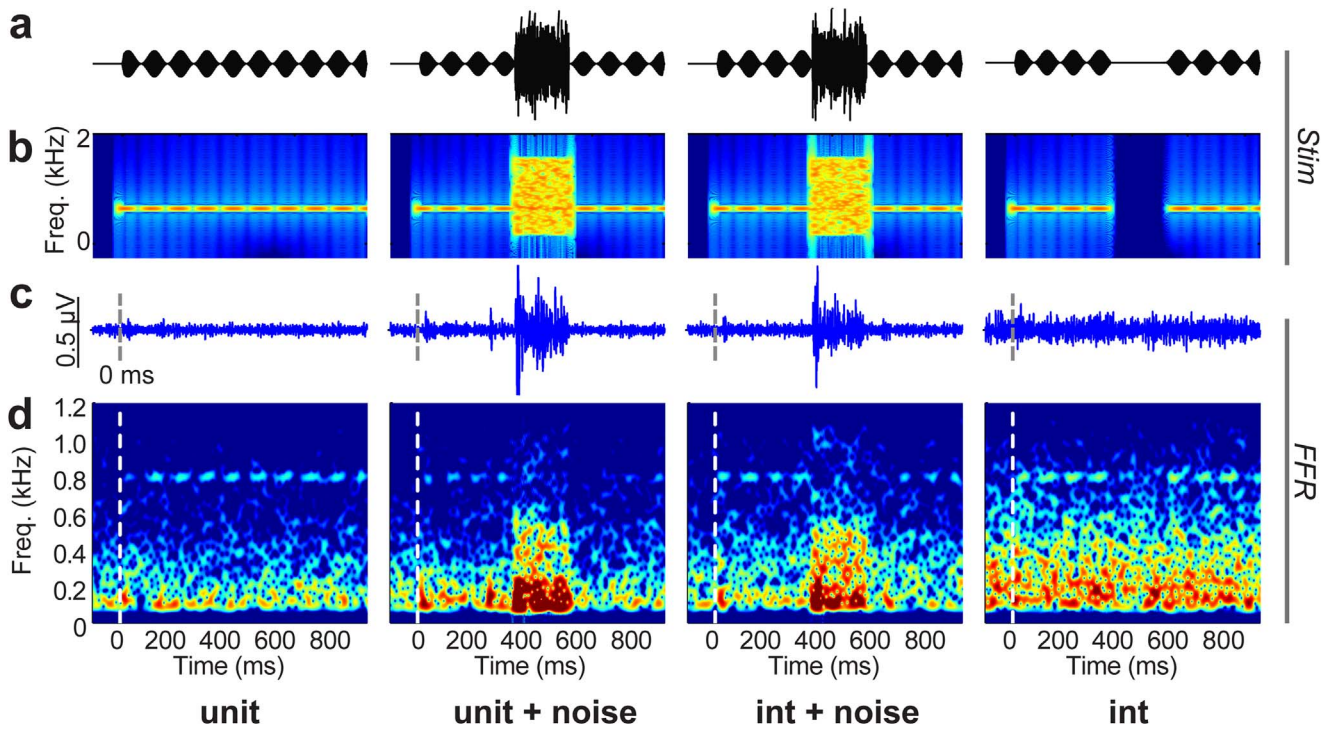
We collected behavioral and neuroelectric responses to illusory tones in noise that varied in their perceived continuity (Riecke et al., 2007). See *Materials and Methods*. In a speeded identification task, listeners labelled auditory stimuli (see Fig. 2A–B) as “continuous” or “discontinuous” based on their perception of temporal breaks in target signals. The interjection of noise occluded the auditory foreground but induced an illusory percept of a continuous tone (Fig. 1A). Tonal continuity was perceived even when targets were physically silent during noise (*int + noise* condition) confirming that stimuli were perceptually restored. RTs did not differ across tokens ( $F_{3,27}=0.52$ ,  $p=0.67$ ,  $\eta_p^2=0.05$ ) (Fig. 1B),

indicating that the speed of listeners’ decision was not modulated by stimulus condition.

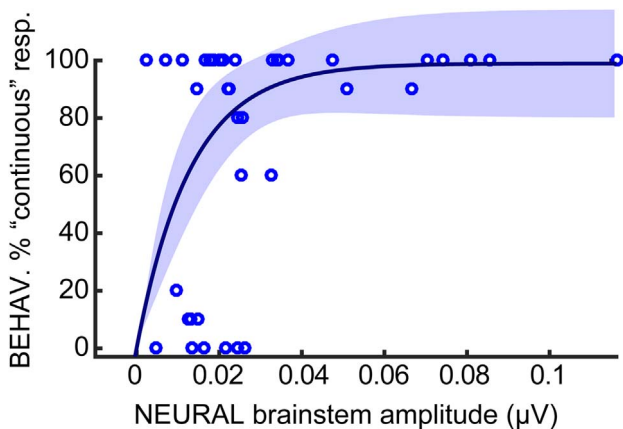
Brainstem FFRs appeared as neurophonic potentials whose phase-locking faithfully mirrored acoustic targets (Fig. 2). Prominent response energy was evident at the stimulus frequency which varied periodically with the modulation rate at  $\sim 800$  Hz (Fig. 2C–D).<sup>1</sup> This high frequency response is well above the known upper phase-locking limit of auditory cortical neurons (i.e., 100–200 Hz) (Joris et al., 2004) and helps further confirm that neural responses were of subcortical origin.

Logistics regression was conducted to assess the relation between perceptual judgments of auditory continuity (Fig. 1) and brainstem responses. In initial analyses, we considered the combination of neural amplitudes measured at both the *fc* and *fm* as predictors. Logistics regression was achieved via a generalized linear model (GLM) using the ‘glmfit’ function in MATLAB. The behavioral responses we aimed to measure were categorical binary judgments. Consequently, we used a binomial distribution and canonical logit link function to model the relation between neural and perceptual responses (Jaeger, 2008). Results revealed that brainstem amplitudes at *fc* predicted the frequency with which listeners’ perceived an illusory percept of a continuous tone [ $t_{37}=8.92$ ,  $p < 0.0001$ ]. That is, larger coding at the tone’s carrier frequency was related to an increased likelihood of auditory induction (Fig. 3). In contrast, we found no relation between brainstem coding at *fm* and behavior [ $t_{37}=1.72$ ,  $p=0.09$ ]. However, this might be expected given that the brainstem encoding of *fm* was much weaker than at *fc* (see also Fig. 4) and previous behavioral work showing that listeners are insensitive to the phase of *fm* modulations during occluding noise (Carlyon et al., 2004). Moreover, we found that the inclusion of *fm* as a predictor did not

<sup>1</sup> Low-frequency energy was observed in neural responses that was band limited to  $< 500$  Hz and arose primarily during the noise occluding segment. We attribute this low-frequency noise to myogenic activity. The response properties of this activity are most consistent with post auricular muscle (PAM) activation, whose spectrum is also band limited to a few hundred hertz and is induced via high-intensity sounds (O’Beirne and Patuzzi, 1999). It should be noted that all FFR response analysis (800 Hz) were well above the PAM bandwidth.



**Fig. 2.** Brainstem encoding of illusory auditory stimuli. (A) Stimulus time waveforms and (B) spectrograms for uninterrupted (*unit*) and interrupted (*int*) target tones with and without perceptual continuity-inducing noise (Riecke et al., 2007). (C) Brainstem FFR time waveforms and (D) response spectrograms illustrate ensemble responses of brainstem neurons to illusory stimuli. Dotted lines, stimulus onset ( $t = 0$ ).



**Fig. 3.** Brain-behavior relations for auditory induction. Individual data points show listeners' brainstem response amplitudes coding the stimulus frequency ( $fc$ ) plotted against their perceptual judgments of illusory continuity. The solid curve reflects a nonlinear fit to the data of the form  $a/(1 - e^{-bx})$ , fit using MATLAB's 'fitlm' routine. The shaded area reflects the 95% CI. More robust brainstem responses are associated with an increased likelihood of hearing a continuous (illusory) tone.

improve the logistics GLM fit above and beyond a model containing only the  $fc$  term alone [ $\chi^2(1) = 3.02$ ,  $p = 0.08$ ].

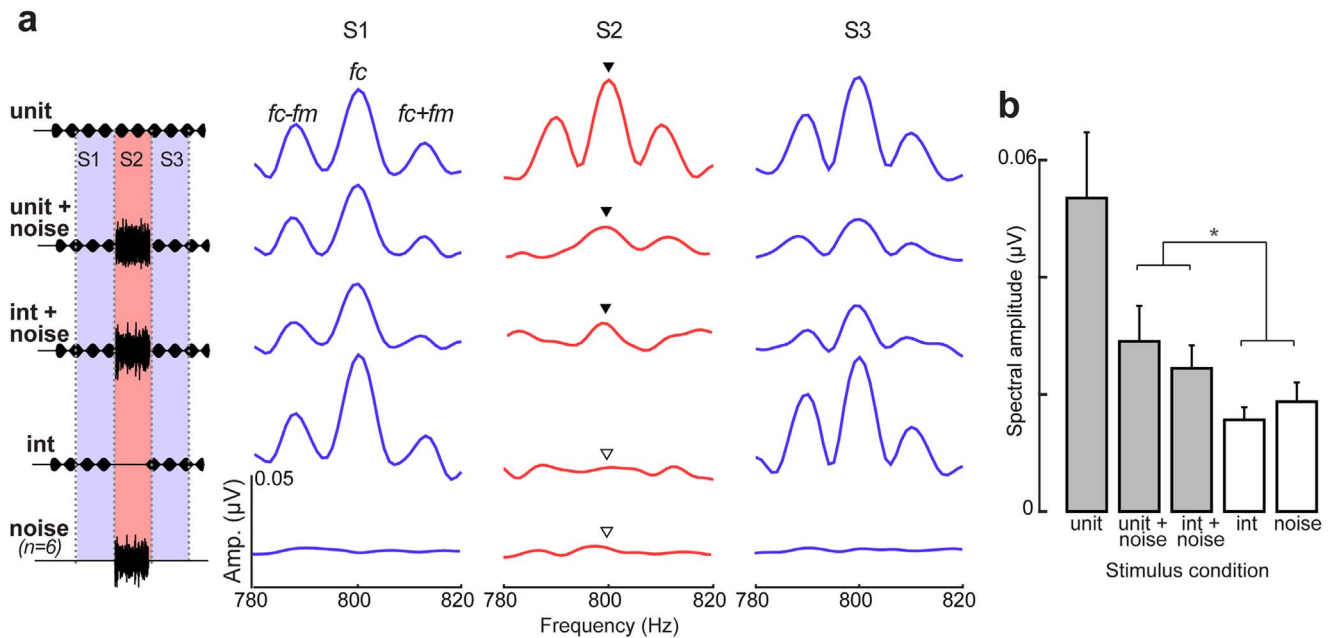
Importantly, the brain-behavior relation between listener's subjective reports of auditory continuity and FFR ( $fc$  encoding) remained significant even after excluding either *int* trials [ $t_{27} = 2.82$ ,  $p = 0.0047$ ] or *unit* trials [ $t_{27} = 7.92$ ,  $p < 0.001$ ] where the tone was unambiguously discontinuous or continuous, respectively. These findings were further bolstered by analysis of the RT data, which showed that the speed of listeners' behavioral judgments for induction-invoking stimuli (i.e., *unit+noise* and *int+noise*) were highly correlated with FFR responses [Spearman- $r = 0.53$ ,  $p = 0.018$ ; data not shown]. That is, larger responses (heard as continuous tones, Fig. 3) were associated with slower RTs, consistent with the well-known speed-accuracy tradeoff of choice

behavioral decisions (Heitz, 2014). Collectively, these findings indicate that the modulation of neural encoding at  $fc$  (but not  $fm$ ) was biologically relevant, predicting the perceptual properties of illusory auditory induction. In subsequent analyses, we focus only on  $fc$  given this was the only reliable predictor of behavior identified in the GLM.

We then assessed whether brainstem responses "tagged" target stimuli even in the presence of noise (i.e., correlate of restoration) using formal signal detection statistics (John and Picton, 2000) and Fourier analysis. We quantified FFR spectra in three, non-overlapping windows before (S1), during (S2), and after (S3) the critical occluding noise (Fig. 4A). We found that perceptually continuous (but not discontinuous) targets contained reliable ( $p \leq 0.01$ ) response energy in all listeners at the signal frequency even during occluding noise (i.e., S2). Across listeners, the average detection statistics ( $F$ -test,  $p$ -value; John and Picton, 2000) for responses to continuous stimulus conditions were: *unit*:  $F_{2,5} = 375.09$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.99$ ; *unit+noise*:  $F_{2,5} = 49.49$ ,  $p = 0.017$ ,  $\eta_p^2 = 0.95$ ; *int+noise*:  $F_{2,5} = 27.06$ ,  $p = 0.014$ ,  $\eta_p^2 = 0.91$ . Contrastively, the discontinuous *int* token did not produce reliable energy at the stimulus frequency according to a stringent ( $p < 0.01$ ) statistical criterion for detection [ $F_{2,5} = 15.22$ ,  $p > 0.01$ ].

An rmANOVA conducted on raw brainstem response amplitudes revealed that neural responses were modulated by the stimulus condition [ $F_{3,27} = 8.14$ ,  $p = 0.0005$ ,  $\eta_p^2 = 0.47$ ]. Multiple comparisons revealed that continuous tokens elicited stronger phase-locked FFRs than interrupted tokens. Moreover, illusory tokens with noise foregrounds (i.e., *int+noise*, *unit+noise*) evoked stronger brainstem responses than the discontinuous *int* token (Fig. 4B), suggesting a neural correlate of auditory restoration.

Both our continuity conditions (*int+noise* and *unit+noise*) contained additive noise whereas the control *int* condition did not. It is possible that the noise masker in these stimulus conditions could alter the neural responses in ways that may not have a direct relation to the continuity illusion (e.g., they may reflect a response to the noise itself; Petkov et al., 2007). To rule out this possibility,



**Fig. 4.** Brainstem responses reflect illusory perceptual continuity during noise. (A) Stimulus time-courses and analysis windows (S1–S3). (right) FFR spectra illustrate brainstem encoding of the carrier ( $fc$ ) and modulation sidebands ( $fc \pm fm$ ) of target tones before (S1), during (S2), and after (S3) the illusory inducing noise. Prominent energy is observed at the target frequency (800 Hz) for uninterrupted tones heard as continuous. Even with occluding foreground noise, FFRs to targets reliably “tag” ( $p < 0.01$ ) the signal frequency relative to the noise floor (John and Picton, 2000) ( $\blacktriangleright$ ) for all but interrupted (discontinuous) tones. (B) Despite noise masking (*unit+noise*) and the physical absence of the signal in the background (*int+noise*), brainstem responses phase-lock throughout occluding noise. No responses are observed for tokens with discontinuous percepts (*int, noise*). \* $p < 0.05$ ; errorbars =  $\pm$  s.e.m.

an additional control experiment was conducted using  $n=6$  listeners who were able to return for follow-up testing. The control condition featured the noise masker alone (see “noise”, Fig. 4A, bottom). This stimulus allowed us to compare FFRs to stimuli that contained noise but induced continuity percepts to those evoked by the noise alone—an important control in neural induction studies (cf. Petkov et al., 2007). Paralleling the discontinuous *int* condition, results showed that the FFRs contained no reliable energy at the stimulus frequency (see Fig. 4A, bottom). A planned comparison contrasting induction stimuli with the two control conditions [i.e.,  $\text{mean}(\text{int}+\text{noise}, \text{unit}+\text{noise})$  vs.  $\text{mean}(\text{int}, \text{noise})$ ] confirmed that FFRs were stronger for perceptually restored compared to both control stimuli. Additionally, FFR amplitudes did not differ between the two induction stimuli (*int+noise, unit+noise*), satisfying an important criterion of induction (Bregman, 1990) that during noise, “neural activity should be indistinguishable from activity that would have occurred had the tone actually continued (Petkov et al., 2007).” Collectively, our findings (i) provide evidence that subcortical neural activity persisted and even reconstructed missing auditory targets during obstructing noise and (ii) indicate the observed effects are not an idiosyncratic response to the occluding noise itself.

### 3. Discussion

Our results offer new evidence that illusory auditory percepts can emerge as early as the human brainstem, prior to the engagement of cerebral cortex and conscious attention. We found that brainstem responses represented ongoing modulated tones despite being occluded by noise and physically absent from the auditory signal. This indicates that subcortical signal processing helps maintain stable auditory representations by partially canceling the negative perceptual effects of masking (Warren, 1970). In demonstrating that nascent properties of sound induction begin in subcortical structures, our data generally support the

interpretation that the illusion originates above the auditory periphery (Petkov et al., 2007; Riecke et al., 2012) in more central auditory processing stages (King, 2007; Micheyl et al., 2003; Petkov et al., 2007; Riecke et al., 2007, 2009). However, our results extend previous studies by implicating the inferior colliculus (IC)—the putative generator of the human FFR (Bidelman, 2015b; Sohmer et al., 1977)—as a possible candidate in creating such illusory auditory restoration. Our findings further support the notion that brainstem auditory processing plays an important role in the perceptual organization of sound by pre-processing target auditory signals in route to cortex (cf. Bidelman and Alain, 2015; Pressnitzer et al., 2008).

At a mechanistic level, neural oscillations in auditory cortex have been shown to account for illusory continuity by entraining to ongoing target stimuli and completing fragmented signals masked by noise (Riecke et al., 2009). While A1 is a suitable candidate for induction (Petkov et al., 2007), evidence for intrinsic oscillatory entrainment in the brainstem is scarce but has been observed in thalamic (Steriade and Deschenes, 1984) and IC neurons (Schwartz et al., 1993). In particular, Schwartz et al. (1993) have reported “oscillating cells” localized to the antero-medial portion of the IC that fire spontaneously with discrete preferred interspike intervals. Provocatively, the intrinsic oscillatory firing of these cells becomes entrained to the same frequencies as the stimulus input. Target stimuli in the present study fell within the bandwidth of these brainstem oscillators (60–840 Hz) (Schwartz et al., 1993) and thus, could account for the FFR restoration effects observed here. Additionally, IC units also respond to sound omissions (Aguillon et al., 2015), an important quality for a candidate neural mechanism of induction. Spontaneous oscillations, induction, and omission responses have not been observed in peripheral auditory nerve (AN) fibers (Petkov et al., 2007; Riecke et al., 2012). That is, current understanding of the phenomenon’s neural basis is that continuity takes form after AN but in or before reaching A1 (Petkov and Sutter, 2011, p. 61). Therefore, our data lead us to infer that rostral brainstem is the first likely candidate for auditory

restoration. It is conceivable that the mesoscopic response properties of IC oscillating neurons (Schwartz et al., 1993) and their sensitivity to omissions in the ongoing auditory stream (Aguillon et al., 2015) may account for the induction-related responses we observe here in scalp-recorded FFRs.

While focused attention and lexical-semantic information can modulate illusory auditory restoration (e.g., Warren, 1970; Warren et al., 1972), induction has been demonstrated under passive listening conditions in which listeners are instructed to ignore auditory presentations (Michey et al., 2003; Petkov et al., 2003, 2007). Similarly, in the present study we found that FFRs showed nascent neural representations of auditory restoration effects under passive listening. This suggests that restoration emerges pre-attentively and in the absence of active engagement of attention. Our results converge and extend recent reports suggesting that properties of induction and perceptual illusions arise at pre-attentive stages of auditory cortical processing and without selective attention (Heinrich et al., 2011; Michey et al., 2003; Ruggles and Oxenham, 2014) by demonstrating neural correlates even lower in the auditory pathway—at the level of the brainstem. While attention no doubt modulates the extraction of information from the auditory scene, our data reveal that induction mechanisms that help “fill in” missing elements of the soundscape can operate automatically, and at pre-perceptual stages (Heinrich et al., 2011; Michey et al., 2003; Ruggles and Oxenham, 2014). As suggested by Heinrich et al. (2011), illusory auditory continuity might reflect an “obligatory perceptual process,” operating independently of attentional state. It is conceivable then that the cortical neural substrates supporting auditory restoration (e.g., Heinrich et al., 2011; Michey et al., 2003; Petkov et al., 2007) are at least partially inherited from lower, subcortical stages of the auditory processing hierarchy (see also, Bidelman and Alain, 2015).

Auditory induction has been popularly viewed as a “top-down” phenomenon, driven by higher-order cortical feedback. On the contrary, the pre-attentive, subcortical origin of induction observed here is more consistent with the notion that auditory continuity results from “bottom-up” mechanisms (Husain et al., 2005). Indeed, computational modeling suggests that lateral inhibitory-competitive networks in A1 (i.e., “bottom-up” synaptic activations) are sufficient to account for illusory auditory percepts. Nevertheless, our data cannot adjudicate other alternate explanations. In particular, it is possible that “top-down” corticofugal pathways modulate brainstem restoration and/or guide its neuronal receptive fields to determine what to tag and subsequently “fill in” based on a signal's behavioral relevance (Suga and Ma, 2003). Thus, it remains possible the observed subcortical correlates of induction seen here, result from a more complex interplay with auditory cortex (Las et al., 2005). Indeed, signal detection in noise is much stronger at increasingly higher levels of the auditory neuroaxis (midbrain < medial geniculate body < auditory cortex) (Las et al., 2005). Consequently, it is possible that the auditory restoration in brainstem FFRs (present study) is at least partially inherited from higher stages via “top-down” corticofugal feedback from thalamocortical structures (e.g., Suga et al., 2000). It is also possible that illusory auditory induction is stronger in cortical relative to subcortical nuclei. This possibility remains to be tested in future studies.

Additionally, the stimuli of this study were designed to maximize the presence or absence of perceptual continuity (i.e., a binary judgment) and thus, the potential to observe a corresponding neural correlate. It would be interesting in future studies to extend present findings by examining stimuli that parametrically vary the strength of perceptual continuity (e.g., Riecke et al., 2007). Such a stimulus design would provide necessary replication of the current results and also enable examination of more nuanced effects in auditory induction (e.g., individual

differences), beyond simply the presence or absence of a percept as examined here. Nevertheless, our findings highlight a potential brainstem mechanism to account for complex, even illusory sound percepts and underscore the importance of early, pre-attentive auditory processing in the perceptual organization of sound (cf. Bidelman and Alain, 2015; Pressnitzer et al., 2008).

## 4. Materials and methods

### 4.1. Participants

Listeners were 10 young adults (4 female;  $M \pm SD$ :  $30.4 \pm 3.8$  years) recruited from the University of Memphis student body and Greater Memphis Area. All participants had normal hearing (< 25 dB HL thresholds), no musical training (< 3 years formal instruction), and were right-handed (Oldfield, 1971). Participants provided written informed consent in accordance with a protocol approved by the University of Memphis Institutional Review Board.

### 4.2. Auditory stimuli

Sinusoidally amplitude modulated (SAM) tones (800 Hz carrier frequency modulated at 11 Hz; 850 ms duration) served as target stimuli (Fig. 2A–B) (Riecke et al., 2007). Using a high tonal carrier was critical as this frequency lies well above the upper phase-locking limit of auditory cortical neurons (i.e., 100–200 Hz) (Joris et al., 2004) and thus, guaranteed that neural responses would be of subcortical origin—where phase-locking persists up to ~1100 Hz (Liu et al., 2006). Target stimuli were either presented with or without a temporal interruption to oppose or promote perceptual continuity of the ongoing modulated tone. This segment was 22% (i.e., 187 ms) of the total stimulus duration, temporally centered on the carrier signal (see Fig. 2A). Uninterrupted stimuli (*unit*) consisted of the original SAM tone targets whereas interrupted stimuli (*int*) contained a gap, temporally centered within the targets. To induce auditory perceptual restoration, masking noise was superimposed onto the *unit* and *int* targets. For interrupted targets, onsets and offsets between the gap and masker were synchronized. The masker itself consisted of band-filtered noise that was spectrotemporally centered on the modulated tones (Fig. 2B). Auditory induction is stronger when occluding noise is of similar spectral neighborhood to targets (Warren et al., 1972). As such, the noise bandwidth was 2 octaves, concentrated logarithmically around the carrier of the target tone (800 Hz) (Riecke et al., 2007). Maskers were combined with the *unit* and *int* target tones at a signal-to-noise-ratio of –5 dB. This yielded two additional stimuli (*unit+noise*, *int+noise*) that differed acoustically, but were perceptually identical. Formal discrimination tests in preliminary control experiments ( $n=5$  listeners) confirmed that these two stimuli were perceptually continuous but indistinguishable from one another ( $t_4=0.17$ ,  $p=0.87$ ). This perceptual equivalence occurred despite the fact that in the *unit* case, the masker occluded the target tone whereas in the *int* case, the masker occluded silence. Critically, this confirmed that no *physical cues* were available to judge auditory stimuli and furthermore, that listeners heard illusory tones based on the *psychological* restoration of stimuli. All stimuli were gated (10 ms  $\cos^2$  ramps) and RMS normalized to equate the intensity of target tones across conditions. Stimuli were synthesized in MATLAB<sup>®</sup> 2013b (The MathWorks, Natick, MA).

### 4.3. Behavioral task

Prior to EEG recording, we conducted an auditory classification

task to gauge listeners' perception of illusory stimuli. Testing was carried out in a sound-attenuating booth (Industrial Acoustics, Inc.) using high-fidelity circumaural headphones (Sennheiser HD 280). Stimuli were presented on a PC at a comfortable volume ( $\sim 70$  dB SPL). Listeners performed a rapid subjective listening task in which they judged the perceived continuity of the four auditory stimuli (*unit*, *int*, *unit + noise*, *int + noise*). Participants were briefly trained to attend to the modulated target tones and rate their perceptual continuity as either "continuous" or "discontinuous" via button press on the computer. The four stimuli were each presented 10 times (40 total trials, random order). We analyzed participants' behavioral responses by calculating the percentage of trials reported as "continuous" (i.e., no perceptible breaks). Trial-by-trial reaction times (RT) were also recorded, computed as the time delay between stimulus presentation and the listener's response. Stimulus presentation and response collection was achieved using custom routines coded in MATLAB.

#### 4.4. Brainstem FFR recordings

Brainstem frequency-following responses (FFRs) are neuromiographic scalp potentials generated in the rostral brainstem (Bidelman, 2015b) whose phase-locked activity faithfully mirrors time-frequency properties of acoustic signals. Previous studies demonstrate that the degree of spectrotemporal information coded in a listener's FFR is predictive of their auditory perceptual skills including speech identification (Weiss and Bidelman, 2015). Brainstem responses were recorded using typical procedures from our laboratory. FFRs were elicited in response to 1800 exemplars of each of the four stimulus tokens (interstimulus interval = 200 ms). Auditory targets were presented binaurally at an intensity of 82 dB SPL.

FFRs overlap in time with the evoking stimulus and thus are highly susceptible to stimulus artifact contaminating the neural response. We used ER-30 inset headphones (Etymotic Research) as they feature extended acoustic tubing (20 ft) that allowed us to place the transducers well outside the testing environment. Spatially separating the headphone transducers from participants ensured that electromagnetic stimulus artifact could in no way contaminate neurophysiological responses (Campbell et al., 2012) and guaranteed that following responses were of a biological origin. All latency measures were corrected for the acoustic delay of the headphone transducer. Similarly, the lowpass frequency response of headphone apparatus (2 kHz cutoff) was corrected with a dual channel 15-band graphical equalizer (dbx EQ Model 215 s; Harman) to achieve a relatively flat frequency response out to 4 kHz. Stimulus intensity was calibrated through a Larson-Davis SPL meter (Model LxT) and measured in a 2-cc coupler (IEC 60126). Left and right ear channels were calibrated separately. Stimulus conditions were randomized within and between participants.

Participants reclined comfortably in an electro-acoustically shielded booth to facilitate recording of neurophysiologic responses. They were instructed to relax and refrain from extraneous body movement (to minimize myogenic artifacts), ignore the sounds they hear (to divert attention to the auditory stimuli), and were allowed to watch a muted subtitled movie to maintain a calm yet wakeful state (i.e., passive listening). EEGs were recorded differentially using a vertical montage with electrodes placed on the high forehead at the hairline ( $\sim$ Fz) referenced to linked mastoids (A1/A2). Neuroelectric activity was digitized at 20 kHz using an online passband of 0.05–8000 Hz (SynAmps RT amplifiers; Compumedics Neuroscan). Traces were segmented ( $-100$ – $900$  ms epoch window), baselined to the pre-stimulus interval, and subsequently averaged in the time domain to obtain FFRs for each listener per stimulus condition. Trials exceeding  $\pm 50 \mu\text{V}$  were

rejected as artifacts prior to averaging. Grand averaged evoked responses were then bandpass filtered (100–1000 Hz) for response quantification and to eradicate low-frequency cortical responses from evoked responses and isolate brainstem neural activity (Bidelman, 2015a; Bidelman and Alain, 2015).

#### 4.5. FFR response analysis

FFRs were windowed (Gaussian function,  $\sigma = 1$ ) into three, non-overlapping 175-ms time segments corresponding to periods before (S1: 50–225 ms), during (S2: 350–525 ms), and after (S3: 550–725 ms) the occluding noise (see Fig. 4A). Segmented traces were then converted to the frequency-domain via the Fast Fourier Transform for spectral analysis.<sup>2</sup> We measured the Fourier magnitude at the stimulus carrier frequency in each of the three response segments to quantify the degree of subcortical phase-locking to the target signal in the S2 segment of interest (i.e., the noise occluding interval).

For each stimulus, the presence of a response in the S2 segment was further confirmed using a stringent statistical criterion (spectral *F*-test; John and Picton, 2000) contrasting response amplitude at the expected target (800 Hz) to the adjacent noise floor (for details, see John and Picton, 2000). We quantified the noise floor in three frequency bins 40 Hz away from either sideband (i.e., 759–761 Hz and 839–841 Hz) to ensure noise estimates fell well outside the range of all stimulation frequencies (carrier and modulation sidebands). The rationale of this approach is that neural phase-locked responses to the signal are localized to a Fourier bin near the stimulus frequency whereas activity in adjacent bins contains only random noise (with zero mean and equal variance distributed across the noise bins). The ratio of signal power to the power in *N* adjacent frequency bins is then distributed according to a *F*-distribution with 2 and  $2N - 1$  degrees of freedom (John and Picton, 2000). This analysis provided a probability (*p*-value) of whether or not the FFR contained energy at the target signal frequency. To satisfy a brainstem correlate of illusory auditory restoration, we required that FFRs be detected at the target frequency during the occluding noise segment (S2) at a  $p = 0.01$  level of significance. We used this stringent criterion for response detection to further safeguard against the possibility that a FFR could be falsely attributed to a neural response to the noise (rather than signal) component.

We analyzed all other dependent measures (e.g., behavioral data) using repeated measures (rm)ANOVA with stimulus condition as the single within-subjects factor (4 levels: *unit*, *int*, *unit + noise*, *int + noise*). Post hoc contrasts were corrected for multiple comparisons via Tukey-Kramer adjustments and assessed at the  $p = 0.05$  level of significance. A generalized linear model (GLM) (logistics regression; binomial distribution with canonical link function) was used to assess the relation between neural and behavioral responses (see Results for details).

#### Author contributions

G. M. B. and C. K. P. designed the experiment, C. K. P. collected the data, G. M. B. and C. K. P. analyzed the data and wrote the paper.

<sup>2</sup> Note that our fixed analysis window (175-ms) was shorter than the duration of any of the three segments themselves (S1/S3 = 331 ms; S2 = 190 ms). Choosing shorter windows for the analysis, temporal windowing of the segments, and latency correction of the headphone transducer prevents possible spillover effects (i.e., temporal bleed) between spectral segments. Evidence that these safeguards were effective is evident in the *int* and *noise control* conditions (Fig. 4A), which showed no measurable response in the critical S2 segment unlike stimuli which invoked perceptual continuity.

## Acknowledgements

Portions of this work were supported by grants from the American Hearing Research Foundation (AHRF) and American Academy of Audiology Foundation (AAAF) awarded to G. M. B.

## References

- Aguillon, B., Nieto, J., Fritz, J., Malmierca, M., 2015. Neurons in the inferior colliculus of the rat response to the omission of stimuli. 38th-MidWinter Meeting, (Assoc. Res. Oto). (Abstract).
- Bidelman, G.M., 2015a. Towards an optimal paradigm for simultaneously recording cortical and brainstem auditory evoked potentials. *J. Neurosci. Methods* 241, 94–100.
- Bidelman, G.M., 2015b. Multichannel recordings of the human brainstem frequency-following response: Scalp topography, source generators, and distinctions from the transient ABR. *Hear Res.* 323, 68–80.
- Bidelman, G.M., Alain, C., 2015. Hierarchical neurocomputations underlying concurrent sound segregation: Connecting periphery to percept. *Neuropsychologia* 68, 38–50.
- Braaten, C.E., Leary, J.C., 1999. Temporal induction of missing birdsong segments in European Starlings. *Psychol. Sci.* 10, 162–166.
- Bregman, A.S., 1990. *Auditory Scene Analysis* Vol.. MIT, Cambridge, MA.
- Campbell, T., Kerlin, J.R., Bishop, C.W., Miller, L.M., 2012. Methods to eliminate stimulus transduction artifact from insert earphones during electroencephalography. *Ear Hear.* 33, 144–150.
- Carlyon, R.P., Micheyl, C., Deeks, J.M., Moore, B.C., 2004. Auditory processing of real and illusory changes in frequency modulation (FM) phase. *J. Acoust. Soc. Am.* 116, 3629–3639.
- Heinrich, A., Carlyon, R.P., Davis, M.H., Johnsrude, I.S., 2011. The continuity illusion does not depend on attentional state: fMRI evidence from illusory vowels. *J. Cogn. Neurosci.* 23, 2675–2689.
- Heitz, R.P., 2014. The speed-accuracy tradeoff: History. *Physiol. Methodol. Behav. Front Neurosci.*, 8.
- Husain, F.T., Lozito, T.P., Ulloa, A., Horwitz, B., 2005. Investigating the neural basis of the auditory continuity illusion. *J. Cogn. Neurosci.* 17, 1275–1292.
- Jaeger, T.F., 2008. Categorical data analysis: Away from ANOVAs (transformation or not) and towards Logit Mixed Models. *J. Mem. Lang.* 59, 434–446.
- John, M.S., Picton, T.W., 2000. MASTER: A Windows program for recording multiple auditory steady-state responses. *Comput. Methods Prog. Biomed.* 61, 125–150.
- Joris, P.X., Schreiner, C.E., Rees, A., 2004. Neural processing of amplitude-modulated sounds. *Physiol. Rev.* 84, 541–577.
- King, A.J., 2007. Auditory neuroscience: Filling in the gaps. *Curr. Biol.* 17, R799–R801.
- Las, L., Stern, E.A., Nelken, I., 2005. Representation of tone in fluctuating maskers in the ascending auditory system. *J. Neurosci.* 25, 1503–1513.
- Liu, L.F., Palmer, A.R., Wallace, M.N., 2006. Phase-locked responses to pure tones in the inferior colliculus. *J. Neurophysiol.* 95, 1926–1935.
- Micheyl, C., Carlyon, R.P., Shtyrov, Y., Hauk, O., Dodson, T., Pullvermuller, F., 2003. The neurophysiological basis of the auditory continuity illusion: A mismatch negativity study. *J. Cogn. Neurosci.* 15, 747–758.
- O'Beirne, G.A., Patuzzi, R.B., 1999. Basic properties of the sound-evoked post-auricular muscle response (PAMR). *Hear. Res.* 138, 115–132.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia* 9, 97–113.
- Petkov, C.I., O'Connor, K.N., Sutter, M.L., 2003. Illusory sound perception in macaque monkeys. *J. Neurosci.* 23, 9155–9161.
- Petkov, C.I., O'Connor, K.N., Sutter, M.L., 2007. Encoding of illusory continuity in primary auditory cortex. *Neuron* 54, 153–165.
- Petkov, C.I., Sutter, M.L., 2011. Evolutionary conservation and neuronal mechanisms of auditory perceptual restoration. *Hear Res.* 271, 54–65.
- Pressnitzer, D., Sayles, M., Micheyl, C., Winter, I.M., 2008. Perceptual organization of sound begins in the auditory periphery. *Curr. Biol.* 18, 1124–1128.
- Riecke, L., van Opstal, A.J., Goebel, R., Formisano, E., 2007. Hearing illusory sounds in noise: Sensory-perceptual transformations in primary auditory cortex. *J. Neurosci.* 27, 12684–12689.
- Riecke, L., Esposito, F., Bonte, M., Formisano, E., 2009. Hearing illusory sounds in noise: The timing of sensory-perceptual transformations in auditory cortex. *Neuron* 64, 550–561.
- Riecke, L., Micheyl, C., Oxenham, A.J., 2012. Global not local masker features govern the auditory continuity illusion. *J. Neurosci.* 32, 4660–4664.
- Ruggles, D.R., Oxenham, A.J., 2014. Perceptual asymmetry induced by the auditory continuity illusion. *J. Exp. Psychol.: Hum. Percept. Perform.* 40, 908–914.
- Schwartz, D.W.F., Dezso, A., Neufeld, P.R., 1993. Frequency selectivity of central auditory neurons without inner ear. *Acta Otolaryngol. -Stockh.*, 113.
- Sohmer, H., Pratt, H., Kinarti, R., 1977. Sources of frequency-following responses (FFR) in man. *Electroencephalogr. Clin. Neurophysiol.* 42, 656–664.
- Steriade, M., Deschenes, M., 1984. The thalamus as a neuronal oscillator. *Brain Res. Rev.* 8, 1–63.
- Suga, N., Gao, E., Zhang, Y., Ma, X., Olsen, J.F., 2000. The corticofugal system for hearing: Recent progress. *Proc. Natl. Acad. Sci. U.S.A.* 97, 11807–11814.
- Suga, N., Ma, X., 2003. Multiparametric corticofugal modulation and plasticity in the auditory system. *Nat. Neurosci.* 4, 783–794.
- Sugita, Y., 1999. Grouping of image fragments in primary visual cortex. *Nature* 401, 269–272.
- Warren, R.M., 1970. Perceptual restoration of missing speech sounds. *Science* 167, 392–393.
- Warren, R.M., Obusek, C.J., Ackroff, J.M., 1972. Auditory induction: Perceptual synthesis of absent sounds. *Science* 176, 1149–1151.
- Weiss, M.W., Bidelman, G.M., 2015. Listening to the brainstem: Musicianship enhances intelligibility of subcortical representations for speech. *J. Neurosci.* 35, 1687–1691.