Localization of complex sounds is modulated by behavioral relevance and sound category

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Meaningful sounds represent the majority of sounds that humans hear and process in everyday life. Yet studies of human sound localization mainly use artificial stimuli such as clicks, pure tones, and noise bursts. The present study investigated the influence of behavioral relevance, sound category, and acoustic properties on the localization of complex, meaningful sounds in the horizontal plane. Participants localized vocalizations and traffic sounds with two levels of behavioral relevance (low and high) within each category, as well as amplitude-modulated tones. Results showed a small but significant effect of behavioral relevance: localization acuity was higher for complex sounds with a high level of behavioral relevance at several target locations. The data also showed category-specific effects: localization biases were lower, and localization precision higher, for vocalizations than for traffic sounds in central space. Several acoustic parameters influenced sound localization performance as well. Correcting localization responses for front-back reversals reduced the overall variability across sounds, but behavioral relevance and sound category still had a modulatory effect on sound localization performance in central auditory space. The results thus demonstrate that spatial hearing performance for complex sounds is influenced not only by acoustic characteristics, but also by sound category and behavioral relevance. *© 2017 Acoustical Society of America.*

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I. INTRODUCTION

Sound localization is a principal mechanism for orientation in the environment and for rapid reaction to significant events. It also enables humans to localize events when visual information is degraded or absent, such as in darkness or in a cluttered environment (e.g., in a crowd). Spatial hearing additionally plays a role in auditory scene analysis, that is, the process through which incoming sounds with overlapping frequencies are decomposed into individual sound sources (Bregman, 1990). Humans are capable of localizing sounds in the horizontal plane within the range of a few degrees for positions close to the midline (e.g., Makous and Middlebrooks, 1990; Oldfield and Parker, 1984). This is achieved mainly through the processing of binaural spatial cues: interaural level differences (ILDs) and interaural time differences (ITDs). Monaural, spectral cues introduced by the pinnae, head, and torso further contribute to vertical sound localization and to the disambiguation of front and back in the horizontal plane (for a review, see Grothe *et al.*, 2010).

Although sound localization in humans and non-primate mammals has been studied intensively for several decades, most psychoacoustic studies presented participants with tones, clicks, or noise bursts (e.g., Butler, 1986; Makous and Middlebrooks, 1990; Musicant and Butler, 1985; Oldfield and Parker, 1984; Van Wanrooij and Van Opstal, 2007; Voss *et al.*, 2015). Little is known about the localization of complex, meaningful sounds, or about the influence of the behavioral relevance of sounds on localization acuity. The present study therefore aimed to investigate the relative effects of behavioral relevance and acoustic properties (spectral bandwidth, amplitude modulation, sound duration, center of spectral gravity, and presence of ILDs and ITDs) on localization performance for complex sounds in the horizontal plane.

Participants localized amplitude-modulated (AM) tones, vocalizations, and traffic sounds. For each category of complex, meaningful sounds (that is, vocalizations and traffic sounds), we selected stimuli that either had a relatively high or a relatively low relevance for ongoing behavior. We hypothesized that behavioral relevance, as well as some acoustic properties, modulate sound localization performance. Specifically, we expected that sounds with high behavioral relevance would be localized more accurately than less relevant ones. We further predicted modulatory effects of bandwidth, center of spectral gravity, and availability of ILDs and ITDs. That is, we hypothesized that localization performance would be better for broadband than narrowband sounds (Butler, 1986; Tollin *et al.*, 2013), as well as for sounds with a spectral content mostly outside of the 1–3 kHz range (Sandel *et al.*, 1955; Stevens and Newman, 1936), and for sounds with a clear presence of ILDs and ITDs.

II. METHODS

A. Participants

Fourteen volunteers [mean age = 23.6 yrs, standard deviation (SD) = 4.6 yrs, 8 males] gave informed consent for participation in the experiment in accordance with the procedures of the Institutional Review Board at Georgetown University. Participants reported a normal neurological history and had normal hearing in both ears as assessed with audiometric testing of pure-tone thresholds at 0.5, 1, 2, 4, and 8 kHz with a Oscilla SM910 Screening Audiometer (Oscilla, Aarhus, Denmark).

B. Stimuli

Stimuli consisted of spatialized audio clips in one of three categories: vocalizations, traffic sounds, and AM tones. We selected vocalizations and traffic sounds because they are meaningful, complex sounds. AM tones were added to investigate the influence of spectral sound properties on spatial hearing performance. We introduced the dimension of behavioral relevance by selecting specific sound items within each category of complex, meaningful sounds (vocalizations and traffic sounds). Specifically, we included neutral (low behavioral relevance) and fearful (high behavioral relevance) vocalizations from the Montreal Affective Voices Database (Belin *et al.*, 2008). Fearful expressions are highly relevant to human behavior as they indicate the possible presence of a threat in the environment. Recordings of traffic sounds were similarly selected based on their potential behavioral relevance. That is, we hypothesized that the siren of a police car would have a larger behavioral relevance than the sound of a car engine. We confirmed the selection of items based on their level of behavioral relevance in a separate validation experiment before implementing the actual experiment (see Sec. II C).

AM tones were generated with MATLAB (The MathWorks, Inc., Natick, MA), modulated at 8 Hz (modulation depth = 1), and comprised three frequency ranges: 0.45, 0.50, and 0.55 kHz; 1.35, 1.50, and 1.65 kHz; and 2.25, 2.50, and 2.75 kHz. In total there were five sound conditions: high relevance vocalizations, low relevance vocalizations, high relevance traffic sounds, low relevance traffic sounds, and AM tones. Nine audio clips were included in each condition, resulting in 45 unique sounds. Audio clips of vocalizations included both male and female voices. Audio clips were cut to a duration of 1000 ms, sampled at 44.1 kHz, and included a 10 ms linear on- and off-ramp. Peak energy [root mean square (RMS) amplitude] was equalized across stimuli.

Participants localized audio clips at five locations in central auditory space (−20°, −10°, 0°, +10°, +20°) and five locations in the right auditory periphery (+70°, +80°, +90°, +100°, +110°; see Fig. 1). We did not include target locations in the left auditory periphery to avoid participant fatigue. Furthermore, to the best of our knowledge, no prior study has shown a difference in localization performance between the left and right hemi-field (Middlebrooks and Green, 1991; Oldfield and Parker, 1984; Voss *et al.*, 2004, 2015). All target locations were at zero elevation and therefore differed only in azimuth position.

Audio clips were presented with professional Sony MDR-V900 studio headphones (Sony, Tokyo, Japan) during the test session. Audio fragments were spatialized prior to the actual test session by making subject-specific binaural recordings. Although this setup may be less natural than free-field listening conditions, it provides the opportunity to assess spatial hearing performance for stimuli that have recently been used in functional magnetic resonance imaging studies investigating the neural mechanisms underlying sound localization (Derey *et al.*, 2015; Moerel *et al.*, 2015). Binaural recordings furthermore enable us to quantify the ILDs and ITDs for each stimulus and to include this information in subsequent analyses.

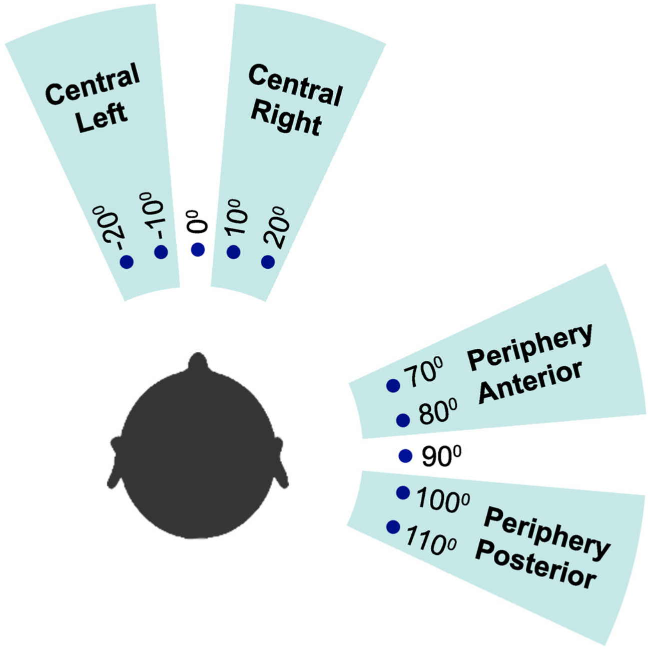

FIG. 1. (Color online) Target locations. Blue dots indicate the position of target locations at which stimuli were presented. Light blue areas indicate portions of the azimuth that constitute location bins for analysis. The measures of sound localization performance employed in the present study—localization acuity, bias, and precision—were averaged across target locations within an individual bin.

Subject-specific binaural recordings of all stimuli were made with microphones placed in the ear canals of participants (OKM II Classic Microphone, Soundman, Germany; sampling rate = 44.1 kHz). Recordings were made in a production studio (internal volume $p = 66$ m^3, walls and ceiling consisted of gypsum board covered with fabric, the floor consisted of concrete covered with a thin carpet). Participants were blindfolded and seated in the middle of the room. Sound clips were played from the designated azimuthal positions in central and peripheral auditory space using a Behringer B205D loudspeaker (Behringer, Willich, Germany). For each azimuthal position, the speaker was placed at a distance of 1.30 m in far auditory space. Audio recordings were edited with Adobe Audition CS6 (Version 5.0.2, Adobe Systems Inc., Mountain View, CA) and Audacity (Version 2.1.1, http://audacityteam.org) to remove any low-frequency noise introduced by the microphones or speaker (<60 Hz).

C. Stimulus validation

Twenty participants (mean age = 33.3 yrs, SD = 8.6 yrs, 8 males) completed the validation experiment. Participants in the validation experiment were excluded from participation in the main experiment. The validation experiment was performed with the Presentation software package (Version 18.1, Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com). Participants were seated in front of a computer, were wearing Sony MDR-V900 dynamic stereo headphones, and were instructed to evaluate two dimensions of each sound: category (that is, human vocalizations or traffic sounds) and behavioral relevance. Category recognition was tested with a two-alternative forced-choice task: participants had to choose between *vocalization* and *traffic sound* for each audio fragment. Participants were also asked how relevant the sound would be to their ongoing behavior if they were to be in a neutral, non-engaging situation (e.g., walking outdoors). The degree of relevance was rated with a slider scale ranging from "not relevant" at the one extreme to "very relevant" at the other extreme. After sound presentation, the response screen was shown until both evaluations were completed. The next trial was presented after a short interval (1000 ms). Behavioral relevance ratings made with the slider scale were translated to a continuous scale with 1 at the one extreme (not relevant) and 100 at the other extreme (very relevant). We normalized the ratings of each participant to have the same mean and SD (z-scoring within participant) and tested for statistical differences between the behavioral relevance groups within a category with paired-samples t-tests.

D. Procedure

For the main experiment participants were blindfolded and seated in a chair with a fixed position in the center of a sound-attenuated room. At the start of each trial and during each sound presentation they were required to maintain a head position pointing straight ahead. The start of a trial was indicated by the presentation of a short (200 ms), non-spatialized high-frequency tone at 5 kHz. When the participant was in the right position (head pointing straight ahead, as described above), the experimenter started the presentation of the spatialized test sound (1000 ms). Following sound offset, participants pointed at the perceived sound location with a laser pointer in their right hand (dominant hand). Rulers with equidistant lines 1° apart were placed on the walls of the sound-attenuated room, and the experimenter recorded each response (Tabry *et al.*, 2013).

Each stimulus was presented once at every target location, amounting to a total of 450 trials. Stimuli were presented in nine blocks of 50 trials each in a randomized order. Blocks were separated by short breaks. Sounds were presented at a level comfortable to the participant.

E. Analysis

We started the analysis by assessing the presence of anterior-to-posterior (AP) and posterior-to-anterior (PA) reversals. Trials for which target and response location were not on the same side of the interaural axis (that is, either both anterior or both posterior) were considered a reversal trial. We then calculated for such trials a "*reversal resolved response*" by subtracting the response from $-180°$ (target and response in the left hemifield) or $+180°$ (target and response in the right hemifield). In subsequent analyses we thus consider two types of localization responses: the original responses and the reversal-resolved responses.

Next, we computed three measures of sound localization performance: signed error, absolute error, and RMS error. These measures reflect localization bias, acuity, and precision, respectively. Localization bias—signed error—was computed as the signed deviation of the localization response from the target location. The signed error of a more anterior response was classified as negative, that of a more posterior response as positive (Oldfield and Parker, 1984). Note that the signed error is invariant to left–right hemifield errors (that is, mistaking locations to the left of the midline with locations to the right of the midline, or vice versa), and includes only the signed deviation of the response from the target location in an anterior–posterior direction. To compute signed error we therefore collapsed locations across hemifields. Localization acuity was computed as the absolute difference between target and response location. Last, localization precision—RMS error—was defined as the SD of the absolute error. Measures were computed for individual locations and subsequently averaged to create four location bins: left central auditory space, right central auditory space, anterior auditory periphery, posterior auditory periphery (Fig. 1). Data from the central speaker (0°) and from the speaker at the interaural midline ($+90°$) were not included in the analysis.

To evaluate which stimulus properties influence human spatial hearing performance we characterized the acoustic properties of each sound (see Appendix A). S*ound duration* was computed by calculating the power (measured as RMS) in bins of 10 ms. Bins with RMS>0 were included in the total duration. *Center of spectral gravity*, a measure of the average frequency of a spectrum, was identified with Praat (version 6.0.18; Boersma and Weenik; University of Amsterdam; www.praat.org) and converted to a logarithmic scale. *Degree of amplitude modulation*, defined as the SD of intensity within the duration of the audio clip, was also determined with Praat. We furthermore computed *spectral bandwidth* as the difference between the minimum and maximum frequency in the spectrum, expressed in octaves. Finally, we assessed the presence of ILDs by computing the arithmetic difference between the signal amplitude in the left and right channel of the binaural recordings in decibel (dB). We also examined ITDs per stimulus by computing the interaural phase difference between the left and right channel in the binaural recordings. This was done for each frequency-time point in the spectrum and subsequently converted to ITD (see Appendix A).

Finally, we assessed with multiple regression analysis the modulatory effect of these stimulus characteristics, sound category, and behavioral relevance on the localization performance of complex sounds. This was done for the original localization responses as well as the reversal-resolved responses at all target location bins and for each response measure (absolute, signed, and RMS error), resulting in a total of 24 models. Note that the AM tones were not included in the multiple regression analysis as the main aim of the study was to investigate the effect of higher order aspects such as behavioral relevance on the localization of complex sounds. In addition, including the AM tones would introduce multicollinearity in the regression model as a result of the acoustical similarities between stimuli in this category. The spectral bandwidth and degree of amplitude modulations, for instance, were comparable across AM tones. Finally, we did not consider ILD cues here or in the remainder of the analysis, as every binaural recording—independent of differences in center of spectral gravity—exhibited level differences to some extent (Appendix A; see also Hartmann *et al.*, 2016).

III. RESULTS

A. Stimulus validation

Prior to the main experiment we performed a validation experiment to obtain independent judgments of the level of behavioral relevance of the stimuli used in the main experiment and to assess sound category recognition. Figure 2 shows that there was a significant difference between the average level of behavioral relevance within each sound category (*vocalizations* and *traffic sounds*: mean z-score *vocalizations low relevance* [SD] = −0.75 [0.15]; mean [SD] *vocalizations high relevance* = 0.67 [0.29]; mean [SD] *traffic sounds low relevance* = −0.44 [0.20]; mean [SD] *traffic sounds high relevance* = 0.51 [0.39]; paired samples t-test *traffic sounds*: $t(8) = -6.425$, $p = 2.0 \times 10^{-4}$; paired samples t-test *vocalizations*: $t(8) = -15.414$, $p = 3.1 \times 10^{-7}$). Category recognition was at ceiling level (mean percent correct *traffic sounds* = 98%; mean percent correct *vocalizations* = 100%).

B. Outliers

Single trials with a localization response more than 3 SDs above or below the mean response—after correction for front-back reversals—for a given location were considered outliers and excluded from subsequent analyses. Outliers were identified in the data set that was corrected for reversals and removed from both the reversal-resolved and the original data set. The average percentage of trials that was identified as outliers across participants was 2.68%.

C. Reversals

On average, the percentage of AP reversals was 17.2% for locations in central auditory space and 19.1% in the auditory periphery. PA reversals, which could only occur in the posterior periphery (see Fig. 1), were much more frequent: these occurred on average during 65.6% of the trials with a target position in posterior auditory space. We observed that participants that make more AP reversals in central auditory space also make more reversals in the auditory periphery [Fig. 3(A); linear regression, adjusted $R^2 = 0.391$, $\beta = 0.609$, $p = 0.0099$; all p values were corrected for multiple comparisons with the False Discovery Rate (FDR) at $q < 0.05$; Benjamini and Hochberg, 1995]. We also observed a directional bias for reversals: participants with a large proportion of AP reversals had a lower proportion of PA reversals in the periphery and vice versa [Fig. 3(B), adjusted $R^2 = 0.700$, $\beta = -1.152$, $p = 0.0001$]. We did not observe a relationship between the occurrence of AP reversals per sound as a function of location [Fig. 3(C); adjusted $R^2 = -0.018$, $p = 0.667$], nor a directional bias for individual sounds [Fig. 3(D); adjusted $R^2 = 0.015$, $p = 0.206$].

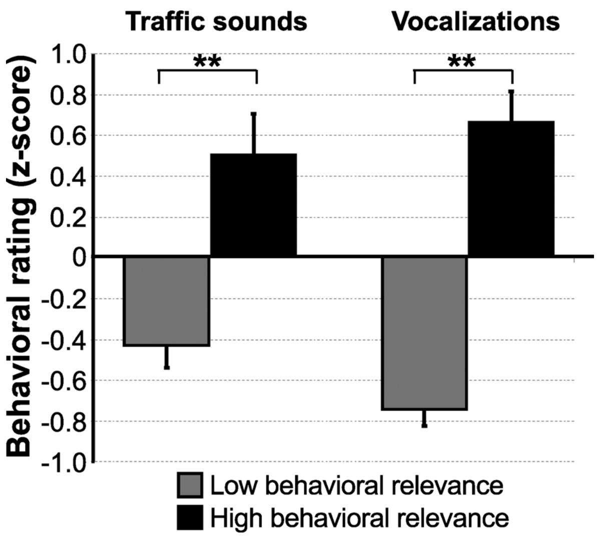

FIG. 2. Judgments of behavioral relevance. Plotted are the results of the stimulus validation experiment. Bars represent the average judgment of behavioral relevance across stimuli within a specific sound category and level of behavioral relevance. Gray bars represent judgments for the low behavioral relevance level, black bars for the high behavioral relevance level. Asterisks indicate a significant difference between the low and high relevance levels (see p values in text). Error bars reflect the SD.

D. Global sound localization performance

The average response per target location across all sounds (AM tones and complex sounds) is depicted in Fig. 4. Figure 5 shows a detailed overview of the localization errors for AM tones and complex sounds separately: the absolute error, signed error, and RMS error, which reflect localization acuity, bias, and precision, respectively. Errors tended to be elevated for AM tones in comparison to complex sounds, although the extent of the difference varied across localization bins and error measures (Fig. 5). Specifically, localization acuity and precision were significantly higher for complex sounds in right central space after correction for reversals (reflected by a lower absolute and RMS error for complex sounds, paired samples t-test, $p < 0.001$, $q[\mathrm{FDR}] < 0.05$). In line with this, the localization bias was smaller for complex sounds in the same location bin (that is, the signed error for reversal-corrected responses was smaller for complex sounds, $p < 0.001$, $q[\mathrm{FDR}] < 0.05$). Finally, for the original responses, localization acuity and precision were higher for complex sounds than for AM tones in the anterior periphery (lower absolute and RMS error, $p < 0.01$, $q[\mathrm{FDR}] < 0.05$).

Examining the AM tones in detail shows that for these sounds, localization acuity was higher in the anterior periphery than in left and right central space both before and after correction for reversals (reflected by a lower absolute error

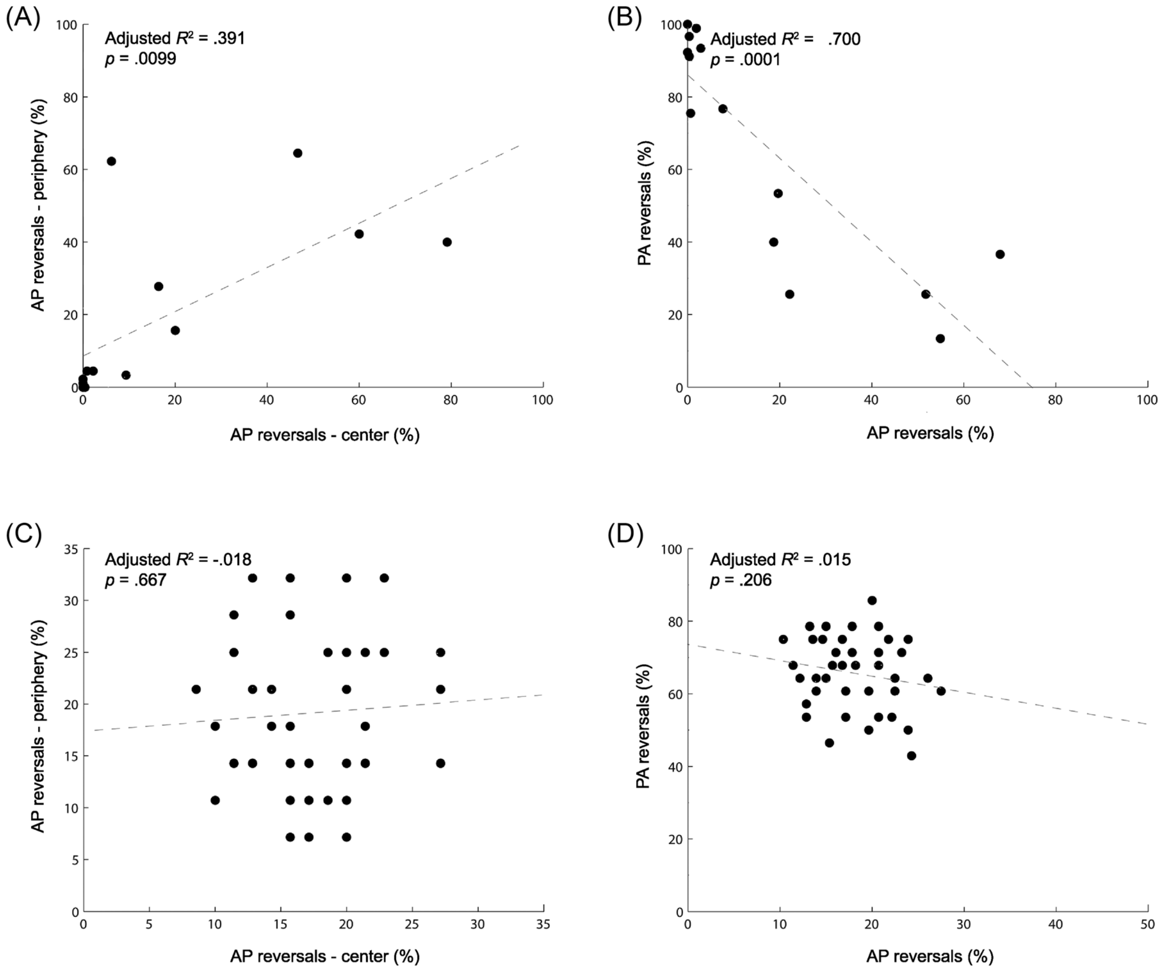

FIG. 3. Localization reversals per participant and per sound. (A) Each dot represents—for a single participant—the percentage of AP reversals in central auditory space plotted against the percentage of AP reversals in peripheral auditory space. The dashed, gray line represents the best fit of the linear model. (B) Percentages of AP reversals per participant (averaged across central and peripheral auditory space) against the percentage of PA reversals (measured only in the periphery). (C) and (D) are similar to (A) and (B), respectively, but computed per sound ($N = 45$).

in Fig. 5; $p < 0.01$ for original responses and $p < 0.001$ for reversal-corrected responses; q[FDR] < 0.05). Further, after correction for reversals, localization acuity was also significantly higher for the posterior periphery than for left and right central space ($p < 0.001$, q[FDR] < 0.05). For complex sounds, the pattern of localization acuity across location bins was slightly different. That is, acuity was higher in the anterior periphery than in left central space both before and after correction for reversals ($p < 0.01$ for both comparisons, q[FDR] < 0.05). Localization acuity was also higher in the posterior periphery than in left central space for reversal-corrected responses. However, there were no significant differences between right central space and the periphery.

The bias toward more peripheral positions ($-90°$ or $+90°$) for target locations in central space that is visible in the average response (Fig. 4) is also reflected in the signed error in Fig. 5. Here, a positive signed error indicates a bias toward posterior locations while a negative signed error indicates a bias toward anterior locations (note that the signed error in Fig. 5 reflects the anterior–posterior bias only and can therefore deviate from the difference between response and target location in Fig. 4; see Sec. II for more details). Signed errors were significantly larger than zero for AM tones and complex sounds in both left and

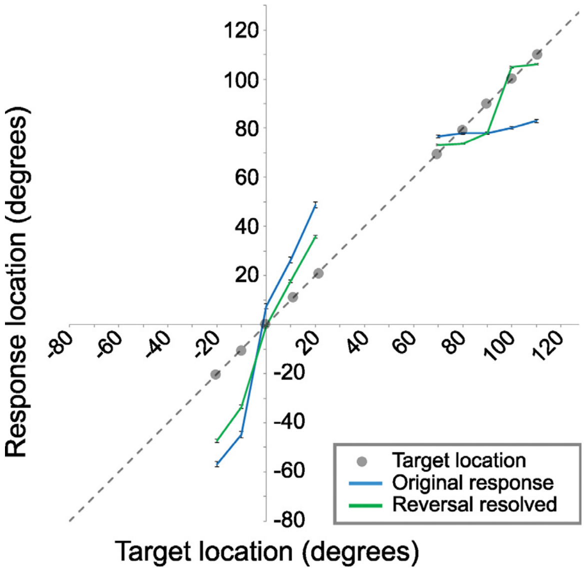

FIG. 4. (Color online) Average sound localization responses. Solid lines represent the localization response averaged across sounds and participants for the original data (blue line), and the reversal resolved data (green line). The dashed, gray line represents the azimuth on which the ten target locations are indicated with gray circles. Error bars reflect the standard error of the mean (SEM).

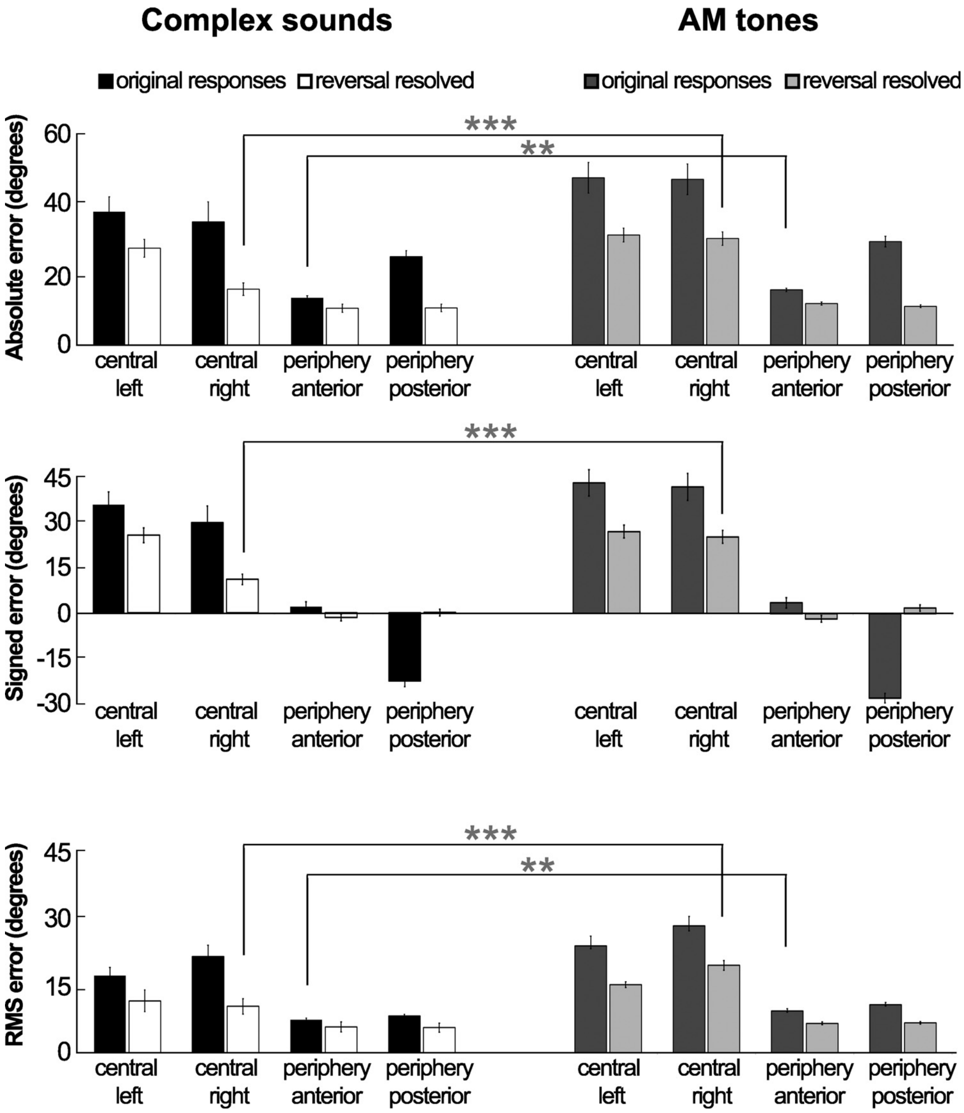

FIG. 5. Sound localization performance. Bars represent the average absolute error (top row), signed error (middle row), and RMS error (bottom row) for complex sounds (left column) and AM tones (right column). Dark colors indicate the original responses, brighter colors indicate the responses corrected for front-back reversals. Horizontal lines indicate a significant difference between complex sounds and AM tones (** $= p < 0.01$; *** $= p < 0.001$; FDR corrected for multiple comparisons). Error bars represent the SEM.

right central space, and for both original and reversal-corrected responses (one-sample *t*-tests, $p < 0.05$ for all comparisons, q[FDR] < 0.05). Figure 5 also confirms that the localization bias in the anterior periphery is minimal for complex sounds and AM tones (signed errors did not deviate from zero, $p > 0.05$), and that localization responses in the posterior periphery were biased toward more anterior positions ($p < 0.01$, q[FDR] < 0.05). Correcting for reversals removed the localization bias for this location bin ($p > 0.05$; see also Fig. 4).

Finally, localization precision was also higher in the anterior and posterior periphery than in left and right central space for complex sounds and AM tones, both before and after correction for reversals (indicated by a lower RMS error in the peripheral location bins, see Fig. 5; paired-samples *t*-tests, $p < 0.05$ for all comparisons, q[FDR] < 0.05).

E. Sound localization performance for individual sounds

1. Original localization responses

Figure 6 shows that localization acuity (absolute error), bias (signed error), and precision (RMS error) varied across sounds, and in particular for the original localization responses without correction for front-back reversals. Visual inspection of Fig. 6 also shows that variation was largest in central auditory space. The results of the multiple regression analysis confirm these observations. Specifically, the model combining several low level acoustic parameters with the higher order parameters behavioral relevance and sound category explained the observed pattern of localization acuity and bias for all location bins tested here well, and the pattern of localization precision in central auditory space (Tables I, II, and III). Examining the regression coefficients shows that there are several acoustic parameters that contributed significantly to the model fit. These include the degree of amplitude modulation, the center of spectral gravity, the presence of ITD cues, and sound duration.

In addition to these low level sound attributes, the higher order aspects behavioral relevance and sound category influenced spatial hearing performance as well (Tables I, II, and III). Specifically, behavioral relevance contributed to the model fit for localization acuity (absolute error) in right central space and in the anterior periphery: sounds with a high level of behavioral relevance have a higher localization acuity (reflected by a negative regression coefficient). In right central space, this effect was mainly driven by

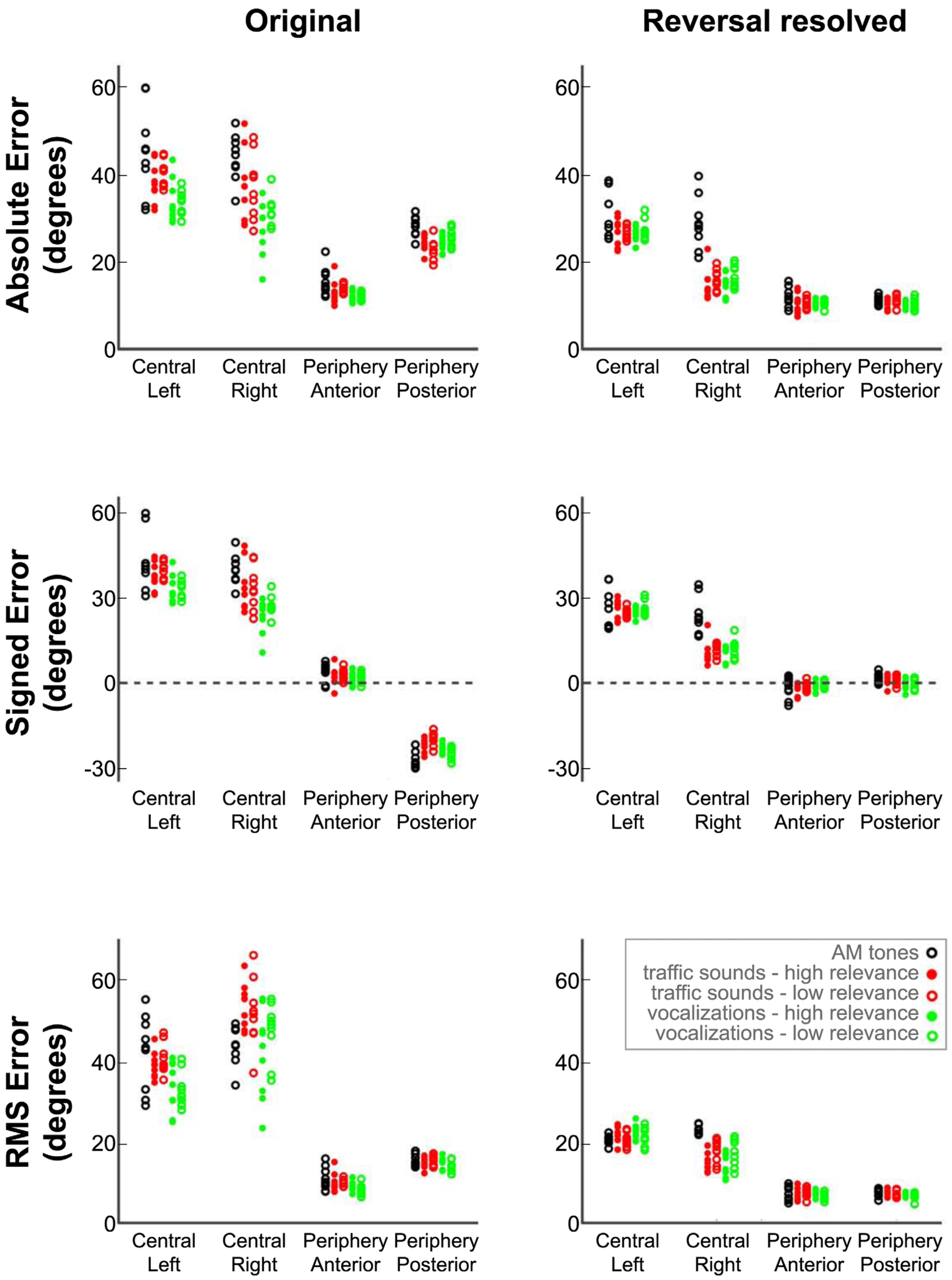

FIG. 6. (Color online) Localization errors per sound. Dots represent the average error per stimulus. Top row shows absolute error, middle row signed error, and bottom row RMS error. Errors for the original data are plotted in the left column, those of the reversal resolved data in the right column. Colors indicate sound category: black circles are AM tones, red circles traffic sounds, and green circles vocalizations. For the latter two categories, filled circles represent high relevance stimuli and open circles low relevance stimuli.

vocalizations: vocalizations with a high level of behavioral relevance (Fig. 6; closed, green circles) tended to have a smaller absolute error than those with a low level of behavioral relevance (Fig. 6; open, green circles). However, in the anterior periphery, the difference between low and high levels of behavioral relevance for traffic sounds followed a similar pattern (Fig. 6; open, red circles versus closed, red circles, respectively).

Further, sound category contributed to the regression model fits for localization bias at nearly all location bins.

TABLE I. Results of the multiple linear regression analysis of the absolute error for the original localization responses. P values in bold indicate a significant model fit. P values are FDR corrected for multiple comparisons at $q < 0.05$, except for the model fit in the posterior periphery (indicated by the symbol ^{x}) where $q = 0.06$. Values reflect standardized regression coefficients with the 95% confidence interval underneath. Note that the intercept is not shown because all variables (including the dependent variable) were z scored. β values in bold are significant ($p < 0.05$). † indicates a regression coefficient with a p value close to significance ($p < 0.07$).

	Central Space Left	Central Space Right	Periphery Anterior	Periphery Posterior
F	5.43	4.01	2.81	2.41
P	**5.7×10^{-4}**	**3.9×10^{-3}**	**0.025**	**0.046**^{x}
Adjusted R2	0.477	0.383	0.278	0.220
Behavioral relevance	−1.05	**−2.56**	**−0.54**	0.28
	[−2.50 0.39]	*[−4.91 −0.22]*	*[−1.00 −0.10]*	*[−0.54 1.11]*
Amplitude modulation	−0.19	2.41	**1.06**	**−1.95**
	[−3.13 2.74]	*[−2.10 6.93]*	*[0.20 1.91]*	*[−3.50 −0.40]*
Bandwidth	1.10	−2.85	−0.83	−1.71
	[−3.08 5.29]	*[−9.60 3.90]*	*[−2.12 0.47]*	*[−4.00 0.59]*
Duration	−0.45	**3.03**	0.48†	−0.50
	[−2.01 1.10]	*[0.54 5.52]*	*[−0.02 0.98]*	*[−1.40 0.39]*
Spectral Gravity	−0.58	2.04†	0.11	**1.00**
	[−1.95 0.79]	*[−0.16 4.24]*	*[−0.35 0.56]*	*[0.21 1.78]*
ITD	**−2.68**	0.09	0.65	0.38
	[−4.96 −0.40]	*[−3.35 3.53]*	*[−0.30 1.60]*	*[−0.85 1.61]*
Sound category	**3.07**	1.70	0.36	−0.03
	[1.33 4.80]	*[−1.29 4.68]*	*[−0.19 0.91]*	*[−1.03 0.97]*

Specifically, in left and right central auditory space, the localization bias was larger for traffic sounds, indicating that traffic sounds are localized more toward the periphery (−90° or +90°) in comparison to vocalizations. In contrast, in the posterior periphery, the localization bias was larger for vocalizations, indicating that vocalizations were biased more toward anterior positions than traffic sounds (note that this is reflected by the positive regression coefficient in Table II, as the sign of the signed error is negative in the posterior periphery). Sound category also contributed significantly to the model fit of localization acuity and precision (RMS error) in left central space. Here the direction of the effect was similar to that for localization bias in central space: vocalizations were localized more accurately and with more precision than traffic sounds.

2. Reversal-resolved localization responses

Resolving front-back reversals reduced the variability in localization acuity, bias, and precision, especially in central auditory space (Fig. 5). The remaining pattern of differences in sound localization bias and precision across sounds was

TABLE II. Results of the multiple linear regression analysis of the signed error for the original localization responses. For a full description of the values in the table, see legend of Table I. Note that no model was estimated for the anterior periphery as signed errors were close to zero for this location bin. N/A = not applicable.

	Central Space Left	Central Space Right	Periphery Anterior	Periphery Posterior
F	5.10	4.52	N/A	6.26
P	**8.73×10^{-4}**	**1.8×10^{-3}**	N/A	**2.0×10^{-4}**
Adjusted R2	0.458	0.413	N/A	0.52
Behavioral relevance	−1.04	−1.87	N/A	−0.18
	[−2.54 0.45]	*[−4.39 0.65]*		*[−1.00 0.64]*
Amplitude modulation	−0.47	−0.85	N/A	**1.83**
	[−3.51 2.56]	*[−5.55 3.86]*		*[0.34 3.33]*
Bandwidth	0.88	**−7.60**	N/A	1.26
	[−3.44 5.20]	*[−14.6 −0.62]*		*[−0.96 3.48]*
Duration	−0.42	1.98	N/A	0.35
	[−2.03 1.19]	*[−0.73 4.70]*		*[−0.51 1.22]*
Spectral Gravity	−0.50	**2.80**	N/A	**−1.12**
	[−1.92 0.91]	*[0.41 5.19]*		*[−1.88 −0.36]*
ITD	**−2.62**	0.28	N/A	−0.47
	[−4.97 −0.26]	*[−3.46 4.01]*		*[−1.66 0.72]*
Sound category	**3.16**	**4.44**	N/A	**1.33**
	[1.37 4.96]	*[1.39 7.48]*		*[0.36 2.30]*

TABLE III. Results of the multiple linear regression analysis of the RMS error for the original localization responses. For a full description of the values in the table, see legend of Table I.

	Central Space Left	Central Space Right	Periphery Anterior	Periphery Posterior
F	3.14	2.83	1.25	1.51
P	**0.014**	**0.023**	0.31	0.21
Adjusted R2	0.30	0.268	0.05	0.09
Behavioral relevance	−0.66	−1.32	0.13	−0.03
	[−2.62 1.31]	*[−4.67 2.04]*	*[−0.41 0.66]*	*[−0.60 0.55]*
Amplitude modulation	0.12	2.95	0.30	0.00
	[−3.54 3.78]	*[−3.32 9.21]*	*[−0.70 1.29]*	*[−1.07 1.06]*
Bandwidth	−0.03	−2.63	−0.26	−0.83
	[−5.46 5.41]	*[−11.93 6.66]*	*[−1.80 1.28]*	*[−2.41 0.75]*
Duration	−0.45	**4.93**	0.27	−0.04
	[−2.56 1.67]	*[1.31 8.55]*	*[−0.31 0.85]*	*[−0.66 0.57]*
Spectral Gravity	−0.92	1.32	−0.17	0.49
	[−2.78 0.94]	*[−1.87 4.50]*	*[0.71 0.37]*	*[−0.05 1.03]*
ITD	−2.10	1.64	0.59	0.89
	[−5.01 0.81]	*[−3.34 6.62]*	*[−0.25 1.43]*	*[0.04 1.73]*
Sound category	**3.59**	1.79	0.40	0.65
	[1.22 5.96]	*[−2.26 5.85]*	*[−0.25 1.06]*	*[−0.04 1.34]*

explained by the model in right central auditory space only (Table IV), but not in the auditory periphery (Appendix B) or in left central space. Of the low level sound characteristics, only bandwidth contributed to the model fit in right central space. Specifically, sounds with a broader bandwidth were localized with more precision and less bias (negative regression coefficient). Of the higher level sound characteristics, behavioral relevance and sound category both contributed to the model fit for localization bias and precision (note that the pattern of coefficients is the same for localization acuity, but here the overall model fit did not reach statistical significance $p = 0.12$). For behavioral relevance, vocalizations and traffic sounds with a high level of behavioral relevance had smaller signed and RMS error values compared to their counterparts with a low level of behavioral relevance (see difference between open and filled circles for each sound category in Fig. 6). For sound category, the direction of the effect was similar to that for the original responses: the localization bias was smaller for vocalizations, and localization precision was higher for vocalizations as well.

TABLE IV. Results of the multiple linear regression models estimated on the absolute, signed, and RMS error computed from the reversal resolved localization responses for complex sounds in right central space. For a full description of the values in the table, see legend of Table I.

	Absolute Error	Signed Error	RMS Error
F	1.83	4.84	3.55
P	0.12	$\mathbf{1.4 \times 10^{-3}}$	$\mathbf{7.8 \times 10^{-3}}$
Adjusted R2	0.143	0.449	0.344
Behavioral relevance	−1.63	**−2.21**	**−2.66**
	[−2.74 −0.52]	*[−3.18 −1.24]*	*[−3.85 −1.48]*
Amplitude modulation	0.40	0.63	1.39
	[−1.67 2.48]	*[−1.17 2.42]*	*[−0.82 3.60]*
Bandwidth	−3.42	**−5.22**	**−4.95**
	[−6.50 −0.34]	*[−7.84 −2.60]*	*[−8.01 −1.88]*
Duration	0.13	−0.79	−0.06
	[−1.07 1.33]	*[−1.71 0.13]*	*[−1.19 1.08]*
Spectral Gravity	0.84	0.51	0.55
	[−0.22 1.89]	*[−0.36 1.37]*	*[−0.45 1.55]*
ITD	0.05	1.16	0.84
	[−1.60 1.70]	*[−0.22 2.54]*	*[−0.79 2.46]*
Sound category	0.46	**1.74**	**1.48**
	[−0.88 1.81]	*[0.64 2.85]*	*[0.15 2.81]*

IV. DISCUSSION

The present study assessed the effect of behavioral relevance, sound category, and acoustic properties on the localization performance for complex sounds of different sound categories. Participants performed a sound localization task while listening to AM tones, vocalizations, and traffic sounds of two levels of behavioral relevance (low and high). Multiple regression analysis of localization acuity (measured as absolute error), bias (signed error), and precision (RMS error) for the complex sounds showed that the differences in performance across individual sounds were explained well by a model consisting of regressors for behavioral relevance, sound category, and five acoustic parameters. There was a small but significant contribution of the higher order factor behavioral relevance to the overall model fits, indicating that localization acuity was higher for sounds with a high level of behavioral relevance (in right central space and in the anterior periphery). In addition, the contribution of sound category to the model fits signaled that localization acuity was higher for vocalizations than traffic sounds (in left central space). Sound category further modulated localization bias (in left and right central space, and in the posterior periphery), and localization precision (in left central space only). Specifically, localization biases were smaller for vocalizations in left and right central space, and localization precision was higher for this sound category. In addition to these higher order parameters, several acoustic properties of the sounds contributed to localization acuity, bias, and precision.

The observed effects were partly driven by the occurrence of front-back reversals. Specifically, a correction for reversals reduced the variability in performance across sounds, lessening differences between high and low relevant sounds, and between traffic sounds and vocalizations. However, in right central space the modulatory effect of behavioral relevance level and sound category was present even after correction for reversals, although it affected different aspects of sound localization (localization bias and precision rather than localization acuity). In conclusion, our data show that in addition to low level acoustic characteristics, higher order factors such as behavioral relevance and sound category can influence sound localization performance as well.

A. Behavioral relevance modulates localization performance

The present data showed—for the original localization responses—an effect of behavioral relevance on sound localization acuity (absolute error) in right central auditory space and in the anterior periphery. In left central space, the regression coefficient for behavioral relevance did not reach statistical significance because the localization of high relevance vocalizations was relatively poor compared to the acuity for this group of sounds in right central space (Fig. 6). As lateralization differences between left and right are not commonly observed in sound localization, it is probable that the diminished acuity for high relevance vocalizations in left central space resulted from the imbalance in target locations in the current experimental design. That is, out of consideration of participant fatigue we only included target locations in central space in the left hemifield (−10° and −20°), while the right hemifield contained targets in both central and peripheral space (+10°, +20°, +70°, +80°, +90°, +100°, +110°; see Sec. II). This imbalance may have resulted in participants overshooting target locations in left central space toward the periphery, which is also reflected in the increased localization bias in this location bin. It is therefore conceivable that in a balanced experimental design, a difference in localization acuity between sounds with a low and high level of behavioral relevance would be observed in left central space as well.

Behavioral relevance did not contribute significantly to the model fit for localization bias (signed error). This indicates that only the magnitude of errors was smaller for high relevance sounds (reflected by the absolute error discussed before), while the direction of errors varied equally between high and low relevance sounds. Localization precision (measured as RMS error) was not modulated by behavioral relevance either, showing that the variability across localization responses was similar for low and high relevance. Together, these results suggest that—for the original localization responses—the level of behavioral relevance of a complex sound mainly affects the magnitude of localization errors (that is, localization acuity).

Correcting for reversals reduced the difference in localization acuity, bias, and precision across sounds. The multiple regression model employed here did not fit the remaining differences in localization acuity (absolute error) at any location bin, although the regression coefficient for behavioral relevance had a similar sign in right central space as for the original localization responses. However, the regression model did explain well the pattern of localization bias (signed error) and precision (RMS error) for reversal-corrected responses in right central space (see Table IV). Moreover, for these measures of localization performance, behavioral relevance did contribute to the overall model fit. This indicates that behavioral relevance may modulate the direction of localization errors (localization bias) and the variability in responses (localization precision) as well, and that the model was not able to detect this in the original localization responses due to a diluting effect of the front-back reversals.

The modulatory effect of behavioral relevance on sound location processing observed in the present study is consistent with recent studies showing that the neural representation of a stimulus in primary sensory cortices—including A1—is modulated by the behavioral relevance of that stimulus (e.g., Fritz *et al.*, 2003; Kato *et al.*, 2015). Kato *et al.* (2015) argue that such a change in neural representation can modulate the saliency of processing of the stimulus in subsequent higher-level areas, which may in turn influence the behavioral response. Further research is needed to assess whether a similar mechanism is at work here. It would be interesting to know if different areas of higher auditory cortex contribute differentially according to their functional specialization (e.g., Tian *et al.*, 2001). Posterior areas of auditory cortex, for instance, are more selective for spatial cues than anterior areas (Lomber and Malhotra, 2008; Rauschecker, 2007; Rauschecker and Tian, 2000).

B. Category-specificity: Localization bias for traffic sounds toward the lateral pole

For the original localization responses, sound category contributed to the model fit for the pattern of localization bias (signed error) at all location bins where a localization bias was observed (that is, in left and right central space, and in the posterior periphery; see also Fig. 5). The modulatory effect of category was such that traffic sounds were localized consistently more towards the lateral pole (−90° or +90°) than vocalizations, both in central space (reflected by a positive signed error) and in the posterior periphery (reflected by a negative signed error). Interestingly, localization acuity—the magnitude of errors—and precision were not modulated by sound category (except for in left central space, see Tables I and III), indicating that the category-specific effect mainly applied to the direction of the localization errors. Following the correction for front-back reversals, sound category maintained a significant contribution to the model fit for localization bias in right central space, and even to localization precision in this location bin (see Table IV). The data thus indicate that the direction of localization errors (that is, localization bias), and also the variability of localization responses (that is, localization precision) can be modulated by sound category.

A possible explanation for the difference in localization bias between traffic sounds and vocalizations is based on prior experience and expectations. Specifically, humans commonly turn their head to face the person they are conversing with, while traffic sounds can originate from any direction. Consequently, participants may have been less inclined to attribute vocalizations to positions close to the lateral pole (−90° or +90°) than traffic sounds. Along similar lines, it could also be argued that the superior localization of vocalizations reflects the special status of voices in human auditory processing. That is, the "cocktail party problem" demonstrates that humans have an extraordinary ability to attend to and localize voices (Cherry, 1953). Future psychoacoustic research testing sound localization performance for a wider variety of sound categories is needed to investigate whether the higher performance that we observed here for vocalizations is specific only to this category.

C. Sound localization performance and acoustic parameters

Several acoustic parameters modulated sound localization performance as well, although the contribution of specific parameters varied across response measures (localization acuity, bias, and precision), as well as location bins. The regressor reflecting the presence of ITD cues contributed to the model fits for localization acuity and bias in left central space for the original responses. This shows that the magnitude of errors was smaller for binaural recordings with ITD cues than for those without ITD cues. In addition, the overshoot to lateral positions was less for sounds with ITD information. Other acoustic parameters of influence included the degree of amplitude modulation, sound duration, and the center of spectral gravity, although the contributions varied across performance measure and location (Tables I–III). For the responses that were corrected for front-back reversals, spectral bandwidth appeared to be the most influential acoustic parameter such that sounds with a broad spectral bandwidth were localized with less bias and with higher precision (Table IV). This is also reflected in the localization performance for the narrowband AM tones, which tended to be poorer than for the complex sounds. This effect of bandwidth on sound localization is in line with previous reports (e.g., Butler, 1986).

The irregularities in the contribution of the acoustic parameters depending on performance measure and location bin may partly be a consequence of the type of stimuli used. Specifically, it was not the aim of the present study to provide an exhaustive test of the modulatory effects of low level acoustic characteristics on sound localization. Instead, we selected complex sounds based on category and behavioral relevance, while including regressors reflecting the acoustic characteristics of these sounds in the multiple linear regression analysis to ensure that the observed effects for the higher order parameters were not secondary to the spectral and temporal sound properties. Thus, future psychoacoustic research is needed to study in depth the effect of these and other acoustic aspects on spatial audition.

D. Reversals

Participants regularly perceived sounds originating from a position anterior to the interaural axis as originating from the posterior quadrants, or vice versa. This phenomenon has been described as the cone of confusion: sounds at an equal azimuthal angle relative to the interaural axis have nearly identical interaural time as well as level differences (Wallach, 1939), making it very difficult to disambiguate front from back on the basis of these binaural cues alone. Prior studies on sound localization reported widely varying results for the occurrence of front-back reversals. For instance, participants in the study of Oldfield and Parker (1984) made few to no reversals in central auditory space and only about 10% in the auditory periphery, while Makous and Middlebrooks (1990) report up to 45% reversals in the periphery. Many recent free-field studies have tested only sound locations in the anterior quadrants and have not reported reversals at all (e.g., Tabry *et al.*, 2013; Van Wanrooij and Van Opstal, 2007; Voss *et al.*, 2015).

The variation in stimuli across studies—that is, clicks, tones, noise bursts of different frequency ranges—is likely to have an impact on the incidence of reversals as well. For example, spectral cues, introduced by the head, pinnae, and torso, arise only for sounds containing frequencies >4 kHz. Given that these monaural cues contribute to the disambiguation of front from back, low-frequency sounds are expected to lead to more reversals. Additionally, several studies demonstrate that narrow band sounds are more difficult to localize for humans and cats than broadband sounds (Butler, 1986; Musicant and Butler, 1985; Tollin *et al.*, 2013) and lead to more frequent front-back reversals (Blauert, 1969; Butler, 1986).

In the present study, the occurrence of reversals as well as the direction of these reversals (PA versus AP) varied across participants. Some participants had relatively high reversal rates, while others had very low reversal rates. Note that the low reversal rates of a group of participants show that the occurrence of reversals was not directly a result of the quality of binaural recordings, but rather of inter-individual differences in sound localization capabilities. Interestingly, participants made reversal errors predominantly in one direction. This suggests that in ambiguous sound localization circumstances, participants had a bias in a specific direction and allocated ambiguous sound sources consistently to either the front or the back. This bias may have been a result of *a priori* expectations about the target sounds. Consequently, it is conceivable that reversal rates would be lower if participants were informed about the range of possible target locations before the experiment.

E. Asymmetry between spatial acuity in central and peripheral auditory space

The magnitude of errors in central auditory space in this study—especially in the left hemifield—is higher than commonly reported (e.g., Makous and Middlebrooks, 1990; Oldfield and Parker, 1984; Voss *et al.*, 2015). As discussed before, the difference in localization performance between left central space and right central space is likely a result of the imbalance in the target locations employed here. Yet, localization errors were also relatively high in right central auditory space. A possible reason for this may be that participants were blindfolded. Specifically, a recent study by Tabry *et al*. (2013) demonstrates that overall sound localization acuity in the horizontal plane deteriorates when participants are blindfolded and thus deprived of visual feedback. It is conceivable, given that sighted people have most of their auditory-visual interactions in central space, that the negative effect of blindfolding on localization performance is stronger in this region. Although participants were also blindfolded in some other studies which report smaller errors in central auditory space, it should be noted that in those studies participants either received extensive training with visual feedback prior to the testing session (Makous and Middlebrooks, 1990), or listened to long-duration stimuli (Oldfield and Parker, 1984).

Alternatively, the relatively poor results in central auditory space could have been a result of the binaural reproduction technique used here. However, if this were the case, the degradation of sound localization should be equal across location bins. Given that the data show an asymmetry in performance between central and peripheral space, it is not probable that the reduced performance in central auditory space is a consequence of the binaural reproduction technique. More research is needed to investigate in detail the effects of blindfolding, training, and binaural reproduction techniques on spatial hearing, as well as the temporal pattern of these effects.

F. Conclusions

The present study shows that the behavioral relevance of complex, meaningful sounds influences spatial hearing performance. Localization performance was also modulated by sound category, and by several acoustic parameters, including the center of spectral gravity, spectral bandwidth, availability of ITDs, and sound duration. These results provide new insights into the mechanisms underlying the localization of complex, natural sounds. Future research combining psychoacoustics with electrophysiological and neuroimaging methods is needed to further explore the interactions between higher-level mechanisms and lower-level acoustic properties that affect sound localization in humans and other higher mammals, as well as the neural mechanisms involved.

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APPENDIX A: STIMULUS CHARACTERISTICS

See Table V and Figs. 7–9.

TABLE V. Stimulus characteristics. For ITD and ILD: 1 = present, 0 = not present. N/A = not applicable.

Stimulus	Relevance	Category	Duration (ms)	Spectral gravity (log)	Amplitude-modulation (dB)	Bandwidth (octaves)	ITD	ILD
1	N/A	1	960	3.439	13.2	0.14	0	1
2	N/A	1	960	3.398	13	0.12	0	1
3	N/A	1	960	3.352	13.2	0.24	0	1
4	N/A	1	960	3.217	13.1	0.28	0	1
5	N/A	1	960	3.176	13	0.29	0	1
6	N/A	1	960	3.130	12.8	0.30	0	1
7	N/A	1	960	2.740	13.1	1.22	1	1
8	N/A	1	960	2.699	12.9	0.77	1	1
9	N/A	1	960	2.653	12.7	0.79	1	1
10	1	2	1000	3.674	6.9	8.26	1	1
11	1	2	1000	3.060	7.9	8.27	1	1
12	1	2	960	3.186	9.3	6.52	0	1
13	1	2	1000	3.136	2.7	6.25	1	1
14	1	2	1000	2.963	4.7	7.14	1	1
15	1	2	880	3.852	9.5	5.21	0	1
16	1	2	1000	2.597	2.6	6.22	1	1
17	1	2	1000	3.042	1.6	5.46	1	1
18	1	2	1000	3.021	3.7	6.39	1	1
19	0	2	320	3.069	8.2	8.20	1	1
20	0	2	570	3.017	9.9	6.34	1	1
21	0	2	1000	2.316	1.9	5.93	1	1
22	0	2	1000	3.192	2.7	7.87	1	1
23	0	2	1000	3.625	1.1	8.26	1	1
24	0	2	1000	2.700	1.1	7.68	1	1
25	0	2	990	2.654	3.5	8.04	1	1
26	0	2	1000	3.560	4.9	8.29	1	1
27	0	2	990	3.390	3.5	7.66	1	1
28	1	3	290	2.996	6.2	5.85	1	1
29	1	3	410	3.299	7.5	4.85	0	1
30	1	3	690	2.875	6.6	5.71	1	1
31	1	3	400	3.152	10.5	4.52	1	1
32	1	3	570	2.867	3	6.61	1	1
33	1	3	740	3.144	5.3	5.72	1	1
34	1	3	590	3.154	6.7	4.54	1	1
35	1	3	340	2.925	5.5	6.79	1	1
36	1	3	720	3.051	4.2	5.21	1	1
37	0	3	990	2.855	1.2	5.67	1	1
38	0	3	990	3.067	0.8	6.69	1	1
39	0	3	510	3.038	1.7	6.97	1	1
40	0	3	1000	2.898	1.8	5.65	1	1
41	0	3	650	2.769	2.8	6.52	1	1
42	0	3	210	3.106	3.8	5.06	1	1
43	0	3	980	2.972	4.9	7.00	1	1
44	0	3	1000	2.866	1.1	6.20	1	1
45	0	3	890	2.954	1.6	5.98	1	1

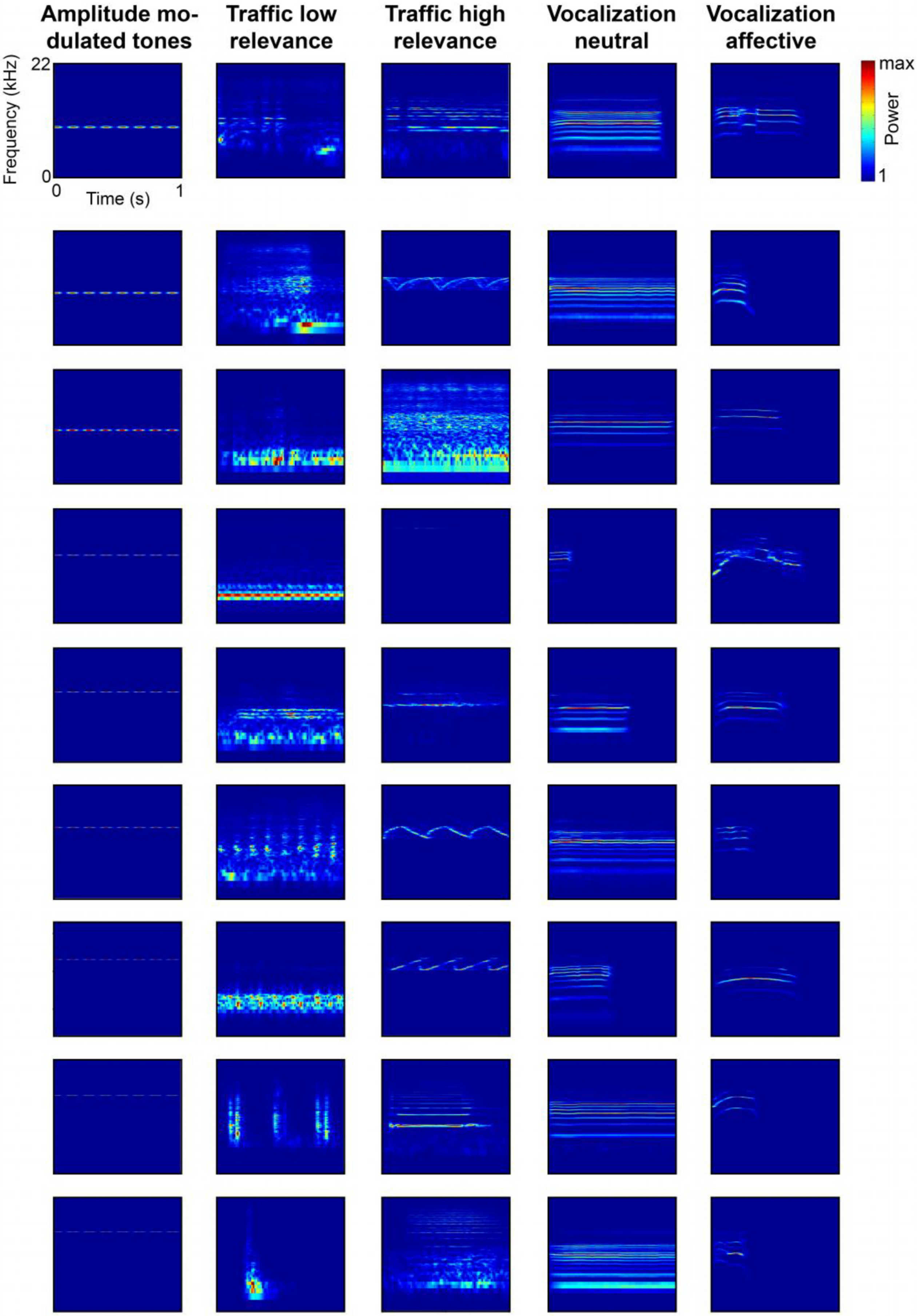

FIG. 7. Spectrograms of individual stimuli. Spectrograms show the frequency-time representation of each stimulus. Colors indicate power.

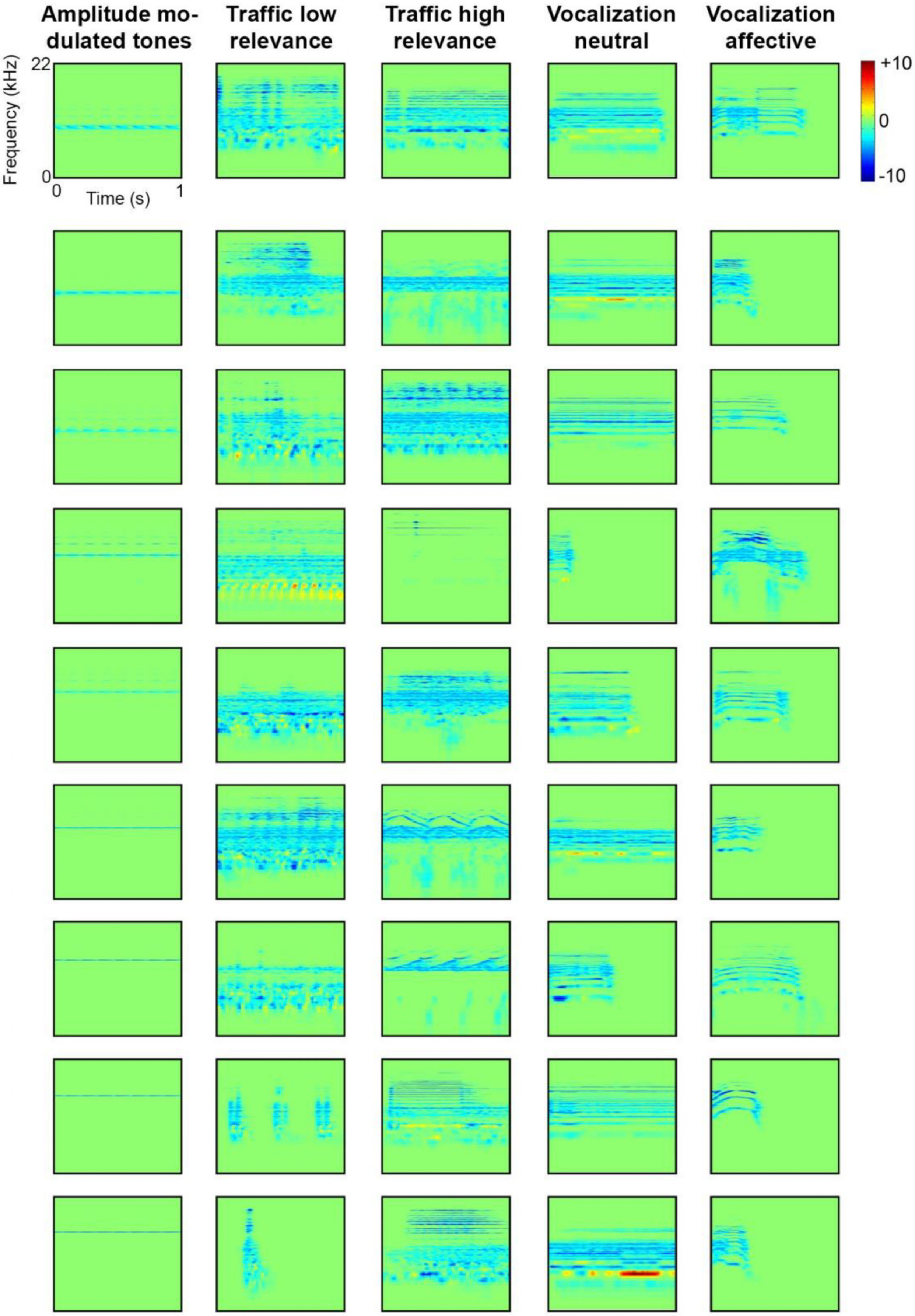

FIG. 8. ILDs in binaural recordings. Colors indicate the difference in intensity in dB between the left and right channel of binaural recordings of each stimulus presented at +90° (right channel subtracted from left channel). Plotted are the intensity differences averaged across the recordings of all participants.

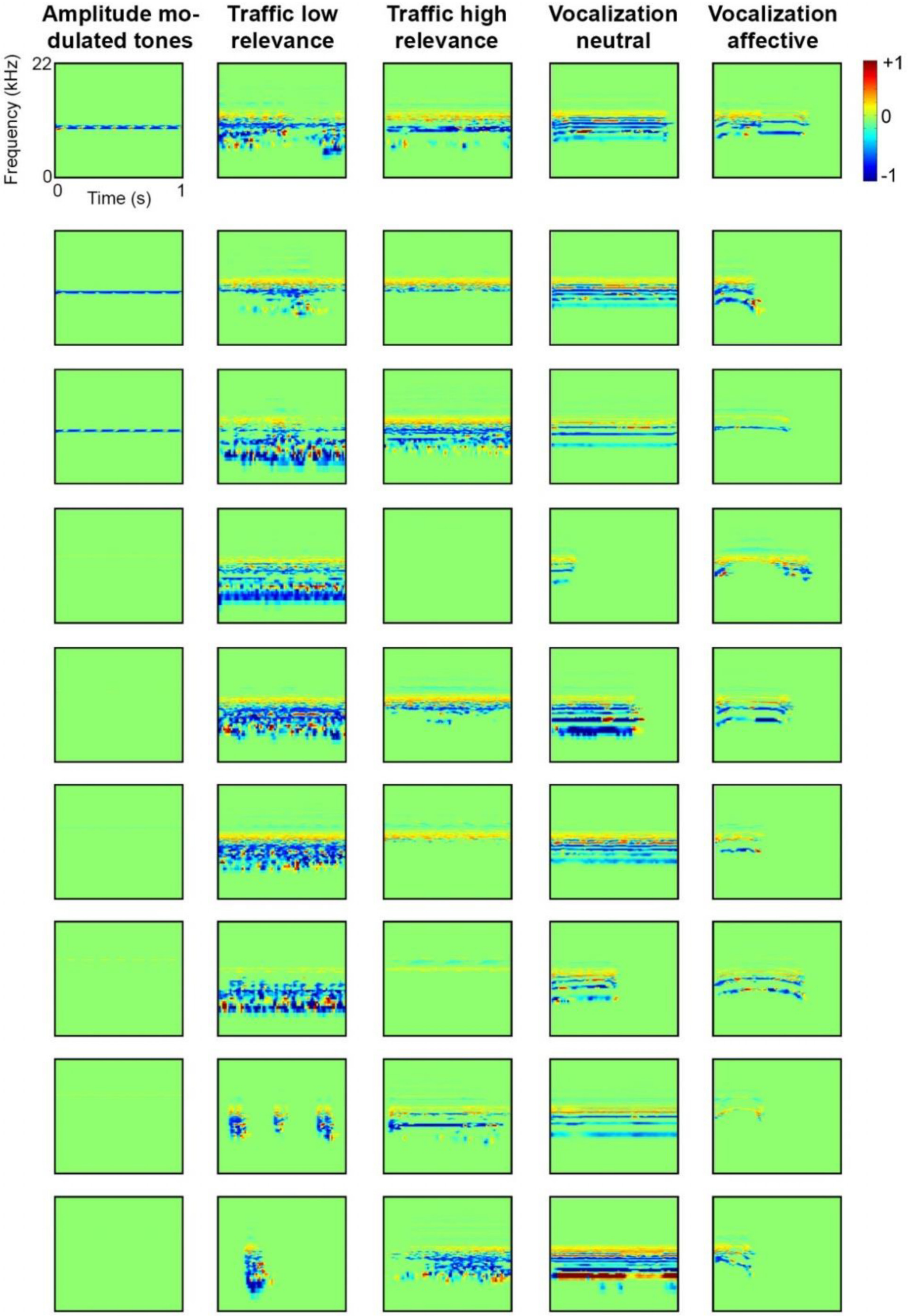

FIG. 9. ITDs in binaural recordings. Colors indicate the time differences in milliseconds between the left and right channel of binaural recordings of each stimulus presented at +90° (right channel subtracted from left channel). Plotted are the time differences averaged across the recordings of all participants.

TABLE VI. Results of the multiple linear regression models estimated on the absolute error computed for the reversal-resolved localization responses for complex sounds. *P* values in bold indicate a significant model fit (FDR corrected for multiple comparisons). Values reflect standardized regression coefficients with the 95% confidence interval underneath. Note that the intercept is not shown because all variables (including the dependent variable) were *z* scored. β values in bold are significant ($p < 0.05$).

	Central Space Left	Central Space Right	Periphery Anterior	Periphery Posterior
F	0.19	1.83	1.13	1.36
P	0.99	0.12	0.376	0.26
Adjusted R2	−0.193	0.143	0.025	0.07
Behavioral relevance	−0.15	−1.63	−0.51	−0.27
	[−1.17 0.88]	*[−2.74 −0.52]*	*[−1.02 −0.01]*	*[−0.71 0.18]*
Amplitude modulation	0.29	0.40	0.10	−0.16
	[−1.63 2.20]	*[−1.67 2.48]*	*[−0.83 1.02]*	*[−0.99 0.67]*
Bandwidth	0.24	−3.42	−1.64	−0.47
	[−2.60 3.08]	*[−6.50 −0.34]*	*[−3.01 −0.26]*	*[−1.70 0.76]*
Duration	0.03	0.13	−0.01	−0.31
	[−1.07 1.14]	*[−1.07 1.33]*	*[−0.55 0.52]*	*[−0.79 0.17]*
Spectral gravity	0.35	0.84	0.21	0.31
	[−0.62 1.32]	*[−0.22 1.89]*	*[−0.26 0.69]*	*[−0.11 0.73]*
ITD	−0.13	0.05	0.15	0.43
	[−1.65 1.40]	*[−1.60 1.70]*	*[−0.59 0.88]*	*[−0.23 1.09]*
Sound category	−0.19	0.46	0.35	0.55
	[−1.43 1.05]	*[−0.88 1.81]*	*[−0.25 0.95]*	*[0.01 1.08]*

APPENDIX B: MULTIPLE REGRESSION ANALYSIS FOR REVERSAL RESOLVED DATA

See Tables VI, VII, and VIII.

TABLE VII. Results of the multiple linear regression models estimated on the signed error computed for the reversal-resolved localization responses for complex sounds. *P* values in bold indicate a significant model fit (FDR corrected for multiple comparisons). Values reflect standardized regression coefficients with the 95% confidence interval underneath. Note that the intercept is not shown because all variables (including the dependent variable) were *z* scored. β values in bold are significant ($p < 0.05$). No regression analysis was performed in peripheral space for this response measure, as signed errors were close to zero at the locations (N/A = not applicable).

	Central Space Left	Central Space Right	Periphery Anterior	Periphery Posterior
F	0.20	4.84	N/A.	N/A
P	0.98	**1.4×10^{-3}**	N/A	N/A
Adjusted R2	−0.192	0.449	N/A	N/A
Behavioral relevance	−0.13	**−2.21**	N/A	N/A
	[−1.25 0.98]	*[−3.18 −1.24]*		
Amplitude modulation	0.07	0.63	N/A	N/A
	[−2.01 2.14]	*[−1.17 2.42]*		
Bandwidth	0.02	**−5.22**	N/A	N/A
	[−3.07 3.10]	*[−7.84 −2.60]*		
Duration	0.09	−0.79	N/A	N/A
	[−1.11 1.29]	*[−1.71 0.13]*		
Spectral gravity	0.51	0.51	N/A	N/A
	[−0.54 1.57]	*[−0.36 1.37]*		
ITD	−0.01	1.16	N/A	N/A
	[−1.67 1.64]	*[−0.22 2.54]*		
Sound category	−0.16	**1.74**	N/A	N/A
	[−1.50 1.19]	*[0.64 2.85]*		

TABLE VIII. Results of the multiple linear regression models estimated on the RMS error computed for the reversal-resolved localization responses for complex sounds. *P* values in bold indicate a significant model fit (FDR corrected for multiple comparisons). Values reflect standardized regression coefficients with the 95% confidence interval underneath. Note that the intercept is not shown because all variables (including the dependent variable) were *z* scored. β values in bold are significant ($p < 0.05$).

	Central Space Left	Central Space Right	Periphery Anterior	Periphery Posterior
F	0.79	3.55	0.88	1.21
P	0.599	**7.8×10^{-3}**	0.532	0.331
Adjusted R2	−0.04	0.344	−0.02	0.04
Behavioral relevance	0.79	**−2.66**	−0.10	0.12
	[−0.07 1.65]	*[−3.85 −1.48]*	*[−0.58 0.38]*	*[−0.16 0.40]*
Amplitude modulation	−0.74	1.39	−0.15	−0.44
	[−2.35 0.88]	*[−0.82 3.60]*	*[−1.05 0.75]*	*[−0.95 0.07]*
Bandwidth	0.96	**−4.95**	−1.30	−0.25
	[−1.43 3.35]	*[−8.01 −1.88]*	*[−2.64 0.03]*	*[−1.01 0.52]*
Duration	−0.39	−0.06	0.11	−0.09
	[−1.32 0.54]	*[−1.19 1.08]*	*[−0.41 0.63]*	*[−0.39 0.22]*
Spectral Gravity	0.20	0.55	0.29	0.01
	[−0.62 1.02]	*[−0.45 1.55]*	*[−0.16 0.75]*	*[−0.25 0.28]*
ITD	0.09	0.84	0.10	−0.06
	[−1.19 1.37]	*[−0.79 2.46]*	*[−0.62 0.81]*	*[−0.47 0.34]*
Sound category	−0.36	**1.48**	0.35	0.35
	[−1.40 0.68]	*[0.15 2.81]*	*[−0.24 0.93]*	*[0.02 0.69]*

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