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Supplementary motor area activations predict individual differences in temporal-change sensitivity and its illusory distortions

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ABSTRACT

Perception of time and temporal change is critical for human cognition. Yet, perception of temporal change is susceptible to contextual influences such as changes of a sound's pitch. Using functional magnetic resonance imaging (fMRI), the current study aimed to investigate perception of temporal rate change and pitch-induced illusory distortions. In a 6 × 6 design, human participants ($N = 19$) listened to frequency-modulated sounds (~4 Hz) that varied over time in both modulation rate and pitch. Participants judged the direction of rate change ('speeding up' vs. 'slowing down'), while ignoring changes in pitch. Behaviorally, rate judgments were strongly biased by pitch changes: Participants perceived rate to slow down when pitch decreased and to speed up when pitch increased ('rate-change illusion'). The fMRI data revealed activation increases with increasing task difficulty in pre-SMA, left putamen, and right IFG/insula. Importantly, activation in pre-SMA was linked to the perceptual sensitivity to discriminate rate changes and, together with the left putamen, to relative reductions in susceptibility to pitch-induced illusory distortions. Right IFG/insula activations, however, only scaled with task difficulty. These data offer a distinction between regions whose activations scale with perceptual sensitivity to features of time (pre-SMA) and those that more generally support behaving in difficult listening conditions (IFG/insula). Hence, the data underscore that individual differences in time perception can be related to different patterns of neurofunctional activation.

Introduction

Almost all environmental events inherently carry temporal information. The most prominent examples are speech and music, which contain variations in item duration and fluctuations in temporal rate. Critically, perceived time does not necessarily precisely reflect physical stimulus features (Eagleman, 2008) but can be influenced by contextual factors such as sound intensity (Alards-Tomalin et al., 2013), visual space (Huang and Jones, 1982; Jones and Huang, 1982) or changes in a sound's pitch (Boltz, 1998, 2011; Henry and McAuley, 2009, 2013; Herrmann et al., 2013; Shigeno, 1986). For example, participants tend to overestimate the rate of a modulated sound when the sound's pitch increases and underestimate the rate of a sound when the sound's pitch decreases (Herrmann et al., 2013).

In order to investigate the neural underpinnings of time perception, functional magnetic resonance imaging (fMRI) studies have been conducted to reveal where in the brain temporal information is processed. Most fMRI studies thus far investigated interval or duration perception (e.g., Coull et al., 2004; Lewis and Miall, 2003; Pouthas et al., 2005; Rao et al., 2001; Tregellas et al., 2006), while a few other studies examined the perception of rate (e.g., Bengtsson et al., 2009; Grahn and McAuley, 2009; Grahn and Rowe, 2009; Henry et al., in press; McAuley et al., 2012). The most prominent regions associated with processing temporal information are the supplementary motor area (SMA), pre-SMA, insular cortex, inferior frontal gyrus (IFG), inferior parietal cortex, cerebellum, and basal ganglia including the caudate and putamen (Bengtsson et al., 2009; Coull et al., 2004, 2008; Grahn and McAuley, 2009; Harrington et al., 1998, 2010; Lewis and Miall, 2003; McAuley et al., 2012; Morillon et al., 2009; Nenadic et al., 2003; Rao et al., 2001; Schwartze et al., 2012; Teki et al., 2011; Tipples et al., 2013; Wiener et al., 2014; for a recent meta-analysis, see Wiener et al., 2010).

Another line of studies focused on the influences of task performance and attentional dynamics in modulating the brain activity in those regions implicated in timing functions (Coull and Nobre, 1998; Coull et al., 2004; Henry et al., in press; Tregellas et al., 2006). For example, increasing the difficulty of discriminating the duration or rate of auditory or visual stimuli leads to increased activation in the pre-SMA, right inferior frontal cortex, basal ganglia, and inferior parietal cortex (Ferrandez et al., 2003; Henry et al., in press; Livesey et al., 2007; Tregellas et al., 2006; Wencil et al., 2010; Wiener et al., 2014). Furthermore, selective attention to a specific temporal feature (e.g., duration) while ignoring a different temporal feature (e.g., modulation rate) leads to a reversal in the pattern of brain activity as a function of task difficulty (Henry et al., in press). In this study, for a to-be-attended

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temporal feature, the largest neural response was observed for small (i.e., difficult to discriminate) stimulus changes, and the smallest neural response occurred for large (i.e., easy to discriminate) stimulus changes. Critically, this differential effect was inverted for the to-be-ignored temporal feature, for which the largest neural response was observed when stimulus change was large (i.e., maximally distracting), while the smallest neural response was observed when stimulus change was small (i.e., easy to ignore; Henry et al., in press). Taking these studies together, it has been concluded that brain activation in regions associated with timing functions is also strongly affected by task performance and attentional dynamics in a timing task (Coull et al., 2004; Ferrandez et al., 2003; Henry et al., in press; Livesey et al., 2007; Tregellas et al., 2006).

Critically, individuals vary in their ability to discriminate, for example, small changes in duration or rate (Erb et al., 2012; Fitzgerald and Wright, 2011; Grahn and McAuley, 2009; Moore et al., 1991), and in their susceptibility to illusory distortions of duration or rate (Dirnberger et al., 2012; Harrington et al., 2004; Herrmann et al., 2013; Tipples et al., 2013). Furthermore, individuals differ in the degree to which brain activation in regions implicated in timing functions is modulated by performance in a timing task (Coull et al., 2008; Wiener et al., 2014), induction of a beat (Grahn and McAuley, 2009; Grahn and Rowe, 2009), emotion-induced time distortions (Dirnberger et al., 2012), and general misestimation of time (Harrington et al., 2004; Tipples et al., 2013).

Regarding distortions in perceived time, there have been a number of previous attempts to relate brain activation to illusory time percepts (using within-participant and across-participant correlations). Several studies have observed a relation between brain activations and distortions of perceived time originating from global context effects (Harrington et al., 2004; Tipples et al., 2013), while others observed a relation between brain activity and illusory percepts originating from manipulations of nontemporal stimulus features such as visual motion, visual looming, audio-visual interaction, or emotional content (Bueti and Macaluso, 2011; Dirnberger et al., 2012; Harrington et al., 2011; Wittmann et al., 2010). With respect to the auditory domain, Bueti and Macaluso (2011) were unable to observe a link between brain activations and temporal illusions, although they observed such a link for the visual domain; this null effect in the auditory domain might be due to the weak perceptual distortions elicited by the non-modulated tone stimuli used in this study (as discussed also in Bueti and Macaluso, 2011). Pitch changes in sounds, on the other hand, are known to strongly influence percepts of time (Boltz, 1998, 2011; Henry and McAuley, 2009, 2013; Herrmann et al., 2013; Shigeno, 1986), and are therefore well suitable for investigating the underlying neural functional activations.

Thus, the current fMRI study focused on time distortions induced by auditory stimulation and followed previous research by focusing on modulations of brain activity by attentional dynamics and task performance in brain regions associated with timing functions. In detail, we used frequency-modulated sounds that changed over time in modulation rate (speeding up vs. slowing down) and pitch (decrease vs. increase). We aimed to investigate (1) which brain regions are modulated by difficulty in a discrimination task when attending to modulation-rate changes while simultaneously ignoring changes in pitch; and (2) whether the degree of modulation in brain activity is linked to individual differences in perceptual sensitivity (to modulation rate) and the magnitude of pitch-induced illusory distortions.

Methods and materials

Participants

Nineteen healthy adults aged 21–32 years (median: 24 years; 10 female) participated in the current study. Participants were right-handed and had no self-reported hearing problems or history of neurological diseases. They gave written informed consent and were paid 8 Euro per hour. The study was in accordance with the Declaration of Helsinki and approved by the local ethics committee of the University of Leipzig.

Acoustic stimulation

Stimuli consisted of frequency-modulated sounds with a duration of 4 s, in which modulation rate and pitch were manipulated in a 6×6 design (see Fig. 1A). Stimuli were created in MATLAB (v7.11; The MathWorks Inc.) using an adapted version of the *vco.m* function, and were sampled at 44.1 kHz with 24-bit resolution. In brief, the *vco.m* function generates a sine wave with time-sensitive frequency modulations by manipulating the phase angles of the waveform. Levels for rate and pitch changes were chosen based on pilot testing, which ensured that rate–pitch combinations would elicit robust illusory rate-change percepts (see also Herrmann et al., 2013).

For the factor modulation rate, the carrier frequency of the sounds was modulated by a sinusoidal function, where the modulation rate linearly changed from 4 Hz to one of six levels (4 Hz $\pm$2.6%, $\pm$7.8%, and $\pm$13%) over the duration of the sound (Fig. 1A). The modulation depth was fixed at $\pm$20% of the mean carrier frequency, which took on one of six values ranging from 1200 Hz to 1500 Hz. Note that we selected a modulation rate of 4 Hz (i.e., a period of 250 ms) which, together with unpredictable starting phases of the modulation, deems using any counting strategy in order to perform the task unlikely.

For the factor Pitch, the carrier frequency itself was manipulated such that it linearly changed around the mean carrier frequency by $\pm$8%, $\pm$24%, or $\pm$40% over the duration of the sound. For carrier frequency manipulations, modulation depth was scaled according to the instantaneous mean carrier frequency and thus remained consistent with the logarithmic frequency scale critical for auditory perception (Attneave and Olson, 1971; Burns, 1999; Fig. 1A).

Note that the stimulus-final phase (and consequently the starting phase) of the frequency modulation was manipulated such that half of the trials ended in the rising phase of the frequency modulation and the other half in the falling phase (uniformly distributed across conditions). Hence, any perceptual differences potentially arising from different final trajectories of the sounds' frequency were controlled for across trials.

Procedure

Sounds were presented at 55 dB sensation level (i.e., above the participants' individual hearing threshold), which was determined for a 1350-Hz pure tone at the beginning of the experiment. Then, participants underwent a short familiarization session prior to scanning (including extreme examples of modulation-rate changes without changes in pitch) in order to familiarize them with the task.

A schematic outline of a trial is shown in Fig. 1B. Each trial in the experiment comprised the presentation of a sound (jittered randomly between 1.45 and 1.95 s following trial onset; Fig. 1B), followed by a visual response prompt showing the letters “S” and “L” next to each other (S — “schneller” and L — “langsamer”, German for “faster” and “slower”, respectively). The response prompt always occurred along with the onset of the 5th fMRI volume (TR) within a trial at 6.4 s. Participants were asked to press the button for “S” whenever the modulation rate increased and the button for “L” whenever the modulation rate decreased. Participants were instructed to ignore changes in pitch. The positions (left vs. right on the screen) of the letters “S” and “L” randomly changed from trial to trial (uniformly distributed across conditions), and the participant was given 2.3 s to indicate his/her response using the index finger (left screen position) and ring finger (right screen position) of the right hand. Subsequently, an additional visual response prompt was presented (2.3 s after the first prompt) which asked participants to judge on a three-point scale how confident they were with their

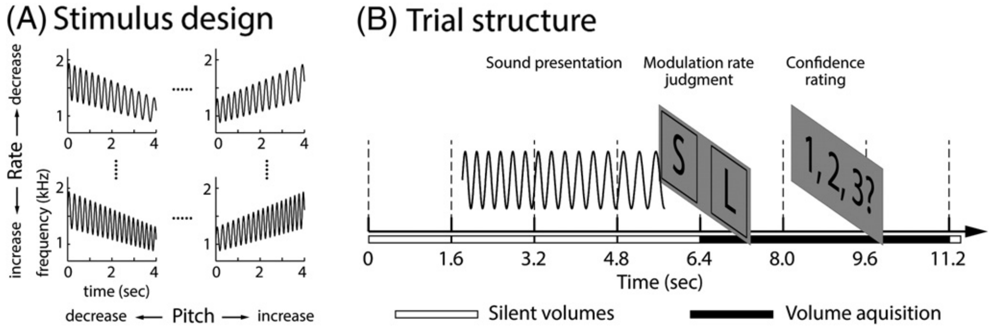

Fig. 1. Stimulus design. A) Schematic of the 6 × 6 rate–pitch stimulus design (only four stimuli examples are shown). Stimuli were frequency-modulated sounds varying in modulation rate and pitch over the duration of the sound. Here, the frequency modulation of example sounds is depicted, with the sounds' frequency displayed on the y-axis and time on the x-axis. Note that changes in modulation rate are schematic and were smaller in the actual stimuli. B) Trial structure of the current fMRI experiment, including sound presentation, modulation rate judgment (S — "schneller" and L — "langsamer", German for "faster" and "slower", respectively), and confidence ratings. The position of "S" and "L" on the screen (left versus right) varied from trial to trial, and thus prohibited specific motor preparation during sound presentation.

decision in the modulation-rate judgment (Fig. 1B; see also Wilsch et al., in press).

The experiment was divided into six blocks. Within each block, each of the 6 × 6 unique modulation rate × pitch combinations was presented once, resulting in 36 stimulus presentations per block. In addition, four silent trials were presented per block, where no acoustic stimulation occurred.

Auditory stimuli were presented via MRI-compatible headphones (Commander XG, Resonance Technology, Inc.). Visual response prompts were projected through an LCD projector onto a mirror screen attached to the head coil. An IBM-compatible computer running with the presentation software (Neurobehavioral Systems, Albany, CA) controlled the stimulation.

Behavioral data analysis

Behavioral data were analyzed in two ways. First, general task difficulty was investigated. In detail, each trial's response was given a binary code (correct; incorrect) and then weighted by the corresponding confidence rating, such that the single-trial response coding could take on one of six values [0 0.2 0.4 0.6 0.8 1]. For example, a response code of 0.6 refers to a correct response for which the participant was unconfident (confidence rating of 1). Single-trial responses were averaged over trials. We refer to the resulting dependent measure as hit rate. In order to test whether rate manipulations affected listeners' rate-change discrimination performance, hit rates were averaged across pitch conditions (rate marginal) and a one-way repeated measures analysis of variance (rmANOVA) was calculated to compare rate conditions. In order to test whether pitch manipulations affected listeners' rate-change discrimination performance, hit rates were averaged across rate conditions (pitch marginal) and a one-way rmANOVA was calculated to compare pitch conditions. Note that here the rate × pitch interaction was not of interest because pitch-induced illusory influences on rate-change discrimination were investigated using proportion of 'speeding up' responses (see below). Whenever the assumption of sphericity was violated (according to a significant Mauchly's test at $P \leq 0.05$), Greenhouse–Geisser correction was applied (Greenhouse and Geisser, 1959).

For the second analysis, each trial's response was again given a binary code (slowing down; speeding up) and then weighted by the corresponding confidence rating, such that the single-trial response coding could take on one of six values [0 0.2 0.4 0.6 0.8 1]. For example, a response code of 0.6 refers to a 'speeding up' response for which the participant was unconfident (confidence rating of 1). Single-trial responses were averaged over trials. We refer to the resulting dependent measure as proportion of 'speeding up' responses. From the proportion of 'speeding up' responses two measures were extracted. First, perceptual sensitivity to discrimination rate changes was estimated as the slope of the linear fit to weighted proportions of 'speeding up' responses as a function of z-normalized rate levels (average across pitch conditions). We henceforth refer to the slope measure as 'discrimination index'. A larger (i.e., steeper) slope indicates better rate-discrimination sensitivity (Macmillan and Creelman, 2005, p. 121). Second, strength of illusory rate-change percepts was estimated as the slope of the linear fit to the proportion of 'speeding up' responses as a function of z-normalized pitch levels (average across rate conditions). We henceforth refer to this measure as 'illusion index'. A larger slope indicates stronger illusory rate-change percepts. In order to test whether participants were able to discriminate rate changes and whether participants were biased in their rate-change percept, the discrimination index and the illusion index were separately tested against zero using one-sample t-tests. Subsequently, the two indices were tested against each other using a paired-sample t-test. Importantly, the discrimination and illusion indices were used as covariates in the fMRI analyses (see below).

fMRI recordings and preprocessing

Data were recorded on a 3-T MedSpec 30/100 scanner (Bruker, Ettlingen, Germany) using a birdcage head coil. T_2^*-weighted images were acquired using an interleaved silent steady state (ISSS) sequence (Mueller et al., 2011; Schwarzbauer et al., 2006), with a TR of 1.6 s, TE of 30.36 ms, flip angle of 73° (Ernst angle), acquisition bandwidth of 101 kHz, matrix = 64 × 64 pixels, and FOV = 19.2 cm^2, resulting in an in-plane resolution of 3 × 3 mm. Slice thickness was 4 mm, with a 1-mm interslice gap. During auditory stimulation, the magnetization was kept in a silent steady state (4 volumes) followed by the subsequent acquisition of 3 volumes during which the visual response prompts and corresponding button presses were delivered (Fig. 1B). Following the experimental blocks, a Fieldmap image was acquired for use during realignment. Existing high-resolution T_1-weighted magnetization-prepared rapid gradient-echo images were taken from the database of the Max Planck Institute for Human Cognitive and Brain Sciences. T_1 images were acquired on a 3-T MAGNETOM TIM Trio scanner (Siemens, Erlangen, Germany) according to the following parameters: TR = 1.3 s, TA = 10 ms, TE = 3.93 ms, matrix = 256 × 240, FOV = 256 × 240, resulting in a resolution of 1 mm × 1 mm × 1.5 mm (interpolated to 1-mm isotropic voxel size during spatial normalization).

Data were analyzed using SPM8 (Welcome Trust Centre for Neuroimaging, London, UK) and custom MATLAB scripts. Preprocessing comprised rigid-body spatial realignment and unwarping using the Fieldmap image, segmentation of the T_1 image, coregistration to the T_1 image according to spatial normalization parameters from segmentation, normalization to Montreal Neurological Institute (MNI) space, interpolation to 3 × 3 × 3-mm voxel size, and smoothing with an 8-mm FWHM isotropic Gaussian kernel. First-level analyses were modeled using a finite impulse response (FIR) function, and a high-pass filter of 0.1 Hz was applied to remove slow drifts in the data.

fMRI analysis: overall brain activation to acoustic stimulation and task performance

In order to test for general brain activations elicited during acoustic stimulation and task performance, one design matrix was constructed for each participant and a general linear model (GLM) was calculated (first-level analysis). The design matrix included one regressor per block indexing sound trials and a second regressor per block indexing silent trials. Blocks were modeled as regressors of no interest. Effects of overall brain activation were calculated as sound trials vs. silent trials (contrast vector: [1–1]). On the second level, the resulting contrast values were compared to zero using a one-sample t-test. t-Values were transformed to z-scores, and activations were cluster-extent threshold corrected for multiple comparisons ($P \leq 0.05$) based on Monte Carlo simulations as described in Slotnick and Schacter (2004) and Slotnick et al. (2003). Voxels with z-scores equal or greater than 3.719 ($P \leq 0.0001$) and a cluster extent of nine voxels were considered statistically significant. Anatomical labels were determined using the xjView toolbox (http://www.alivelearn.net/xjview) implemented in SPM8.

fMRI analysis: neural activation as a function of increasing task difficulty

Next, two GLMs were calculated for each participant (first-level analysis), one for the six rate conditions and one for the six pitch conditions. Each design matrix included six regressors per block (six rate or pitch conditions) and blocks were modeled as regressors of no interest. The resulting beta values for rate conditions and the beta values for pitch conditions were separately subjected to the analyses described in the following.

In order to investigate neural responses related to task performance (i.e., increasing task difficulty), hit rates were correlated with neural activation (Fig. 4). In detail, for each participant and separately for each voxel, a linear function was fitted to the estimated coefficients (beta values) from each GLM as a function of hit rate. In order to allow for a possible separation of task-difficulty increases due to rate versus pitch changes, linear fits were separately calculated for the rate conditions and for the pitch conditions (see Fig. 4B). On the second level, voxels that significantly scaled with increasing task difficulty (decreasing hit rate) were determined by testing the slopes of the linear fits against zero using a one-sample t-test. t-Values were transformed to z-scores and activations were cluster-extent threshold corrected for multiple comparisons ($P \leq 0.05$; Slotnick et al., 2003; Slotnick and Schacter, 2004). Voxels with z-scores equal or greater than 2.576 ($P \leq 0.005$) and a cluster extent of twenty-four voxels were considered statistically significant. Anatomical labels were determined using the xjView toolbox (http://www.alivelearn.net/xjview) implemented in SPM8.

Further correlations were carried out using the slopes of the above-described linear fits to investigate whether the modulation in neural activation as a function of increased task difficulty (decreasing hit rate) has perceptual consequences related to either (a) sensitivity to discriminate changes in rate or (b) pitch-induced distortions of rate changes. For each significant cluster, individual slopes from the linear fit to beta values as a function of hit rate (reflecting the degree of modulation in brain activation with increasing task difficulty) were extracted from the voxel yielding the highest z-score within the cluster. Extracted slopes were then correlated with the discrimination index and the illusion index estimated from the behavioral data.

Results

Behavioral results

Fig. 2A depicts hit rates (weighted proportion correct) for rate conditions and pitch conditions. One-way rmANOVAs conducted separately for rate conditions and for pitch conditions revealed significant differences in hit rate for both rate and pitch conditions (rate: $F_{5,90} = 78.72$, $P < 0.001$, $\varepsilon = 0.485$; pitch: $F_{5,90} = 25.21$, $P < 0.001$, $\varepsilon = 0.596$). These differences in performance were best captured by subtracting hit rate averaged across the two conditions with the largest stimulus change from hit rate averaged across the two conditions with the smallest stimulus change. For rate conditions, this difference was significantly smaller than zero ($t_{18} = -13.52$, $P < 0.001$), indicating that discrimination of rate change was most difficult for small changes in modulation rate. For pitch conditions, the difference between small and large stimulus changes was significantly greater than zero ($t_{18} = 4.49$, $P < 0.001$), indicating that discrimination of rate change was most difficult for large changes in pitch (Fig. 2A, top right).

The analyses reported in the previous paragraph for hit rate are informative regarding general task difficulty. The sensitivity to discriminate rate changes and the degree to which changes in pitch induced illusory rate-change percepts are more clearly investigated using proportion of ‘speeding up’ responses (Fig. 2B). The slope of a linear fit to proportions of ‘speeding up’ responses as a function of rate levels (z-normalized) provides an individual measure of rate-discrimination sensitivity (discrimination index). The slope of a linear fit to proportions of ‘speeding up’ responses as a function of pitch levels (z-normalized) provides an individual measure of the strength of rate-change illusion (illusion index). Both indices (slopes) were significantly larger than zero (rate: $t_{18} = 11.96$, $P < 0.001$; pitch: $t_{18} = 7.41$, $P < 0.001$; Fig. 2B, top right), thus indicating that participants were able to discriminate rate changes, but at the same time were biased in their rate-change percepts by changes in pitch. Noteworthy, rate slopes (discrimination index) were larger than pitch slopes (illusion index), indicating that percepts of rate change were, as expected, more strongly driven by rate changes than by pitch changes ($t_{18} = 2.98$, $P = 0.008$).

In addition, we tested whether perceptual sensitivity for rate changes was linked to pitch-induced illusions by correlating the discrimination index with the illusion index. We observed a significant negative correlation ($r = -0.638$, $t_{18} = 3.42$, $P = 0.003$), indicating that participants who were more sensitive to rate changes tended to perceive weaker illusions. This correlation reflects the necessity of reduced illusions with increased perceptual sensitivity to rate changes, while reduced perceptual sensitivity could in principle be independent from changes in pitch.

Overall brain activation related to sound processing and task performance

Fig. 3 depicts brain regions that were more strongly activated during sound presentation and general task performance than during silent trials. Activated brain regions included the bilateral superior temporal gyri, left inferior frontal gyrus (pars opercularis), left precentral gyrus and pre-SMA. Table 1 shows MNI peak voxel coordinates and the corresponding statistical results.

Neural activation as a function of task performance (increasing task difficulty)

In order to investigate changes in neural activation coupled to task performance, for each participant a linear function was fitted to neural activation (beta values from separate GLMs using rate and pitch conditions as covariates) as a function of hit rate, separately for rate and for pitch conditions. The resulting slopes reflect a measure of brain activation modulation by increasing task difficulty, which we refer to as

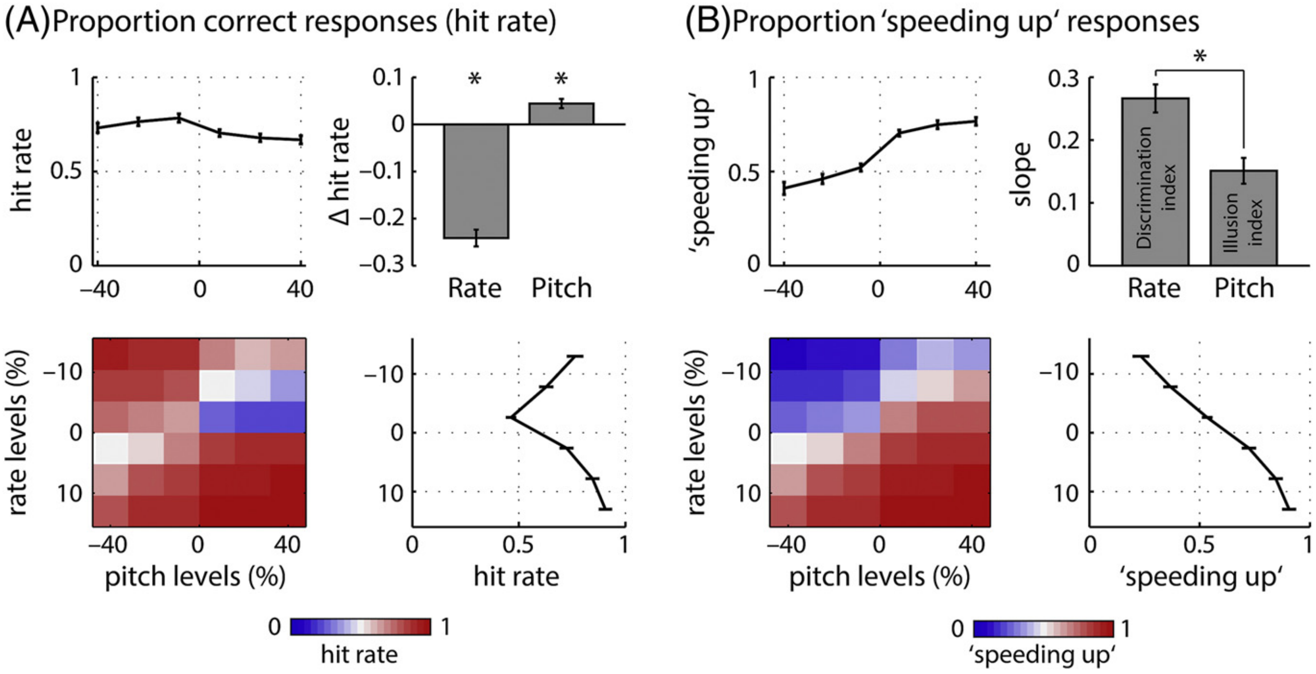

Fig. 2. Behavioral performance. A) Bottom left: Mean hit rate (proportion correct weighted by confidence ratings) for the 6 × 6 rate–pitch conditions. Rate and pitch marginal means are provided at the bottom right and top left, respectively. Top right: Hit rates for large changes in rate or pitch subtracted from hit rates for small changes (Δhit rate). For both rate and pitch conditions, this difference is significantly different from zero. B) Bottom left: Mean proportion of 'speeding up' responses (weighted by confidence ratings) for the 6 × 6 rate–pitch conditions. Rate and pitch marginal means are provided at the bottom right and top left, respectively. Top right: Discrimination index (slope of linear fit to rate marginal) and illusion index (slope of linear fit to pitch marginal). Both indices are significantly larger than zero, and also significantly different from each other. $^{*}P < 0.05$.

'neural task-difficulty index'. Fig. 4 describes the analysis using the data of one participant.

Individual slopes were then tested against zero on the group (second) level (Fig. 5A). Significant activation clusters for rate conditions were observed in pre-SMA and in the right IFG (pars opercularis)/insula. That is, activation strength (beta values) in pre-SMA and right IFG/insula increased with decreasing hit rate (increasing task difficulty). For pitch conditions, a similar modulation of activation strength was observed in the left putamen, such that activation strength (beta values) increased with decreasing hit rate (increasing task difficulty). For illustration purposes, the predicted neural activation as a function of hit rate (calculated from the linear coefficients) for each participant is depicted in Fig. 5A (middle panels). Table 2 summarizes the results.

Neural activation linked to rate-change discrimination and pitch-induced illusions

Further correlations were conducted for maximally-activated voxels within each significant region. The slope of the linear fit to beta values as a function of hit rate (reflecting the degree of modulation of brain activation with increasing task difficulty; neural task-difficulty index; Figs. 4C and 5A middle panel) was extracted for each participant. Slopes were subsequently correlated with the discrimination index (slope of linear fit to behavioral proportions of 'speeding up' responses as a function of rate levels) and the illusion index (slope of linear fit to behavioral proportions of 'speeding up' responses as a function of pitch levels).

Significant correlations of the neural task-difficulty index (for rate conditions) with the discrimination index and illusion index were observed in pre-SMA ($r = -0.536$, $t_{18} = -2.618$, $P = 0.018$; $r = 0.456$, $t_{18} = 2.115$, $P = 0.049$; respectively), but not in the right IFG/insula ($r = -0.136$, $t_{18} = -0.566$, $P = 0.579$; $r = 0.001$, $t_{18} = 0.006$, $P = 0.996$; respectively). In other words, participants showing stronger modulation of pre-SMA activation with increasing task difficulty were more sensitive to discriminate rate changes and showed smaller pitch-induced rate-change illusions. Activations in the right IFG/ insula cortex, on the other hand, only scaled with task difficulty, but were unrelated to individual differences in perceptual sensitivity or illusion strength (Fig. 5B).

In left putamen, neural task-difficulty index (for pitch conditions) was correlated with the illusion index ($r = 0.483$, $t_{18} = 2.275$, $P = 0.036$),

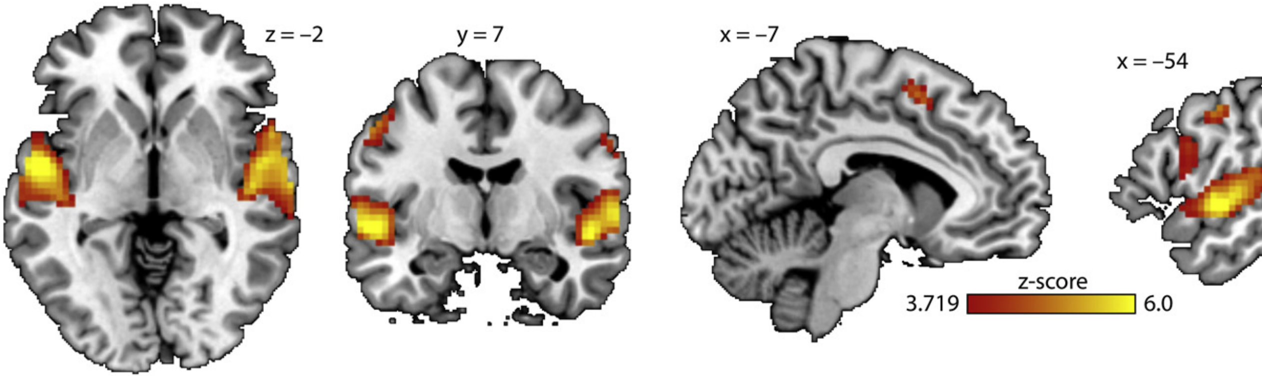

Fig. 3. Brain regions more strongly activated during sound presentation than during silence.

Table 1
MNI coordinates and statistics for peak voxels in significant clusters arising from contrasting neural activation to sound trials with neural activation to silent trials. SMA — supplementary motor area, STG — superior temporal gyrus, IFG — inferior frontal gyrus.

Region	MNI peak coordinate (mm)	z-Score	Number of voxels	Volume (cm^3)
Right STG	51 −4 −8	6.62	634	17.12
Left STG	−57 −4 −2	6.68	674	18.20
Left IFG	−57 8 25	4.96	65	1.76
Left precentral gyrus	−54 −7 43	4.95	49	1.32
Pre-SMA	−6 8 55	4.73	27	0.73

but not with the discrimination index ($r = -0.054$, $t_{18} = -0.222$, $P = 0.827$). In other words, participants showing stronger modulation of left putamen activation with increasing task difficulty showed smaller pitch-induced rate-change illusions, while activity modulations in left putamen were not related to the sensitivity to discriminate rate changes (Fig. 5B). Note that although the discrimination index and the illusion index share some variance (as indicated by the significant correlation reported above), they dissociate on the neural level such that the degree of brain activity modulation in left putamen is correlated only with the illusion index, but not with the discrimination index.

In order to test whether overall activations are related to behavioral performance, we also correlated the discrimination index and the illusion index with the activity from the baseline contrast. For this analysis, we used the sound vs. silence contrast images (baseline, see above) and extracted values from the same voxels in pre-SMA, right IFG/insula, and left putamen as identified by the linear fit analysis (modulation of brain activity by hit rate). Overall brain activity in these regions was correlated neither with the discrimination index nor with the illusion index (for all; $P > 0.25$), indicating that overall brain activity is unrelated to being sensitive to modulation rate changes and to the magnitude of illusory distortions.

Finally, in order to confirm that the observed across-participant correlation effects are not due to the specific selection of brain regions using all data in the linear fit analysis (Kriegeskorte et al., 2009), we also split the six data blocks into two independent data sets (three blocks each) at the first level. One half of the blocks (1, 3, and 5) was used to test for brain regions that were modulated by increasing task difficulty (linear fits to betas as a function of hit rate; neural task-difficulty index). Given the reduced number of data points, only the pre-SMA out of the three regions (pre-SMA, right IFG/insula, left putamen) survived the whole-brain significance threshold (data not shown). Critically, using the other half of the data (block 2, 4, and 6), modulation of brain activity by increasing task difficulty (linear fits; neural task-difficulty index) was calculated for the identified pre-SMA region. The magnitude of brain activity modulation (neural task-difficulty index for rate conditions) was then correlated with the discrimination index and the illusion index (also derived from blocks 2, 4, and 6). In accordance with the analysis using all blocks, both correlations were significant (discrimination index: $r = -0.555$, $t_{18} = -2.751$, $P = 0.014$; illusion index: $r = 0.469$, $t_{18} = 2.190$, $P = 0.043$), confirming that participants showing stronger modulation of pre-SMA activation with increasing task difficulty were more sensitive to discriminate rate changes and showed smaller pitch-induced rate-change illusions.

Discussion

This functional imaging study investigated individual patterns of neural activations in response to temporal rate change and illusory distortions thereof. We observed the following: (1) Perception of temporal rate change is biased by changes in pitch; (2) Neural activations in pre-SMA, right IFG/insula and the left putamen were modulated by the difficulty of rate-change discrimination; (3) However, only activation changes in pre-SMA and the left putamen were linked to the perceptual sensitivity to discriminate rate changes and to relative reductions of illusory distortions. The present data provide evidence that individual differences in time perception can be related to different patterns of neurofunctional activation. In particular the results offer a dissociation of pre-SMA and left putamen versus the right IFG/insula. In the following sections, these findings are discussed in more detail.

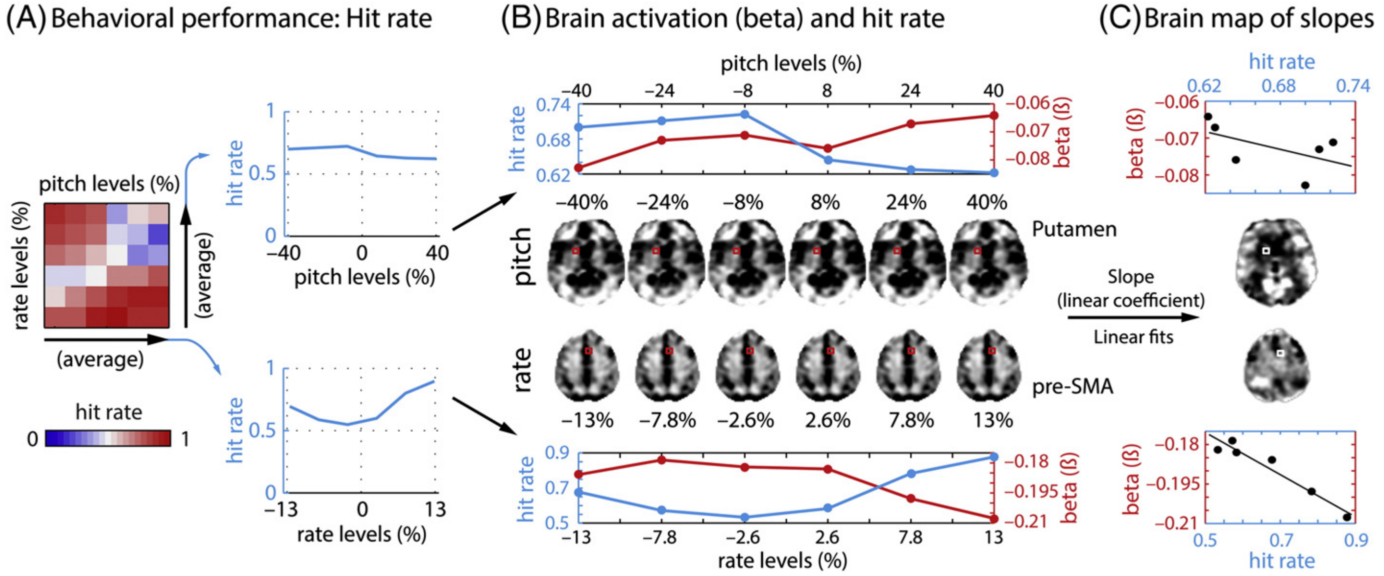

Fig. 4. Single-participant (first-level) analysis of brain activation–hit rate correlation. A) Hit rates (proportion correct weighted by confidence ratings) for one participant, illustrated similar to those of Fig. 2A. On the right, mean hit rates are depicted for pitch conditions (averaged over rate) and rate conditions (averaged over pitch). B) Brain activations (beta values; red; calculated for all voxels) for the six rate and the six pitch conditions (top and bottom, respectively) and the corresponding hit rates (from A; blue). Single-participant brain activation is shown for the peak voxel from the group analysis (marked in red) in left putamen (pitch; MNI coordinate: [−18 8 4]) and in pre-SMA (rate; MNI coordinate: [3 17 46]). C) Linear fits to brain activation data (beta values) as a function of hit rate from the same peak voxel (here marked in white). This analysis is separately conducted for rate and pitch conditions. Linear fits were calculated for each voxel. The slope (linear coefficient) provides a measure of modulation of brain activation as a function of hit rate (task difficulty). The participant-specific brain map of slopes (neural task-difficulty index) is subsequently subjected to the second-level analysis.

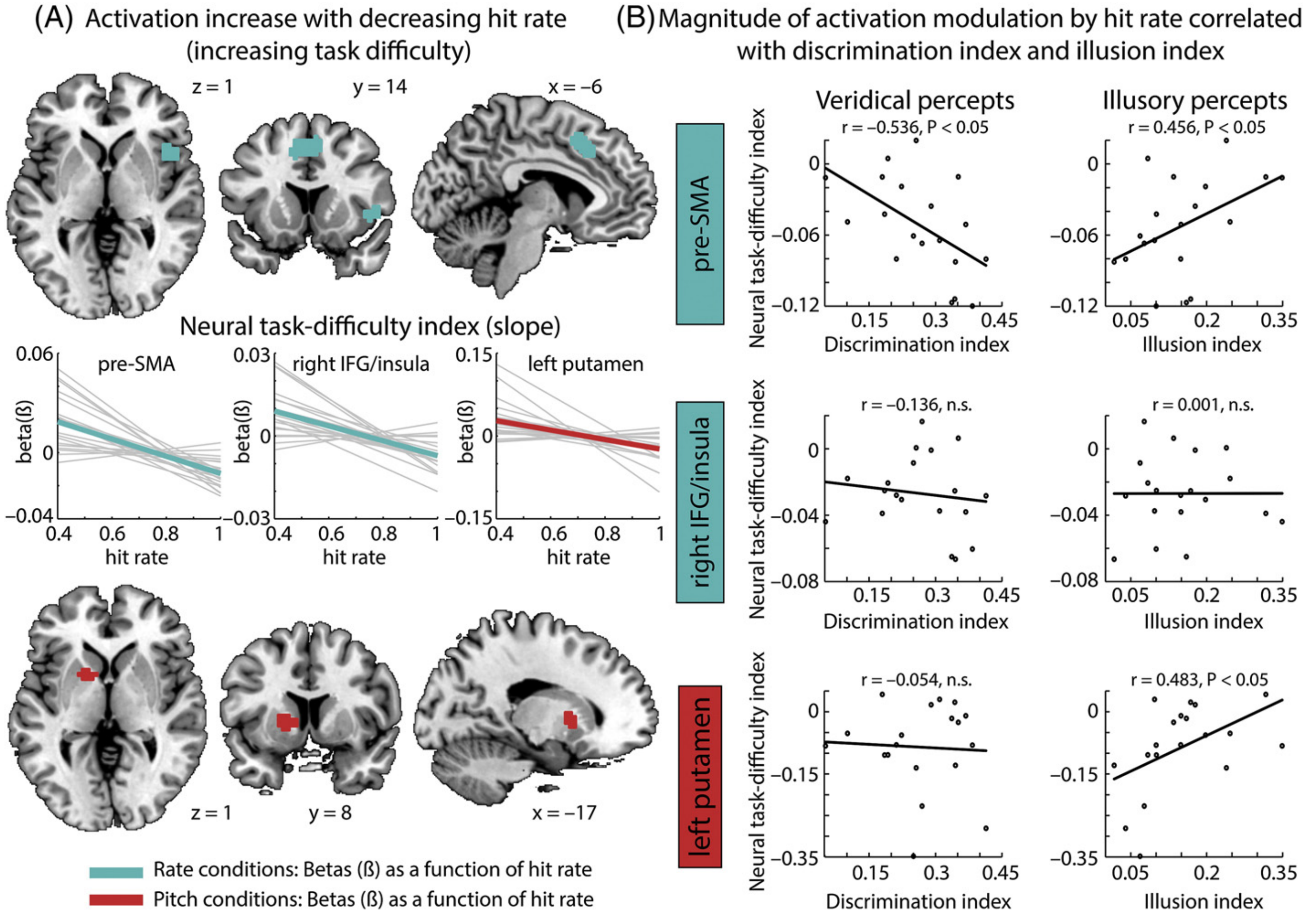

Fig. 5. Brain activation as a function of perceptual performance. A) Activation increase with task difficulty (decrease in hit rate) for rate conditions (cyan) and pitch conditions (red). The middle panels show the predicted betas (zero-centered) from linear fits for the peak voxel of each significant cluster (individuals — gray; mean — colored). The slope of the linear fit reflects an index of neural task difficulty. B) The degree of brain activity modulation by hit rate (neural task-difficulty index in A) correlated with the discrimination index and the illusion index. n.s. — not significant, SMA — supplementary motor area, IFG — inferior frontal gyrus.

Perceptual interdependence of temporal rate and pitch

In the current study, participants were presented with stimuli that changed simultaneously in modulation rate and pitch over the duration of the sound. The two measures derived from the proportion of 'speeding up' responses (i.e., the 'discrimination index' and the 'illusion index') indicate that participants judged the modulation rate but at the same time were biased in their judgments by changes in pitch. That is, pitch increases led to overestimations of the sound's modulation rate and pitch decreases led to underestimations of the sound's modulation rate. This finding is in line with a previous magnetoencephalography (MEG) study using similar stimulation (Herrmann et al., 2013) and agrees with reports of pitch-induced biases in perceived musical tempo (Boltz, 1998, 2011), interval length (Crowder and Neath, 1994; Henry and McAuley, 2009; Pfeuty and Peretz, 2010; Shigeno, 1986), and sound duration (Henry and McAuley, 2013; Yoblick and Salvendy, 1970).

It has been proposed that pitch-induced illusory distortions of temporal rate percepts are related to learned structural covariations of time and pitch in natural sounds, which coincide with expectations about how stimuli in the acoustic environment will unfold (Boltz, 2011; Jones et al., 1978). For example, the speeding up of rate in music and speech is often accompanied by increases in pitch and vice versa. When such structural covariations are violated perception can become biased in a direction that would fulfill the violated expectation (Boltz, 2011; Henry and McAuley, 2013) — in the current study, participants were biased towards perceiving stimuli with increasing pitch as speeding up and stimuli with decreasing pitch as slowing down.

Modulation of brain activation by increasing task difficulty during temporal rate-change discrimination

Our first analysis aimed to investigate activation changes related to task difficulty during temporal rate-change discrimination. Analyses

Table 2
MNI coordinates and statistics for peak voxels in significant clusters arising from linear fits to individual neural activation (beta values) as a function of hit rate (task difficulty). Right-most column: correlation of brain activation modulation with discrimination index and illusion index. n.s. — not significant, SMA — supplementary motor area, IFG — inferior frontal gyrus.

Region	Contrast	MNI peak coordinate (mm)	z-score	Number of voxels	Volume (cm^3)	Correlation (r): discrimination index / illusion index
pre-SMA	Rate	3 17 46	−4.17	154	4.16	−0.536* / 0.456*
Right IFG/ insula	Rate	48 14 1	−3.94	32	0.86	−0.136$^{\text{n.s.}}$ / 0.001$^{\text{n.s.}}$
Left putamen	Pitch	−18 8 4	−3.03	28	0.76	−0.054$^{\text{n.s.}}$ / 0.483*

* $P < 0.05$.

were separately carried out for rate and for pitch conditions, given that the behavioral data indicated opposite task performance effects for rate conditions (hit rate decreased with smaller changes in the sound's modulation rate) compared to pitch conditions (hit rate decreased with larger changes in the sound's pitch).

For rate conditions, brain activation linearly increased with increasing task difficulty (decreasing hit rate) in the pre-supplementary motor area (pre-SMA) and the right-hemispheric inferior frontal gyrus (IFG, pars opercularis), extending into the insula. For pitch conditions, brain activation linearly increased with increasing task difficulty (decreasing hit rate) in the left putamen (Fig. 5 and Table 2). These observations are in line with previous studies showing the strongest activation in the pre-SMA, basal ganglia and right IFG for time discriminations that were most challenging (Ferrandez et al., 2003; Henry et al., in press; Livesey et al., 2007; Tregellas et al., 2006; Wencil et al., 2010; Wiener et al., 2014).

Although a number of studies have failed to control for systematic differences in task difficulty between timing and control conditions (e.g., Hinton et al., 2004; Kudo et al., 2004; Pouthas et al., 2005), those that have highlight the role of the pre-SMA, IFG, and putamen in processing specifically temporal information (Coull et al., 2004, 2008; Harrington et al., 2010; Morillon et al., 2009; Rao et al., 2001). In these previous studies, however, it has proven challenging to separate brain activations to timing functions per se from processes related to attention to time (Henry et al., in press). In fact, following research on feature-selective attention (e.g., Corbetta et al., 1990; Saenz et al., 2002; Schoenfeld et al., 2007; Treue and Martinez Trujillo, 1999), Coull et al. (2004) reasoned that attending to the temporal features of a stimulus leads to modulations of brain activation in regions specifically tuned to temporal information (see also Coull, 2004; Macar et al., 2006). Under the assumption that participants in the current study might have focused more strongly on the modulation rate when rate changes were small and more strongly ignored the pitch when pitch changes were large (both of which led to decreasing hit rate), stronger activations for more difficult stimulus conditions might have been observed in regions tuned specifically to temporal information.

However, another possibility comes from a recent MEG study, which used similar stimulation as employed in the current study and emphasized the role of modality-specific auditory sensory encoding of rate–pitch interdependence (Herrmann et al., 2013; see also Shigeno, 1986). In this study, perception of temporal rate change and illusory distortions thereof was linked to neural phase patterns of low-frequency oscillatory responses in auditory cortex. While acknowledging the fundamental differences between MEG versus fMRI recordings (Bowman et al., 2007; D'Esposito et al., 1999; Hämäläinen et al., 1993; Horwitz et al., 2000), these MEG findings raise the possibility that temporal information per se is encoded already early in the sensory system (Kanai et al., 2011), while activity modulations in pre-SMA, right IFG/insula and putamen are indeed linked to changes in task difficulty and/or attentional dynamics during temporal rate-change discrimination.

Perceptual sensitivity and illusory distortions are related to modulation of neural activation in pre-SMA and putamen

In the current study, two measures were extracted from behavioral performance patterns that relate to the ability with which a participant discriminates temporal rate changes. The ‘discrimination index’, on the one hand, is a measure of the participant's sensitivity to discriminate modulation rate changes, while the ‘illusion index’ captures the degree to which a participant is biased in his/her modulation rate judgment by changes in pitch.

While previous timing studies investigated modulations of brain activity due to task difficulty and attentional dynamics (Coull et al., 2004; Ferrandez et al., 2003; Henry et al., in press; Livesey et al., 2007; Tregellas et al., 2006), the current study extended this research by examining the link between brain activity changes and individual perceptual abilities. We observed that the degree of brain activity modulation by task difficulty in pre-SMA correlated with the individuals' sensitivity to and illusory distortions of perceived temporal rate. That is, individuals whose brain activity was strongly modulated by task difficulty showed higher perceptual sensitivity to modulation rate changes and were relatively less influenced by changes in pitch. Furthermore, similar to pre-SMA, the degree to which brain activity was modulated by task difficulty in left putamen correlated with the illusion index. In contrast, activity in the right IFG/insula only scaled with task difficulty but was unrelated to perceptual sensitivity or illusion strength.

Functionally, activity modulations in pre-SMA and left putamen might be related to complementary aspects of attending to versus ignoring features of temporally varying sounds. In particular, pre-SMA activity modulations were related to the difficulty in discriminating/attending to rate changes (decreasing hit rate with small rate changes), while left putamen activity modulations were related to the difficulty in ignoring pitch changes (decreasing hit rate with large pitch changes). Thus, enhanced activity modulation in pre-SMA might reflect the degree of attention to rate changes, which in turn led to higher sensitivity to discriminate rate changes and to a reduction in illusory distortions. On the other hand, enhanced modulation of brain activity in putamen might reflect the degree to which pitch changes could be ignored, which in turn led to reduced illusory rate-change distortions, but did not necessarily result in better perceptual sensitivity.

Previous fMRI studies reported individual differences in brain activation in regions implicated in temporal processing (pre-SMA, insula, basal ganglia, inferior parietal cortex) as a function of task performance (Coull et al., 2008; Wiener et al., 2014), general time distortions (Harrington et al., 2004; Tipples et al., 2013), and emotion-induced time illusions (Dirnberger et al., 2012). The current results are generally in line with these previous observations, but are also critically different with respect to the previously observed relation between brain activity in IFG/insula (among other areas) and temporal illusions (Bueti and Macaluso, 2011; Dirnberger et al., 2012; Tipples et al., 2013; Wittmann et al., 2010) — such a relation was notably absent in the current study. This discrepancy could be due to differences in experimental stimuli (visual versus auditory), features inducing illusory percepts (global versus local; emotional versus non-emotional) as well as the specific fMRI and behavioral contrasts chosen for between-participant correlations. In fact, in order to examine task performance and attentional dynamics in a temporal discrimination task, the current study focused explicitly on behavior-related modulations of brain activity which in turn were related to individual differences in perceptual sensitivity and the degree of illusory distortions.

Consequently, the current study reveals a distinction between brain areas in which difficulty-related activation is correlated with individual differences in perceptual sensitivity and the magnitude of illusory distortions (pre-SMA, left putamen), and those that are not (right IFG/insula). The absence of a relationship between perceptual sensitivity and activity modulation in the right IFG/insula suggests that these areas support difficult listening tasks rather unspecifically. Consistent with this suggestion, activity modulations in the right IFG/insula have been reported for a variety of challenging task conditions (Dosenbach et al., 2008; Duncan and Owen, 2000; Nelson et al., 2010) including but not limited to temporal discriminations (e.g., Binder et al., 2004; Erb et al., 2013; Pastor et al., 2006; Wencil et al., 2010). For a detailed discussion of the right IFG/insula see Eckert et al. (2009).

In contrast, activations in pre-SMA were related to the individuals' sensitivity to discriminate temporal rate changes and, together with the left putamen, to relative reductions in pitch-induced illusory distortions. Two alternative interpretations are viable. On the one hand, these findings support the role of the pre-SMA and basal ganglia in general timing functions as suggested previously (Grahn and Rowe, 2009; Harrington et al., 2010; Meck et al., 2008; Pouthas et al., 2005; Schwartze et al., 2012). That is, activations in the respective regions are important for temporal rate-change discriminations and for reductions of the illusion magnitude via sharpening the rate-change representation. On the other hand, the current data also support a feature-selective attention interpretation (Coull et al., 2004; Henry et al., in press; Livesey et al., 2007; Tregellas et al., 2006). That is, brain activation might have been more strongly modulated for participants who intensively focused on the modulation rate changes and at the same time intensively ignored changes in pitch. In turn, perceptual sensitivity increased in these participants relative to the ones who less intensively focused on rate changes and were more susceptible to pitch changes. Although it is unlikely that perceptual sensitivity is solely dependent on attentional factors, the current results critically demonstrate that activation changes in pre-SMA support the behavioral outcome of time perception, and allow a functional dissociation from the IFG/insula.

Conclusions

The current study investigated perception of temporal rate change and illusory distortions thereof using functional imaging. Neural activations in the pre-SMA, right IFG/insula and left putamen increased with increasing difficulty to discriminate rate changes. Critically, the data offer a distinction between regions whose activations scale with individuals' perceptual sensitivity to features of time (pre-SMA, putamen) and those that more generally support difficult listening conditions (IFG/insula). As such, the data underscore that individual differences in time perception can be related to different patterns of neurofunctional activation.

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