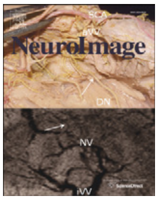
NeuroImage 101 (2014) 370–379

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg



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

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ARTICLE INFO

Article history:
Accepted 16 July 2014
Available online 23 July 2014

Keywords:
Temporal rate change
Time–pitch interdependence
Functional magnetic resonance imaging
Feature-selective attention
Perceptual illusion

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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http://dx.doi.org/10.1016/j.neuroimage.2014.07.026

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 ±2.6%, ±7.8%, and ±13%) over the duration of the sound (Fig. 1A). The modulation depth was fixed at ±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 ±8%, ±24%, or ±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