Neural bases of individual differences in beat perception

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ABSTRACT

When people listen to music, they often move their body in time with the beat. However, people differ widely in their tendency to 'feel a beat'. Why? Here we combined functional magnetic resonance imaging with a timing task that is diagnostic of individual differences in beat perception and compared the brain activity of individuals who readily perceive an implied beat with those who do not. Activation in auditory and motor areas was correlated with individual differences in beat perception, even when participants performed a timing task in which no behavioral differences occurred. The results support two conclusions. First, a bias toward beat perception is mediated by the activation of cortical circuits involved in rhythm production. Second, some individuals more readily engage these cortical beat-based circuits when making timing judgments than do others.

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Rhythm is fundamental to auditory communication and arguably all social interaction (Patel, 2007). An important element in the perception of most rhythms is the sense of a periodic pulse or 'beat' (Parncutt, 1994; Large and Palmer, 2002). When people listen to music, for example, it is evident that they are sensitive to the beat by the way they readily clap, tap their feet, or generally move their body in time with the rhythm. One question that has generated much debate is whether spontaneous entrainment (synchronization) with a beat is a behavior that is unique to the human species or a function that may be shared with at least some other vocal-learning species (Donald, 1991; Bispham, 2006; Fitch, 2006; Patel et al., 2008). Even within the human species, however, there are numerous anecdotal reports that there are large individual differences in the ability to perceive a beat; i.e., some people appear to have much more difficulty perceiving a beat than others. Research into the neural mechanisms of timing is extensive, and the specific issue of beat perception has recently begun to attract attention (Jongsma et al., 2004; Jantzen et al., 2005; Grahn and Brett, 2007). Individual differences in neural mechanisms of beat perception, however, remain largely unaddressed. The aim of this research was to examine the nature of individual differences in beat perception by combining functional magnetic resonance imaging (fMRI) with a behavioral paradigm that indexes individual differences in sensitivity to an implied beat.

In the past twenty years, there have been significant advances in our understanding of the neural circuits involved in timing and temporal processing for a variety of tasks in a wide range of stimulus conditions (Macar et al., 2002; Meck, 2003; Ivry and Spencer, 2004).

In neuroimaging studies, common subcortical and cortical brain areas activated in perceptual and motor timing tasks include the cerebellum (Jeuptner et al., 1997; Jeuptner and Weiller, 1998), basal ganglia (Harrington et al., 1998a; Schubotz et al., 2000; Rao et al., 2001; Ferrandez et al., 2003; Nenadic et al., 2003; Lewis et al., 2004; Grahn and Brett, 2007), supplementary motor area (Macar et al., 2002; Ferrandez et al., 2003; Coull, 2004; Macar et al., 2004; Grahn and Brett, 2007), premotor cortex (Schubotz et al., 2000; Schubotz and von Cramon, 2001), and prefrontal regions (Rubia et al., 1998; Lewis and Miall, 2002) Neuropsychological data parallel the involvement of these brain areas in timing. Notably, focal lesions of the basal ganglia (Harrington et al., 1998a; Harrington and Haaland, 1999), supplementary motor area and premotor cortex (Halsband et al., 1993), cerebellum (Ivry et al., 1988; Ivry and Keele, 1989), and prefrontal cortex (Mangels et al., 1998) have all been shown to produce deficits in timing.

An issue that emerges from this research is that these interconnected brain regions are unlikely to subserve identical functions, and identifying the unique contribution of each area has proved challenging in many respects (Macar et al., 2002; Lewis and Miall, 2003). It has been suggested that one distinction between commonly activated neural structures may be their respective roles in 'automatic' timing, defined as 'the continuous measurement of predictable sub-second intervals defined by movement', and 'cognitively controlled' timing, defined as the 'measurement of supra-second intervals not defined by movement and occurring as discrete epochs' (Lewis and Miall, 2003). Beat perception has the characteristics of both automatic and cognitively controlled timing, as the length of the beat humans perceive can exceed the sub-second threshold (Warren, 1993; Parncutt, 1994) and the beat may or may not be marked by movement. Thus, one function of beat perception may be to co-opt the automatic,

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less attention-demanding, timing system for the perception and production of rhythmic sequences that generally span several seconds.

The neural basis of beat perception has been studied in fMRI (Grahn and Brett, 2007) and in Parkinson disease patients (Grahn and Rowe in press). The fMRI study showed greater basal ganglia and supplementary motor area (SMA) activity when participants listened to short auditory sequences in which a beat could be readily perceived (compared to temporally matched control sequences in which the beat was more difficult to perceive or not present at all). In addition, healthy adults discriminated changes in the beat sequences significantly better than changes in the control sequences, as perception of a beat provided a regular structure against which the temporal intervals comprising the sequence could be measured. Parkinson disease patients, however, did not show the same benefit for beat sequences: they were significantly impaired with respect to healthy adults in discriminating the regular beat rhythms, but, importantly, were not significantly impaired in discrimination of control rhythms. Patients with inherited speech and language impairment also show impairments in rhythmic, but not melodic, tasks (Alcock et al., 2000b). This disorder is linked to mutations in the *FOXP2* gene, which is expressed in the basal ganglia (Haesler et al., 2004). Thus, both fMRI and patient data point to a role for the basal ganglia and SMA in beat perception. These converging data provide evidence for a separable beat-based timing mechanism that is impaired in patients with Parkinson disease. However, individual differences in beat perception for neurologically normal volunteers (widely acknowledged anecdotally) have not been systematically investigated, and nothing is known about how these individual differences may be reflected in the different neural networks engaged by particular timing tasks.

The present study extends previous research by focusing on individual differences in sensitivity to an implied beat. The approach taken was to combine fMRI with a tempo judgment task developed by McAuley et al. (2006a) that demonstrates large individual differences in sensitivity to an implied beat. In this paradigm, participants listen to short tone sequences and judge whether the sequences are 'speeding up' or 'slowing down' at the end. The two types of sequence that are of interest are shown in Fig. 1a. Five-tone (test) sequences, which consist

of an initial 3 tones that mark two 300-ms intervals followed by 2 tones that specify a variable final interval (600 ms $\pm \Delta T$). The key element of the test sequences is that a periodic 600-ms beat is implied, but not explicitly emphasized, by the temporal structure of the sequence (Povel and Okkerman, 1981; Povel and Essens, 1985). Four-tone (control) sequences, in contrast, consist of 2 tones that specify an explicit 600-ms interval followed by 2 tones marking the same variable final interval (600 ms $\pm \Delta T$).

McAuley et al. (2006a) found that for control sequences, individuals generally responded in a manner that suggested they were comparing the duration of the final interval to the initial 600-ms interval. Tempo judgments for test sequences, in contrast, revealed large and robust individual differences. Some individuals appeared to pick up on the implied 600-ms beat and responded identically to individuals who heard the control sequences. However, other individuals did not appear to hear the implied 600-ms beat and tended to compare the final interval to a 300-ms referent marked by the first three tones; this meant that these individuals responded that all of the sequences were 'slowing down'. Thus, somewhat surprisingly, opposite perceptions occurred for identical stimulus sequences. Individuals who did not pick up on the implied beat tended to respond that sequences with final intervals between 300 and 600 ms were 'slowing down', whereas those individuals who did pick up on the implied beat frequently responded that sequences with the same final intervals were 'speeding up' (Fig. 1b).

Of central interest in the present study was whether the opposite tempo perceptions observed for identical test stimulus sequences, indicative of individual differences in sensitivity to an implied beat, were mediated by different neural circuits. In addition, do individual differences in neural activity persist when behavior is identical, or are differences in neural activity only observed when behavior also differs? To address these questions, we used a within-subject design in which participants were presented with both test and control sequences of the type examined by McAuley et al. (2006a) and indicated whether the sequences were 'speeding up' or 'slowing down' while we monitored their brain activity using fMRI. Tempo judgment responses were fit with a signal detection model, based on
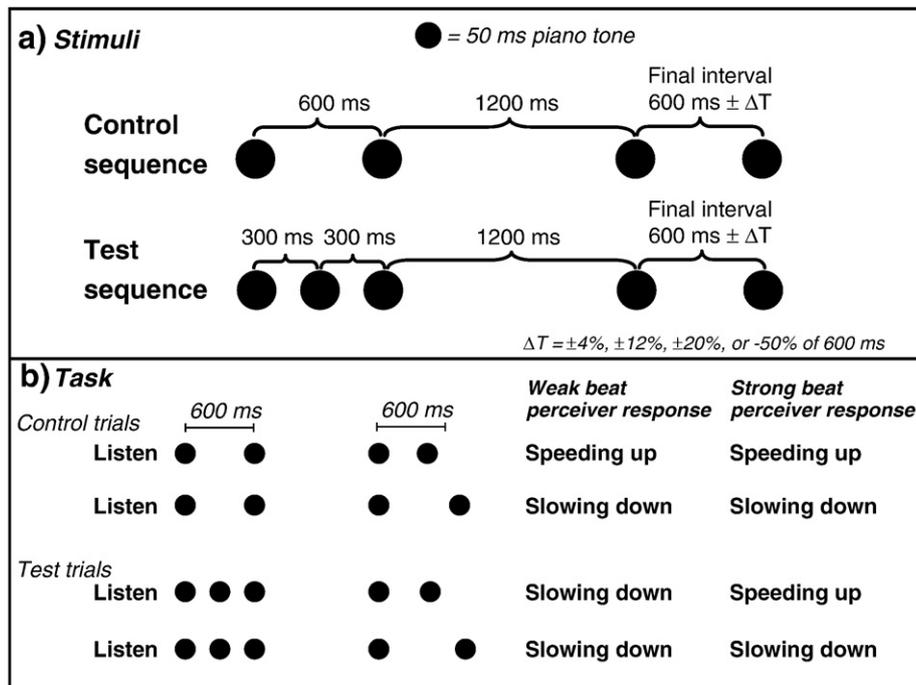

Fig. 1. Ambiguous tempo judgment paradigm: (a) Illustration of control and test sequences. (b) Task and general pattern of responses to control and test sequences by individuals who hear the implied beat (strong beat-perceivers) and by individuals who tend not hear the implied beat (weak beat-perceivers).

the expectation that some listeners would show opposite perceptions about test sequences with final intervals in the 300 to 600 ms range. Because some individuals may time more accurately than others, the model fits enabled us to derive a behavior-based quantitative measure of sensitivity to the implied beat that, critically, was distinct from overall timing ability for each participant. Derived estimates of the beat perception strength parameter were used to examine the relationship between beat perception strength and neural activity. Based on previous research, we expected that individuals showing greater sensitivity to the implied beat would show greater activity in the basal ganglia and SMA.

Materials and methods

Participants

Thirty-five right-handed neurologically normal volunteers ($n = 23$, male) between the ages of 22 and 46 years ($M = 29.9$, $SD = 7.2$) participated. Informed consent was obtained from all participants.

Stimuli

Stimulus sequences were composed of 50-ms piano tones with a fundamental frequency of 440 Hz, initially generated by a Yamaha PSR-270 MIDI keyboard and converted to wav format using CoolEdit 2000 (Syntrillium software corporation, Phoenix, AZ). Control sequences were composed of 4 tones and test sequences were composed of 5 tones (see Fig. 1). For control sequences, the first inter-onset-interval was 600 ms, the second was 1200 ms, and the third was a variable final interval of 600 ms ± 4%, ± 12%, or ± 20%, and −50%. For test sequences, the first two inter-onset-intervals were 300 ms, the third was 1200 ms, and the fourth was a variable final interval of 600 ms ± 4%, ± 12%, or ± 20%, and −50%; test and control sequences differed in temporal structure, but not in total duration.

Procedure

Participants listened to the auditory sequences and judged (by pressing one of two buttons on a response box) whether at the end of the sequence, they felt the sequence was 'speeding up' or 'slowing down'. We emphasized to participants that we were simply interested in their impressions of the sequences and that if they heard all sequences in one particular way, then they should indicate so throughout the experiment. That is, it was fine for them to respond that all of the sequences they heard were 'speeding up', that all of the sequences were 'slowing down' or that they were sometimes 'speeding up' and other times 'slowing down'. Participants were not shown a diagram of the task or told anything about the sequences other than the number of tones.

Prior to scanning, there were 24 practice trials. During scanning, 2/3 of trials required a button-press response, while 1/3 of trials required a 'mental decision' (no button-press) to dissociate hemo-dynamic responses elicited by the stimulus and the button-press. Blocks of 32 button-press trials alternated with blocks of 16 mental-decision trials, resulting in 4 blocks of each per session. Two sessions were run. Test and control trials were randomized within each block. Participants were given 2.5 s to respond with an ITI of 1 s between trials and thirty-two 'null' events of 4.5 s randomly interspersed in order to resolve the hemodynamic response in analysis.

For test and control sequences, there were 24 trials of each final interval per session, except for the −50% interval, which had 48 trials per session; in total, there were 192 trials per session. The −50% trials were included so that individuals who generally heard test trials with the other final intervals as 'slowing down' could not prepare their response earlier than individuals who heard test trials as either 'slowing down' or 'speeding up'.

Image acquisition and preprocessing

Participants were scanned in a 3 T Siemens Tim Trio using a head coil gradient set. To ensure participants were comfortable, foam pads were placed around the head and supported the legs. Stimuli were presented over headphones; attenuation of scanner noise was achieved with insert earplugs rated to attenuate by ∼30 dB (3M 1100 earplugs, 3M United Kingdom PLC, Bracknell, UK). The participants also wore ear defenders. When wearing earplugs and ear defenders, none of the participants reported difficulty in hearing the stimuli or focusing on the task. Participants were instructed not to move any part of their body during the scan other than to respond. Button press responses were recorded with millisecond accuracy.

There were 545 echoplanar imaging (EPI) volumes per session (36 slices, matrix size of 64×64, TE = 30 ms, TR = 2.19 s, FOV = 19.2×19.2 cm, flip angle = 78°). EPIs had a slice thickness of 3 mm, interslice distance of 0.75 mm, and in-plane resolution of 3×3 mm. These EPI parameters enabled whole-brain coverage, including the cerebellum, for all participants. High-resolution 1×1×1 mm MPRAGE anatomical images were collected for anatomic localization and coregistration. SPM5 was used for preprocessing and analysis (SPM5; Wellcome Department of Cognitive Neurology, London, UK). Images were slice-timing corrected, then realigned spatially (to correct for motion) to the first image in the series, using a least squares approach with 6 rigid body parameters, and trilinear interpolation. The MPRAGE image was segmented and normalized (using affine and smoothly nonlinear transformations) to a brain template in Montreal Neurological Institute (MNI) space. The resulting normalization parameters were applied to the coregistered EPIs and EPI images were smoothed with an 8 mm full-width half-maximum Gaussian kernel.

Stimuli and button presses were modeled using a regressor made from an on–off boxcar convolved with a canonical hemodynamic response function. EPI volumes with more than 4 mm movement in any plane were included as covariates of no interest to minimize movement artifacts. Low-frequency noise was removed with a 128 s high-pass filter. Results estimated from single-subject models were entered into second-level random effects analyses for standard SPM group inference (Penny and Holmes, 2003). Region of interest (ROI) analyses were conducted using MarsBar (http://marsbar.sourceforge.net) to extract mean signal intensity for each condition in each ROI.

Data analyses

Behavioral data

To quantify individual differences in responses to the test sequences, we applied a signal detection model to the behavioral judgment response proportions. Binary ('speeding up'/'slowing down') judgments were based on two temporal referents: $P = 300$ ms corresponding to the explicit time interval marked by the first three tones of the sequences and $P = 600$ ms corresponding to the implied beat. We then calculated, for each final interval of the sequence, T_i, a temporal contrast metric, C_i, which measured the normalized difference between the final interval and each referent, P:

$$C_i = \frac{(T_i - P)}{P}.$$

In previous work, we've shown that the temporal contrast metric is a good index of the information that participants use to make time judgments decisions (McAuley and Jones, 2003). Because there were two possible temporal referents, each final interval, T_i, resulted in two values of C_i, labeled here as $C_{i_{300}}$ for the $P = 300$ ms referent and $C_{i_{600}}$ for the $P = 600$ ms referent. In line with standard signal detection

assumptions (Macmillan and Creelman, 1991), values of temporal contrast for each referent were assumed to be normally distributed with standard deviation, σ; the values of $C_{i_{300}}$ and $C_{i_{600}}$ were then z-transformed and combined using a simple weighted average:

$$z = (1 - w)z_{i_{300}} + wz_{i_{600}}.$$

Predicted proportions of 'speeding up' responses, P('Speeding Up'), for each final interval, T_i, were then generated using cumulative normal distribution function:

$$P('\text{Speeding Up}') = 1 - \Phi(z).$$

To fit the model to data, we allowed both $w \in [0, 1]$ and σ to vary and minimize the root-mean-square error (RMSE) between the observed and predicted response proportions. Estimates of w were used as an index of beat perception strength, while estimates of σ provided a separate index of temporal sensitivity. Based on the formulation of the model, values of w closer to 1 indicated greater sensitivity to the implied 600-ms beat.

fMRI data

The contrast images for test and control sequences estimated from single-subject analyses were entered into a second-level random effects analysis. The data were subjected to a repeated-measures analysis of covariance with one factor: condition (test, control), and 1 covariate, w score. In order to increase sensitivity to the perhaps subtle individual differences correlated with w score, the same analysis was conducted on contrast images estimated from second session data only. Then, areas found to show an effect of the w score covariate at a reduced threshold (.01 uncorrected) were used define regions of interest (ROI), analyses of which were conducted on the independent first session data.

Results

A consistent pattern of responses across individuals was observed for control sequences, but not for test sequences. As expected, most participants judged control sequences with final intervals longer than 600 ms as 'slowing down', and sequences with final intervals shorter than 600 ms as 'speeding up'. Test sequences, in contrast, tended to yield opposite judgments when the final intervals were shorter than 600 ms. Some individuals tended to indicate that test sequences with final intervals shorter than 600 ms were 'speeding up', demonstrating sensitivity to the implied 600-ms beat; others responded that the same sequences were slowing down, suggesting that these individuals were not sensitive to the implied 600-ms beat (and instead made a judgment based on the 300-ms interval).

To quantify the individual differences in responses to test sequences, we fit the proposed signal detection model to the proportions of 'speeding up' responses of each participant. The obtained estimate of beat perception strength, w, was then used as a regressor in the fMRI analyses; values of w could vary between 0 and 1, with larger values of w indicating a greater reliance on the implied 600-ms beat. In addition, a median split on w was performed in order to provide a group comparison between strong beat-perceivers ($M = 0.93$, $SD = 0.06$) and weak beat-perceivers ($M = 0.53$, $SD = 0.20$).[1] An independent-samples

t-test showed that the w scores significantly differed between the two groups, $t(33) = 8.10$, $p < 0.001$.

Behavioral results

Proportions of 'speeding up' responses, P('speeding up'), as a function of final interval for the strong beat-perceivers and weak beat-perceivers are shown in Fig. 2 along with predicted response proportions derived from the proposed signal detection model (Average RMSE < 0.05). Strong beat-perceivers responded almost identically to control and test sequences, demonstrating sensitivity to the implied 600-ms beat in the test sequences (see Fig. 2a). In contrast, weak beat-perceivers tended to respond oppositely to control and test sequences for final intervals shorter than 600 ms, demonstrating very little sensitivity to the implied 600-ms beat (see Fig. 2b). A three-way (Group × Sequence Type × Final Interval) mixed measures ANOVA on P('speeding up') revealed main effects of group, $F(1,33) = 43.3$, $p < 0.001$, sequence type, $F(1,33) = 81.78$, $p < 0.001$, and final interval, $F(6,198) = 429.09$, $p < 0.001$, and critically, significant two-way interactions between group and sequence type, $F(1,33) = 34.33$, $p < 0.001$, group and final interval, $F(6,198) = 23.32$, $p < 0.001$, and a significant three-way interaction between group, sequence type and final interval, $F(6,198) = 21.78$, $p < 0.001$.

With respect to overall temporal sensitivity, an independent-samples t-test revealed that discrimination thresholds for control sequences did not significantly differ between strong beat-perceivers ($M = 8.00\%$, $SD = 2.68\%$) and weak beat-perceivers ($M = 9.80\%$,
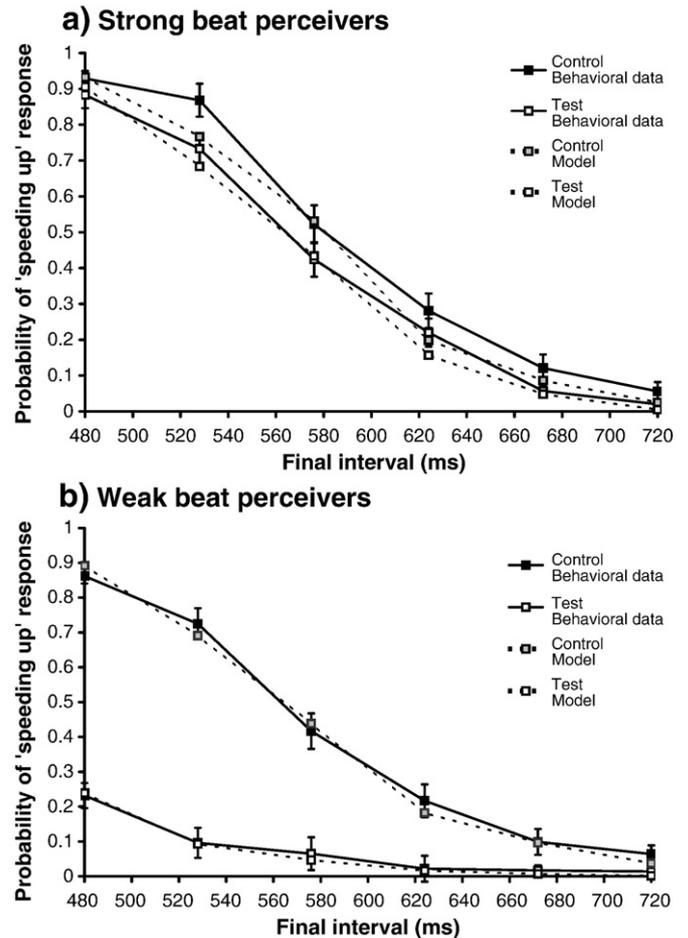

Fig. 2. Summary of behavioral data from participants during scanning and corresponding model fits to the probability of responding 'speeding up', for both (b) strong beat-perceivers and (b) weak beat-perceivers. Error bars indicate standard error of the mean.

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[1] Because there were an odd number of subjects in the study ($n = 35$), the median split on w required an unequal number of participants in the two groups. Based on an inspection of the distribution of w values, which was negatively skewed, we decided to place the middle participant in the weak beat-perceiver group; our rationale was that the w value for the middle participant was closer to the next smaller w value than the next larger w value. Based on this decision, all $n = 17$ values of w for strong beat-perceivers were > 0.8 and tightly clustered, while all $n = 18$ values of w for weak beat-perceivers were less than 0.8 and tended to be more spread out, representing the extended tail of the distribution.

$SD = 3.58\%$), $t(33) = -1.67$, $p = 0.10$; thus, it was not simply the case that the weak beat-perceivers were especially 'poor timers'. Moreover, there was a non-significant correlation between estimated w and discrimination thresholds, $r(35) = -0.217$, $p = 0.17$. A paired-samples t-test comparing strong beat-perceivers across sequence conditions revealed no difference in thresholds for control and test sequences, $t(16) = 0.232$, $p = 0.82$. This latter finding is interesting because it suggests that timing judgments based on an implied beat are as accurate as those for sequences that mark an explicit 600-ms referent.

Finally, there was a significant correlation between w and years of musical training, $r(34) = 0.348$, $p = 0.04$. This relationship needs to be interpreted cautiously; however, as it appears to be driven by a single subject with 40 years of musical training; when this subject was eliminated from the analysis, the correlation was no longer significant. There were also no significant correlations between w and self-reported rhythm ability (on a 1 to 10 scale) or hours of music listening per week.

fMRI results

All stimuli (test and control sequences) versus rest activated task-relevant areas, including superior temporal gyri, premotor and supplementary motor cortex, basal ganglia, cerebellum, dorsolateral prefrontal cortex, inferior frontal cortex, insula, and inferior parietal cortex at a whole-brain corrected ($pFDR < 0.05$) level of significance (see Fig. 3 and Table 1).

The test versus control sequences contrast activated the bilateral superior temporal gyri (maxima coordinates: 54, −16, 4; −52, −16, 4) and right Heschl's gyrus (maximum coordinates: 46, −22, 10) at a whole-brain corrected ($pFDR < 0.05$) level of significance; this was likely due to the greater auditory stimulation for the 5-tone (test) sequences compared with the 4-tone (control) sequences. No whole-brain corrected significant activations were found for the reverse contrast (control–test sequences). We also tested for areas significantly correlated with w score. One area's activity was significantly correlated with decreasing w score at whole-brain corrected levels: the right premotor cortex ($t = 5.43$, $pFDR = 0.013$, $x = 56$, $y = -14$, $z = 52$). No other areas survived whole-brain correction.

ROIs (see Table 2) were defined from areas showing correlations with w in the second session ($p < 0.01$ uncorrected, and only areas also significant in the all sequences–rest contrast were used). Mean voxel values for each ROI were extracted from the first session data and analyzed using a 2×2 mixed measures ANOVA with condition (test/control) and group (strong beat-perceiver versus weak beat-perceiver). See Fig. 4 for activity levels in each ROI across conditions and groups. Overall, test sequences elicited greater activation than control sequences in the left posterior superior temporal gyrus, $F(1,33) = 5.12$, $p = 0.03$. Strong beat-perceivers showed significantly higher activity than weak beat-perceivers in the SMA, $F(1,33) = 5.43$, $p = 0.026$, left premotor cortex, $F(1,33) = 4.60$, $p = 0.04$, and left insula, $F(1,33) = 4.24$, $p = 0.047$. Strong beat-perceivers also showed marginally significantly higher activity in the left inferior frontal gyrus, $F(1,33) = 3.13$, $p = 0.086$. Weak beat-perceivers, in contrast, showed significantly higher activity than strong beat-perceivers in the right premotor cortex, $F(1,33) = 7.74$, $p = 0.009$, and the left posterior superior and middle temporal gyri ($F(1,33) = 6.23$, $p = 0.018$; $F(1,33) = 4.19$, $p = 0.049$). No significant interactions between group and sequence type were observed in the ROI analysis.

To determine more directly whether activation differences occurred in the absence of behavioral differences, we conducted an analysis that was restricted to control sequences only. The results were generally unchanged. For control sequences, strong beat-perceivers showed significantly higher activity than weak beat-perceivers in the SMA, $F(1,33) = 6.11$, $p = 0.019$, left premotor cortex, $F(1,33) = 5.63$, $p = 0.024$, left insula, $F(1,33) = 4.61$, $p = 0.039$, and marginally significantly higher activity in the left inferior frontal gyrus, $F(1,33) = 3.83$, $p = 0.059$. Weak beat-perceivers showed significantly higher activity than strong beat-perceivers in the right premotor cortex, $F(1,33) = 7.12$, $p = 0.012$, and the left posterior superior temporal gyrus, $F(1,33) = 6.23$, $p = 0.018$, but only marginally significant higher activity in the posterior middle temporal gyrus, $F(1,33) = 3.65$, $p = 0.065$.

We conducted analyses of laterality effects, to determine if the group differences at each ROI were confined to only that hemisphere. Each ROI was flipped to the opposite hemisphere, and the data were extracted from each pair of homologous ROIs. Each pair was tested for a significant interaction between group (strong and weak beat-perceivers) and hemisphere. Only one ROI showed this interaction: the right premotor cortex ($F(1,33) = 4.60$, $p = 0.036$), indicating that the group effect (Weak Beat>Strong Beat) at this ROI was only present in the right hemisphere, and not present in the homologous left ROI. All other ROIs did not show a significant interaction, indicating that the group effect in the contralateral ROI did not significantly differ from the group effect at the original ROI, and thus any appearance of laterality effects for these regions was quantitative, not qualitative.
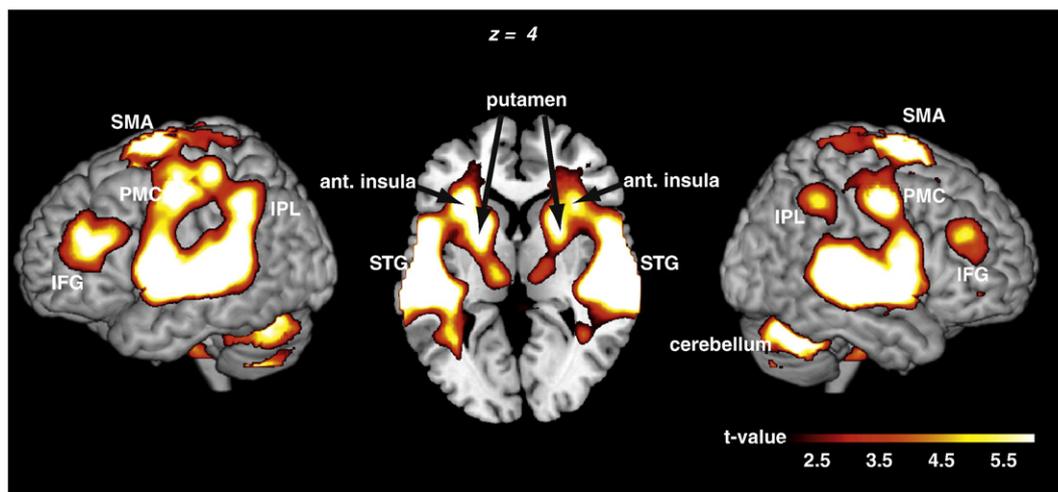

Fig. 3. Areas significantly active in the all stimuli versus rest SPM contrast overlaid on a standardized brain in MNI space. Peak voxels survive $p < 0.05$ whole-brain FDR correction. Z refers to the level of the axial slice shown in stereotaxic MNI space. Ant = anterior, IFG = inferior frontal gyrus, IPL = inferior parietal lobule, PMC = premotor cortex, STG = superior temporal gyrus.

Table 1
Brain regions activated during all stimuli–rest contrast.

Brain region	t-value	x	y	z	Brodmann area
Left superior orbital gyrus	2.9	−22	46	−4	Area 11
Left superior orbital gyrus	2.5	−18	42	−12	Area 11
Right superior orbital gyrus	4.0	24	44	−6	Area 11
Left middle orbital gyrus	3.2	−28	48	−6	Area 11/47
Left middle orbital gyrus	2.4	−22	44	−10	Area 11/47
Left middle frontal gyrus	6.9	−32	42	26	Area 46
Right middle frontal gyrus	3.6	34	40	20	Area 46
Right middle frontal gyrus	2.4	40	48	10	Area 46
Right middle frontal gyrus	4.2	32	−8	58	Area 6
Left inferior frontal gyrus p. opercularis	11.1	−54	4	12	Area 44
Right inferior frontal gyrus p. opercularis	7.5	58	6	20	Area 44
Left inferior frontal gyrus p. triangularis	5.5	−50	28	30	Area 45
Left inferior frontal gyrus p. triangularis	6.3	−42	32	26	Area 45
Right inferior frontal gyrus p. triangularis	5.0	42	16	10	Area 45
Right middle frontal gyrus p. triangularis	5.0	40	38	30	Area 45
Right middle cingulate cortex	5.8	12	14	38	Area 32
Left SMA	14.2	−4	−4	68	Area 6
Left SMA	13.8	−6	0	60	Area 6
Right SMA	13.8	6	0	70	Area 6
Left precentral gyrus	8.9	−50	−8	54	Area 6
Left precentral gyrus	6.9	−28	−10	54	Area 6
Right precentral gyrus	3.2	34	−26	56	Area 4
Right precentral gyrus	10.1	52	−2	50	Area 6
Right precentral gyrus	3.5	26	−6	48	Area 6
Right precentral gyrus	3.4	16	−36	78	Area 6
Left postcentral gyrus	5.5	−36	−30	60	Area 4
Left paracentral lobule	3.7	−10	−40	76	Area 3
Left paracentral lobule	3.5	−8	−36	68	Area 4
Left paracentral lobule	3.4	−12	−30	72	Area 4
Right paracentral lobule	3.6	12	−34	72	Area 4
Right paracentral lobule	3.3	8	−42	76	Area 5
Left insula	7.2	−28	22	4	
Left insula	7.5	−30	18	10	
Right insula	6.8	34	26	6	
Left rolandic operculum	10.9	−54	4	8	
Left superior temporal gyrus	16.0	−62	−34	14	Area 42
Left superior temporal gyrus	15.8	−62	−28	10	Area 22
Left superior temporal gyrus	14.6	−52	−16	2	Area 22
Left superior temporal gyrus	13.9	−54	−42	20	Area 42
Left superior temporal gyrus	13.2	−42	−34	14	Area 41
Right superior temporal gyrus	18.0	66	−20	6	Area 22
Right superior temporal gyrus	18.0	58	−16	2	Area 22
Right superior temporal gyrus	14.6	68	−32	12	Area 22
Left middle temporal gyrus	2.7	−42	−4	−22	Area 20
Left inferior temporal gyrus	2.7	−38	0	−28	Area 36
Left inferior parietal lobule	7.0	−42	−46	44	Area 40
Right inferior parietal lobule	5.6	42	−44	46	Area 40
Right amygdala	2.2	32	−8	−22	
Left hippocampus	3.3	−22	−40	12	
Right parahippocampal gyrus	2.8	24	−14	−18	
Right caudate nucleus	4.0	22	0	26	
Left putamen	7.3	−22	4	6	
Left putamen	7.2	−22	10	6	
Right putamen	6.7	22	12	6	
Right putamen	5.3	24	10	16	
Right putamen	4.4	24	−6	16	
Left thalamus	5.2	−14	−16	6	
Left thalamus	3.0	−4	−14	24	
Left thalamus	2.4	−2	−10	8	
Right thalamus	4.5	16	−14	6	
Cerebellar vermis 4/5	3.6	0	−56	−8	
Cerebellar vermis 6	4.4	2	−62	−20	
Cerebellar vermis 8	3.2	2	−68	−44	
Cerebellar vermis 10	3.6	−8	−50	−26	
Left cerebellum crus 2	2.9	−10	−78	−32	
Left cerebellum crus 2	2.5	−30	−82	−34	
Left cerebellar lobules IV–V	3.2	−4	−52	−14	
Left cerebellar lobule VI	10.0	−28	−62	−26	
Left cerebellar lobule VII	2.9	−12	−78	−36	
Left cerebellar lobule VIII	8.0	−24	−64	−50	
Left cerebellar lobule VIII	7.9	−34	−56	−50	
Right cerebellum crus 2	3.7	6	−82	−26	
Right cerebellum crus 2	3.0	20	−82	−38	
Right cerebellar lobule VI	9.1	32	−58	−30	
Right cerebellar lobule VII	2.8	8	−80	−38	

Table 1 (continued)

Brain region	t-value	x	y	z	Brodmann area
Right cerebellar lobule VII	2.7	6	−78	−36	
Right cerebellar lobule VIII	7.6	32	−56	−50	
Right cerebellar lobule VIII	5.7	20	−66	−50	
Right cerebellar lobule VIII	2.5	8	−76	−34	

All reported peaks significant at $p < 0.05$ whole-brain corrected (FDR) threshold.

A final whole-brain analysis found no areas in which activation correlated with years of musical training, even at a liberal statistical threshold (pFDR<0.05).

Discussion

In this study, we examined the neural bases of individual differences in the bias toward perception of a beat by combining fMRI with a novel tempo judgment task that assesses sensitivity to an implied beat. In the overall stimuli–rest contrast, we found greater activity of the superior temporal gyri, premotor and supplementary motor cortices, basal ganglia, cerebellum, dorsolateral prefrontal cortex, inferior frontal cortex, insula, and inferior parietal cortex. These brain areas are commonly activated in both perceptual and motor timing tasks involving auditory stimuli (Harrington et al., 1998b; Schubotz et al., 2000; Rao et al., 2001; Nenadic et al., 2003; Coull, 2004; Grahn and Brett, 2007). The dorsolateral prefrontal and parietal activations are likely involved in working memory and decision-making aspects of the task (Duncan and Owen, 2000), although parietal cortex has also been suggested to play a role in temporal expectation (Coull and Nobre, 2008). The insula has been implicated specifically in working memory for auditory material (Bamiou et al., 2003; Koelsch et al., 2008). The premotor and supplementary motor area, as well as cerebellar and basal ganglia responses are strongly associated with the temporal aspects of stimulus processing (Hazeltine et al., 1997; Harrington and Haaland, 1999; Ferrandez et al., 2003), particularly for sub-second intervals (Lewis and Miall, 2003).

With respect to individual differences in sensitivity to the implied beat, strong beat-perceivers showed greater brain activity in only a subset of these areas, namely the SMA, left premotor cortex, and left insula, whereas weak beat-perceivers showed comparatively greater activation in left posterior superior and middle temporal gyri and right premotor cortex. Notably, these differences in brain activity were not related to general timing ability, as they occurred during the control sequences in which temporal discrimination thresholds for the two groups were similar.

At first glance, one possible explanation of the activation differences between groups could have been the degree of musical training. However, we found no evidence for this in our data. Even at a greatly reduced statistical threshold, areas correlated with musical training were distinct from the areas correlated with beat perception

Table 2
Regions of interest that show differential activation between strong beat-perceivers and weak beat-perceivers.

	Region of interest (ROI)	Center of mass	Brodmann area
Strong>weak ROIs	L inferior frontal gyrus	−52 13 14	Area 44
	L supplementary motor area	−8 2 72	Area 6
	L medial premotor cortex	−30 −4 55	Area 6
	L insula/ventrolateral prefrontal cortex	−28 24 1	Area 47
Weak>strong ROIs	R premotor cortex	54 −12 50	Area 6
	L superior temporal gyrus	−55 −35 11	Area 22/42
	L middle temporal gyrus	−48 −46 19	Area 41

The location, Brodmann area, and center of mass are given for each region.

Activation differences between Strong beat and Weak beat perceivers
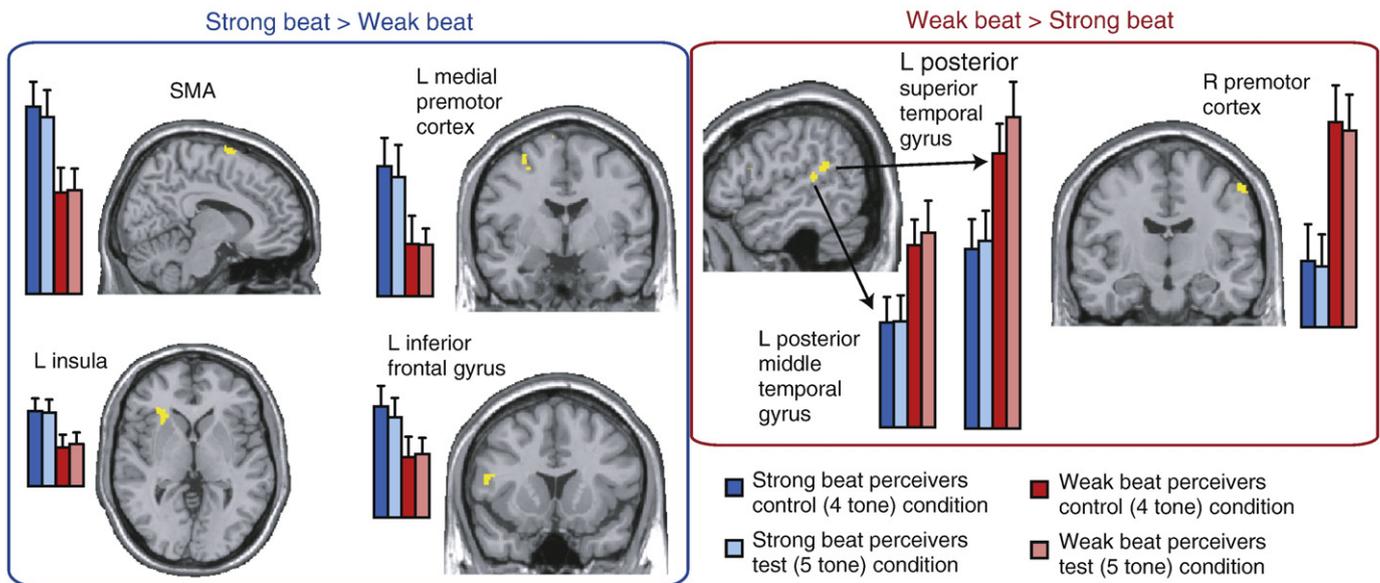

Fig. 4. Areas in which activation differences between strong beat-perceivers and weak beat-perceivers are observed. Mean activation from the first session for each region of interest is shown in the graphs. Blue bars represent activity for strong beat-perceivers; red bars represent activity for weak beat-perceivers, with darker colors representing the control condition and lighter colors representing the test condition. Activation is in arbitrary units, and error bars represent standard error of the mean. Regions of interest are shown on a standardized brain in MNI space.

strength, w (i.e., the areas where strong beat-perceivers and weak beat-perceivers differed). Another possible reason for the differences between the two groups could have been that weak beat-perceivers engaged in a beat-based mode of timing using a 300-ms (rather than 600-ms) beat period, and the difference in periods used gave rise to activation differences. Although we cannot entirely rule out this possibility, it seems unlikely for at least two reasons. First, if this were the case, there is no reason to expect the activation differences between the two groups for the control sequences when there were no differences in behavior. Second, the implied 600-ms beat is close to the preferred tempo of individuals in the tested age range and thus would be expected to yield a much stronger sense of a beat than would 300 ms (Drake et al., 2000; McAuley et al., 2006b).

Another (not mutually exclusive) view of the group differences may be in terms of a local versus global distinction, rather than a weak beat versus strong beat distinction. From this perspective, local listeners use the two smaller (more 'local') intervals as comparators for the final interval, whereas global listeners use the combined intervals to create a more global percept (the 'beat') against which they compare the final interval. Interestingly, this view predicts that the differences between groups might be expected to persist across stretching or shrinking of the temporal intervals used in the stimuli. That is, local listeners should show similar response patterns if the intervals are, for example, 500 and 1000 ms, rather than the 300 and 600 ms. If w is an index of beat sensitivity, however, the prediction is different. Beat sensitivity is thought to be maximal around 600 ms (Parncutt, 1994; Drake et al., 2000; London, 2004). As the intervals become much longer or shorter than the accepted beat range, strong beat-perceivers should show decreases in w (as a beat is less likely to be perceived at the more extreme ranges). At interval ranges well outside the beat range, a behavioral distinction between groups would weaken, as strong beat-perceivers would be expected to respond similarly to weak beat-perceivers. Pilot data currently under collection supports the latter prediction, but these theories remain to be fully investigated.

Previous work on discrimination of auditory sequences with and without a beat has implicated both the basal ganglia and SMA in

beat processing (Grahn and Brett, 2007; Grahn and Rowe in press). In the present study we observed greater SMA activity for strong beat-perceivers compared with weak beat-perceivers, but we did not observe significant basal ganglia activation differences between groups (though the basal ganglia were significantly active in the all stimuli–rest contrast). One potential reason for the difference between our findings and earlier work is that previous studies found robust basal ganglia activity when comparing regular sequences in which a beat was perceived to irregular sequences in which no beat could be perceived (Grahn and Brett, 2007). The stimuli in the present study, however, were always regular; each stimulus was therefore highly predictable, apart from the final onset (the first 2.1 s of every sequence was one of two identically timed patterns). Irregular stimuli were not employed, thus, the contrast in previous work that reveals robust basal ganglia activity (regular beat–irregular non beat stimuli) does not exist. Previous work also could not distinguish whether the basal ganglia response was due to extracting/finding the beat, or predicting future onsets in accordance with the beat after it has been extracted (Grahn and Brett, 2007). If the basal ganglia role is in prediction, rather than extraction, then, in the current study, the basal ganglia may be equally able to provide predictions about incoming stimuli in both strong and weak beat-perceivers. For the task used in the present study, neither mode of timing necessarily makes a better or stronger prediction than the other.

These results can be interpreted within the framework of the striatal beat frequency model (Matell and Meck, 2004; Buhusi and Meck, 2005), in which timing is based on the coincident activation of neurons in the basal ganglia by a distributed set of cortical neural oscillators (potential locations include the SMA and prefrontal areas). These cortical oscillators are assumed to be synchronized at timing onset, and to continue activity throughout the to-be-timed interval. From this perspective, both strong and weak beat-perceivers generate predictions about the end of the sequence (against which they measure the actual perceived interval) resulting in similar levels of basal ganglia activity in both groups; however, greater 'tuning into' into the implied beat by strong beat-perceivers

may involve the recruitment and entrainment of specific sets of cortical oscillators. Taking this view, what differs between the groups is not necessarily inherent difference in the ability to feel a beat (or by extension, a rhythm), but rather the bias to tune into that beat when it is weakly implied in the stimuli. The lack of a strong correlation between w and musical training, self-reported rhythm ability, or amount of music listening provides some additional support that differences in w are not necessarily differences in rhythmic ability. Further work is needed to disentangle how beat perception, predictability, and individual differences influence basal ganglia activity.

The results appeared suggestive of laterality effects, with left hemisphere structures playing a larger role than right hemisphere structures for strong beat-participants. Specific tests of laterality, however, show that these differences are generally quantitative, not qualitative. Activation patterns were not significantly different between most ROIs and their respective homologous contralateral structures (apart from the right premotor cortex effect in the weak beat-perceivers). Laterality findings in the literature are mixed: several neuroimaging and lesion studies find no laterality effects in perceptual timing tasks (Liegeois-Chauvel et al., 1998; Dennis and Hopyan, 2001; Grahn and Brett, 2007), whereas others have found evidence for a greater involvement of left hemisphere structures (Mavlov, 1980; Alcock et al., 2000a; Samson et al., 2001) and yet others for right hemisphere structures (Penhune et al., 1999; Kagerer et al., 2001). A recent review of perceptual timing studies suggests that differences between left and right activations reflect differential engagement of implicit versus explicit perceptual timing processes (Coull and Nobre, 2008), with greater right-sided activity for explicit timing, and greater left-sided activity for more implicit timing. In one study, this laterality difference was observed even when the stimuli were identical (temporally predictable rhythmic speech patterns), but the task required either implicit or explicit processing of the stimuli (Geiser et al., 2008). These findings suggest that in the current study, strong beat-perceivers may rely more on implicit beat perception to do the task, and consequently show increased activity in left hemisphere structures, whereas weak beat-perceivers, who engaged in a more explicit comparison of the intervals in the stimuli, show greater right-sided activity.

Coull and Nobre also point out that motor prediction is predominantly left-lateralized (for a review, see Serrien et al., 2006), suggesting neural overlap between implicit perceptual timing and predictive motor timing. Interestingly, motor actions (e.g., tapping) are a common spontaneous manifestation of beat perception in natural settings. It is therefore suggestive that strong beat-perceivers show greater SMA and left inferior frontal activation than weak beat-perceivers: activation in these areas has been observed during motor imagery and subvocalization (Binkofski et al., 2000; Kawashima et al., 2000), and during auditory imagery of sequences (Halpern and Zatorre, 1999). Again, this is not evidence that strong beat-perceivers necessarily would be better at rhythm processing, but rather that they have a stronger bias to feeling a beat.

Broader implications

In the past decade, there has been a notable increase in research on the neural bases of timing (Gibbon et al., 1997; Harrington et al., 2004; Ivry and Spencer, 2004). One area of active discussion concerns the location and functional characteristics of a putative central 'clock' mechanism. In this regard, much of the behavioral focus has been on the timing of isolated (single) durations in human and non-human animals (Hills, 2003; Lejeune and Wearden, 2006). Two general assumptions in this work have been that (1) human and animal timing involve similar neural mechanisms and (2) the functional characteristics of the internal clock are the same whether timing an isolated duration, such as a stoplight, or dancing to music, even

though the latter requires perceiving a periodic beat, while the former does not. Central to both assumptions is the view that the internal clock is best conceptualized as a pacemaker-accumulator mechanism that measures time according to the number of 'ticks' that accumulate over a given temporal interval (Treisman, 1963; Gibbon et al., 1984; Meck, 2003).

Although the literature generally provides support for pacemaker-accumulator (interval) timing models, these models do not provide an adequate account of human temporal behavior for tasks involving time judgments in extended rhythmic contexts (McAuley and Jones, 2003; Jones and McAuley, 2005). To this end, recent proposals of beat-based (entrainment) mechanisms, in which regular periodicities play a prominent role in guiding temporal behavior, have provided a useful alternative (Large and Jones, 1999; McAuley and Jones, 2003). Moreover, because there is relatively little evidence that animals spontaneously synchronize to the beat in the way that humans do (Wearden, 1988; Bispham, 2006; Fitch, 2006), some of the support for interval timing models may be the result of an over-reliance on animal data.

Our view is that timing engages both beat-based and interval-based timing circuits. In some cases these circuits can have a redundant function; for example, the present tempo judgment task and many others in the literature could be accomplished in either a 'beat' or 'interval' mode (Ivry and Hazeltine, 1995; Pashler, 2001; McAuley and Jones, 2003). From this perspective, the present research suggests that when either mode can be used to accomplish the task, individuals differ in their tendency to spontaneously engage in one or other of these timing modes. Individuals identified as strong beat-perceivers more readily engaged beat-based circuits (a beat-based mode) when judging sequence timing than did weak beat-perceivers.

Additional support for the existence of beat-based timing distinct from interval-based timing comes from behavioral data showing improved timing in sequences where a beat is perceived compared to matched sequences in which no beat can be found (Essens and Povel, 1985; Grahn and Brett, 2007). Thus, it is plausible that most individuals can engage in either interval-based timing or beat-based timing, depending on the task at hand, but that when the sequences can be timed using either mechanism, certain individuals are more likely to engage in beat-based timing than others.

One intriguing possibility for future research offered by this work is that individuals with neurological disorders or diseases that affect brain areas involved in perceiving a beat (e.g., Parkinson's disease) may evidence shifts in spontaneous timing mode; for some tasks, these individuals may show no timing deficits because the task can be accomplished in either a beat or interval mode. Initial support for a beat perception deficit in Parkinson disease was recently provided by Grahn and Brett (2009). Combining the tempo judgment paradigm investigated here with the proposed mathematical model that provides a continuous measure of beat perception strength may provide a behavioral marker to characterize and track disease progression.

In conclusion, we find that individual differences in behavioral bias toward beat perception correspond to activation differences in left cortical motor areas and insula, whereas the opposite bias is correlated with right premotor and posterior auditory cortex activation. We suggest that these cortical activation differences reflect the engagement of different neural timing mechanisms.

Acknowledgments

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