Ψ Psychology Press
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Lateralisation of non-metric rhythm

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There are contradictory results on lateralisation and localisation of rhythm
processing. Our aim was to test whether there is a hemispheric dissociation of
metric and non-metric rhythm processing. We created a non-metric rhythm stimulus
without a sense of metre and we measured brain activities during passive rhythm
perception. A total of 11 healthy, right-handed, native female Hungarian speakers
aged 21.3 ± 1.1 were investigated by functional magnetic resonance imaging
(fMRI) using a 3T MR scanner. The experimental acoustic stimulus consisted of
comprehensive sentences transformed to Morse code, which represent a non-metric
rhythm with irregular perceptual accent structure. Activations were found in the
right hemisphere, in the posterior parts of the right-sided superior and middle
temporal gyri and temporal pole as well as in the orbital part of the right inferior
frontal gyrus. Additional activation appeared in the left-sided superior temporal
region. Our study suggests that non-metric rhythm with irregular perceptual accents
structure is confined to the right hemisphere. Furthermore, a right-lateralised
fronto-temporal network extracts the continuously altering temporal structure of
the non-metric rhythm.

Keywords: Non-metric rhythm processing; Lateralisation; fMRI; Rhythm
perception.

Beyond language, the other structured auditory stimulus that plays a crucial role in human life is music. The nature of hemispheric specialisation for language and music processing is still a central issue. In contrast to the rigid distinction of the classical view (left/language; right/music), to date many findings have demonstrated that this hemispheric asymmetry is relative rather than absolute. However, the dominant role of the left hemisphere in speech processing and the dominant role of the right hemisphere in music processing have been highlighted.

In contrast to music, language comprehension is primarily processed in the left hemisphere, including separate circuits for phonological, syntactic, and semantic information (Dapretto & Bookheimer, 1999; Friederici, Meyer, & von Cramon, 2000; Friederici, Rüschemeyer, Hahne, & Fiebach, 2003) whereas sentence-level prosody ("speech melody") might recruit the right-hemispheric fronto-temporal network (Meyer, Alter, Friederici, Lohmann, & von Cramon, 2002). Processing of music is based on distinct neural processes corresponding to the basic perceptual features (Levitin, 1999; Pierce, 1983). It has been suggested that the left hemisphere appears to be devoted to processing of integer-based rhythm (Sakai et al., 1999) while there is a clear tendency for right-asymmetric activation in frontal and temporal lobe sites for pitch and melodic contour processing (Zatorre, Evan & Meyer, 1994). Lesion studies on perception of timbre have reported that right temporal lobe lesions result in greater impairment in timbre discrimination than left temporal lobe lesions (Milner, 1962; Samson & Zatorre, 1994). However, a recent neuroimaging study indicates that focal regions of the left and right temporal lobes are also involved in timbre processing (Menon et al., 2002).

In general, the temporal features of acoustic perception can be examined both macroscopically (on the scale of seconds) and microscopically (on the scale of milliseconds). Several studies have investigated the lateralisation of auditory processing from a microscopic perspective using signals with differing spectrotemporal characteristics supporting a model in which the left hemisphere is sensitive to temporal stimulus attributes (Robin, Tranel, & Damasio, 1990; Sidtis & Volpe, 1988; Yamasaki et al., 2005), while the right hemisphere is more sensitive to spectral stimulus attributes (Alcock, Wade, Anslow, & Passingham, 2000; Jamison, Watkins, Bishop, & Matthews, 2006; Johnsrude, Penhune, & Zatorre, 2000; Robin et al., 1990; Sidtis & Volpe, 1988; Zatorre & Belin, 2001). Conversely, other investigations have argued that both hemispheres are sensitive to the temporal structure of speech or non-speech sound stimuli. These approaches are in accord with the AST ("asymmetric sampling in time") hypothesis. This model assumes that auditory fields in the two hemispheres prefer different temporal integration windows. This hypothesis proposes that acoustical processing of spoken language is elaborated asymmetrically in the time domain: left auditory

areas preferentially extract information from short temporal integration windows (rapidly changing cues, 20–50 Hz), while the right hemisphere homologues preferentially extract information from long integration windows (slowly changing cues, 4–10 Hz) (Poeppel, 2003). It is further proposed that the posterior portion of the auditory association cortex is the candidate region that accommodates this temporal processing.

From a macroscopic perspective, rhythm, which could be defined as a general sense of movement in time that characterises our experience of music (Apel, 1972), takes place on the scale of seconds or longer. There are contradictory results in the literature on rhythm production and perception. Previous studies with brain-damaged patients on neural processing of rhythm have found a right hemispheric contribution to rhythm processing (Kester et al., 1991; Penhune, Zatorre, & Feindel, 1999; Peretz, 1990; Samson, 2003), although others have suggested left hemispheric dominance for rhythm perception (Polk & Kertesz, 1993; Robin et al., 1990; Sherwin & Efron, 1980). Many rhythm studies have used tapping tasks involving active behavioural responses corresponding to the stimulus pattern (Desain & Honing, 2003; Krampe, Kliegl, Mayr, Engbert, & Vorberg, 2000) and suggested that premotor areas, SMA, preSMA, and the cerebellum are engaged (Rao, Mayer, & Harrington, 2001; Schubotz, Friederici, & Von Cramon, 2000). Investigation of musicians could supply evidence for enhanced and altered activation patterns in right dorsolateral prefrontal cortex and right inferior frontal gyrus as well in response to synchronisation to varying levels of rhythm complexity in contrast to non-musicians. These regions are also involved in working memory function for music (Petrides, 2005). By means of these results it could be assumed that participants with long-term musical training have a higher capacity to monitor and retrieve the temporal interval duration in rhythmic sequences (Chen, Penhune, & Zatorre, 2008). However, the correlates of passive rhythmic perception without motor reproduction are less understood. Recent neuroimaging studies have suggested that musical training leads to the employment of left-sided perisylvian brain areas during passive rhythm perception (Limb, Kemeny, Ortigoza, Rouhani, & Braun, 2006). Another fMRI study has also confirmed the left hemisphere contribution in rhythm perception, but only in the case of metric rhythm processing. This result has suggested that there are two neural representations for rhythm depending on the interval ratio, which correspond to metric and non-metric representations (Sakai et al., 1999). These results are in line with the previous psychological studies which have shown that integer-based rhythm can be reproduced more precisely and easily than rhythms with larger intervallic values or non-integer values (Povel, 1984; Povel & Essen, 1985).

The inconsistency among these studies may be attributable to using various types of rhythms that have also contained aspects of pitch and

melody in some cases, thus making the definition of neural substrate for rhythmic processing more complicated. The specialisation and complex interactions between the left and the right hemispheres in the perception of temporally structured auditory stimuli still require further research. The aim of this study is to investigate neural correlates of passive non-metric rhythm perception. According to the previous studies, we might assume that perception of non-metric rhythms is related to the right hemisphere in the case of non-musician participants. It can be assumed that the processing of metric and non-metric rhythm might apply at least partly different strategies, leading to different activation patterns.

With non-metric rhythm, time intervals are not fractions or multiples of an event or beat, and each duration simply adds to the other. Extracting regularities from temporal sequences of events is characteristic to human cognition. Behavioural evidence indicates that the identification of patterns within event sequences is automatic and obligatory (Canfield & Haith, 1991). The human brain tries to determine patterns in sequences of events, regardless of whether a pattern truly exists, in order to predict future events. Bearing in mind these phenomena we assume that non-metric rhythm processing might activate such mechanism.

To produce non-metric rhythm without a sense of metre we transformed Hungarian sentences into Morse code, to provide irregular perceptual accent structure to participants who were not familiar with Morse code.

METHOD AND MATERIALS

Participants

The participants in this experiment were 11 healthy, right-handed, non-musician women with Hungarian native language. Their mean age was 21.3 ± 1.1, and they had no history of speech or hearing difficulties. They were all undergraduate medical students, without knowledge of Morse code. Handedness was determined by the Edinburgh Handedness Inventory. All experiments on human participants were conducted in accordance with the Declaration of Helsinki. An approval by the Institutional Review Board was obtained. Written informed consent was obtained from all participants prior to the examinations.

fMRI paradigm

The experimental stimuli consisted of two types of sounds: (i) comprehensive Hungarian simple sentences transformed to Morse code, encoding characters digitally by combinations of short and long signs (dots and dashes) with

varying longitude of intervals (on average at a speed of 3/s; intra-character gap 70 ms; gap between letters 230 ms; gap between words 750 ms). These sequences had non-integer intervallic ratio and were employed as a non-metric rhythm (test condition), and due to the different duration of the signs the sequences had irregular perceptual accent structure but without higher-level periodicity. We expected that this stimulus would enhance listeners' subjective perception of the rhythm of sequences and keep their attention at the same level during the whole task. (ii) Monotonic Morse sounds (repeated dots on average at a speed of 7/s) with equal inter-stimulus interval, known as an isochronic sequence, served as baseline. Identical inter-onset intervals provided a regular pulse and did not cause a sense of metre. The tones had a duration of 70 ms and the onset interval was 70 ms.

The frequency range and volume of the Morse sounds were kept at a constant level, whereas the signal sequence had a complex temporal structure. Both types of sound stimuli (Morse-coded text and baseline sounds) had similar spectral complexity with a frequency peak at 700 Hz.

Acoustic stimuli were presented binaurally to the participants through a commercially available fMRI-compatible system (Siemens AG, Erlangen, Germany), and were presented at a comfortable listening level that was clearly audible above the MRI scanner noise. The tone frequency was the same during both task and baseline conditions. Sound pressure level at the participant's ear was approximately + 65 dB.

Experimental design

Participants were instructed to listen passively to the sounds and their alteration. Seven cycles of baseline (isochronic sequence) and test (non-metric rhythm with irregular perceptual accent structure) stimuli were presented and each condition lasted 20 s (block-design), total design length was 4 min 40 s. Participants were told not to move and to keep their eyes closed during the whole investigation.

Data acquisition

Functional imaging was performed in a 3T MR scanner (Siemens Magnetom Trio, Simmens AG, Erlangen, Germany) with 12-channel phased array TIM head coil for radio frequency reception. We used a standard EPI sequence to obtain functional MR images with the following parameters: TR: 2000 ms; TE: 36 ms; voxel size: $2 \times 2 \times 3$ mm^3; FoV: 192×192 cm^2; 23 axial slices with a thickness of 3-mm and 1-mm gap; $80°$ flip angle; 1446-Hz receiver bandwidth. We acquired 280 volumes per session. Anatomical images were acquired using a magnetisation-prepared rapid gradient echo (MP-RAGE)

sequence (TR: 1900 ms; TE: 3.44 ms, 9° flip angle, 180-Hz receiver bandwidth, $0.9 \times 0.9 \times 0.9$ mm^3 isotropic voxel size).

fMRI data processing

Data analysis was performed using the software package SPM5 (Wellcome Department of Imaging Neuroscience, University College of London, UK) (Friston et al., 1995). The first three scans for each session were excluded from data analysis because of the non-equilibrium state of magnetisation. For each participant, images underwent motion correction, and each volume was realigned to the mean of the series. The anatomical scan was then co-registered to the mean of all functional images, previously corrected for intensity inhomogeneities through the bias correction algorithm implemented in SPM5. EPI images were then normalised adopting the MNI152 template, supplied by the Montreal Neurological Institute and distributed with the spm5 hig. Finally, images were smoothed with Gaussian kernel of 5 mm. High-pass filtering (0.0078 Hz) was applied to remove low-frequency drifts in signal.

Each participant's data were analysed by the general linear model (GLM) (Friston et al., 1995). The GLM was fitted to the individual data, with the experimental blocks modelled as a boxcar functions and convolved with the canonical haemodynamic response function (HRF). Individual models were separately estimated and contrasts were defined in order to pick out the effects of test condition. The first-level analysis was carried out for the following contrast: non-metric rhythm with irregular perceptual accent structure (auditory presented Morse-coded text) versus isochronic sequence (monotonic Morse sounds).

First level-analysis results were then entered into the second-level analysis using a one-sample t-test. The statistical significance levels were set to $p = .01$, FDR-corrected for multiple comparisons. Concurrent activation of a cluster of > 5 neighbouring voxels was assumed to represent a true spot of activation.

Characterising right–left asymmetry

We calculated an asymmetry index (AI) for the whole brain activation as used in earlier works (Auer et al., 2009; Janszky et al., 2004):

AI = (activation in the *left* hemisphere – activationin the *right* hemisphere)
/total activation

Thus positive values indicate that the activation is more pronounced on the left than on the right side. AI = 1 corresponds a complete left-sided lateralisation, AI = − 1 a complete right-sided speech lateralisation. According to previous

fMRI studies (Janszky et al., 2004; Springer et al., 1999) AI > 0.2 suggests a left-sided dominance and AI < − 0.2 suggests a right-sided dominance of a particular function.
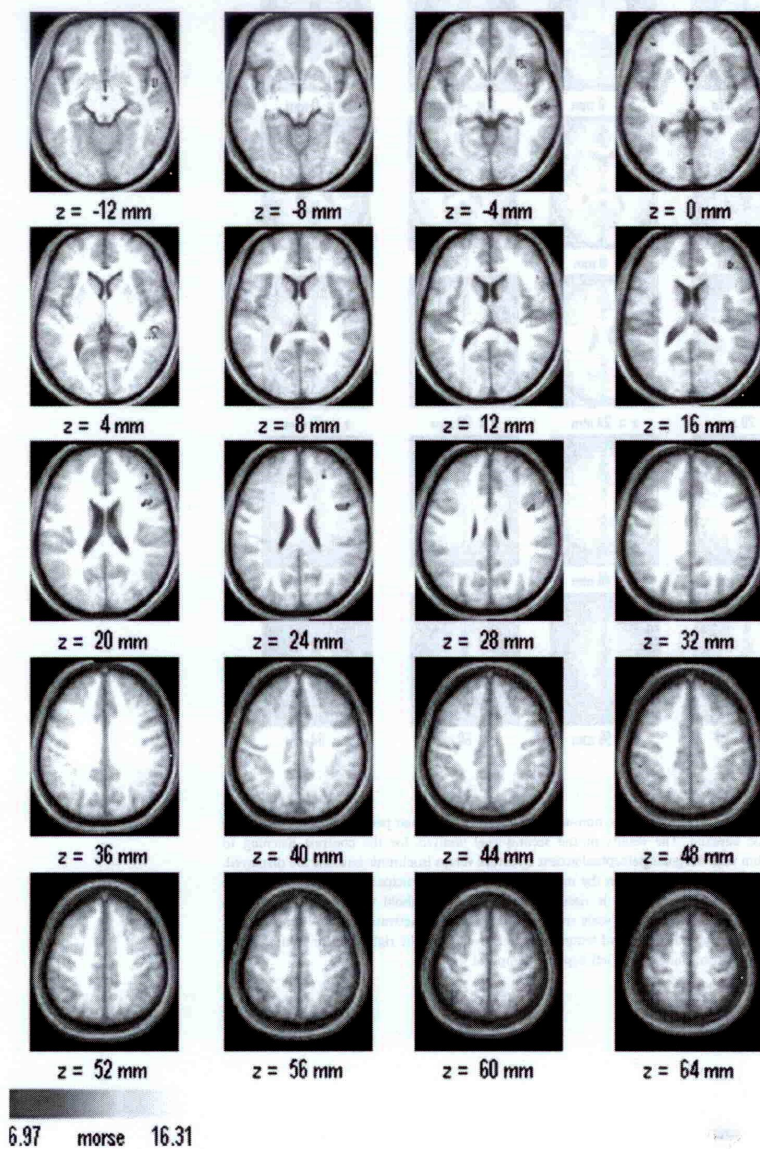
RESULTS

The comparison of passive perception of non-metric rhythm vs the isochronous baseline showed significant brain activations (presented in Figure 1 and listed in Table 1). Activations were primarily found in the right hemisphere, in the posterior parts of the right-sided superior and middle temporal gyri and the right temporal pole as well as in the orbital part of the right inferior frontal gyrus. Additional activation appeared in the left-sided superior temporal region. The asymmetry index (AI) was –0.77, indicating a strong right-sided dominance. We also tested the reverse comparison, in order to search for regions more activated during baseline than task. This "reverse" comparison did not reveal any activated areas (see Table 1 and Figure 1).

DISCUSSION

To examine the lateralisation and localisation of perception of the complex, non-metrically structured, auditory stimuli, we aimed to determine brain structures showing activation during listening to Morse code, which represents a non-metric rhythm with irregular accent structure. Morse-coded text was made by the rules of the native language, resulting in a structured complex auditory stimulus that might be processed as a non-metric rhythm in naive participants.

The main finding of this fMRI study is in concordance with our working hypothesis. Activation caused by non-metrically structured auditory stimuli with irregular perceptual accent is lateralised to the right hemisphere including the orbital part of the right inferior frontal gyrus (IFGr) as well as the right middle and superior temporal gyrus (STGr, MTGr) and right temporal pole. A considerably less extended activation was found in the left-sided STG.

Povel and Essen (1985) argued that there are two types of representation of rhythm: metric and non-metric. Metric rhythm has interval durations of integer ratios relative to the shortest interval, and this type of rhythm is reproduced with higher accuracy and more easily in a tapping task than in non-metric rhythm (Povel & Essen, 1985). Moreover, perception of metric rhythm often causes spontaneous synchronised movements. The experience of feeling the beat during perception of metric rhythm, which is the most common in music, and synchronisation of body movement with it, are consistent with behavioural- and neuropsychological-based motor theories of rhythm perception (Todd, O'Boyle, & Lee, 1999). Beat perception and

Figure 1. Activation during listening to non-metric rhythm with irregular perceptual accent structure versus isochronic baseline. The results of the second-level analysis for the contrast listening to non-metric rhythm with irregular perceptual accent structure versus isochronic baseline are displayed. Activations are shown superimposed on the mean image of the 11 participants' T1 images. Displays follow neurological convention (right is right). The statistical threshold was $p < .01$ (corrected), resulted in $T = 6.97$. The colour-coded scale represents the T values. Activations were found in right superior and middle temporal gyrus and temporal pole as well as in the right inferior frontal gyrus. Some activation was also found in the left superior temporal gyrus.

TABLE 1
Brain regions activated by listening of non-metric rhythm with irregular perceptual accent structure vs isochronic baseline

Hemisphere	Lobe	Gyrus	Brodmann Area	Volume	Coordinates
		Middle temporal	21	168 mm^3	62, −36, −12
		Middle and Superior temporal	21, 22	96 mm^3	60, −30, 0
Right	Temporal	Superior temporal	21	108 mm^3	62, −22, −4
		Superior temporal	22	276 mm^3	52, −32, 4
		Superior temporal	38	108 mm^3	54, 0, −12
	Frontal	Inferior frontal	47	108 mm^3	36, 18, −4
Left	Temporal	Superior temporal	21, 22	108 mm^3	−54, −40, 8

For each activated cluster, the table lists the cluster extent and the anatomical localisations. Stereotactic coordinates (x, y, z in mm) in MNI space are also given for representative local maxima in each anatomical subdivision.

movement synchronisation are immediate, effortless, and automatic processing of timed acoustic patterns. It is also known that rhythm with integer intervallic ratio (metric) and regular perceptual accent structure can induce the strongest beat perception in participants (Grahn & Brett, 2007). An accent can induce a beat intensification highlighted by the manipulation of physical properties of sound, such as intensity or duration (Lerdahl & Jackendoff, 1983). In general, metre (regular accent structure) refers to the emergent temporal structure due to regularly accented events in auditory sequences; however, in sequences without regular accented events, listeners will not be able to extract the metre, so the perception of rhythm and metre are interdependent. In metric sequences the parallel presence of a regular accentuation enables a more accurate perception and encoding of rhythms, and can facilitate movement synchronisation with rhythm by inducing strong beat perception (Parncutt, 1994; Patel, Iversen, Chen, & Repp, 2005). According to the motor theory of rhythm perception, many imaging studies on rhythm processing have described the activation of motor cortices including premotor, preSMA, SMA, cerebellar areas, and basal ganglia. It has been well established that not only were these regions active in movement synchronisation tasks with auditory rhythms (Chen et al., 2008; Chen, Zatorre, & Penhune, 2006; Rao et al., 1997), but they also showed activation during rhythm perception tasks (Rao et al., 2001; Sakai et al., 1999; Schubotz et al., 2000). These areas have also been observed as active in motor preparation tasks (Deiber, Ibanez, Sadato, & Hallett, 1996). As for the basal ganglia and cerebellum, these regions may play an important role in time perception and motor timing (Harrington, Haaland, & Hermanowicz, 1998;

Ivry, 1996; Ivry & Hazeltine, 1995; Ivry & Schlerf, 2008) and may contribute to our sense of tempo as well (Levitin & Cook, 1996).

It can be suggested that a natural link between the auditory and motor systems may exist, and that beat perception innately relates to automatic rhythmic motor responses. A direct relation between movement and beat perception has been found in infants (Phillips-Silver & Trainor, 2005), confirming the role of the motor area. When 9-month-old infants listen to metric and non-metric rhythmic patterns, their ability to detect rhythmic changes is evident only in the context of metric patterns (Bergeson & Trehub, 2006). It means that the metric rhythm preference can be identified in infants relatively early in the developmental phase. These results attest that rhythm is represented by default in a metric form that is also favoured by previous psychological studies (Povel, 1984; Povel & Essen, 1985), and it appears that the capability to detect beat in rhythmic sound sequences is already functional at birth as well (Winkler, Háden, Ladinigd, Szillere, & Honing 2009). An internal temporal reference frame is likely to exist, which may prefer the processing of small-integer ratio temporal intervals, irrespectively of musical training. Moreover, the presence of regular accent structure can shape our perception and expectations of the rhythm within this temporal framework (Handel, 1998; Ivry & Hazeltine, 1995; Pöppel, 1997; Sternberg, Knoll, & Zukofsky, 1982; Povel, 1984; Povel & Essen, 1985).

From the evolutionary point of view, it seems that the ability to perceive a beat in music and synchronisation of movements is not a unique human phenomenon, and this may raise a further questions over the evolution of human music (Schachner, Brady, Pepperberg, & Hauser, 2009; Patel, Iversen, Bregman, & Schulz, 2009).

These results may suggest that this system uses a prediction mechanism that is used for the preparation of motor responses. The brain could predict the patterns in sequences of events, and it may depend on the predictability of the stimuli as well. The predictable nature of the stimuli could be varied at different levels; one of them consists of metricality (integer or non-integer ratio) and the perceptual accent structure. The most predictable rhythm stimuli could be metric rhythm with a regular perceptual accent structure, and this type of rhythm could also induce the strongest beat perception in participants. It could explain why activation of motor areas has often been observed during rhythm processing. We assume that here we could present indirect evidence to support this view, because we could not observe activation in any motor regions mentioned before, our stimulus is unpredictable (non-metric rhythm with irregular accent structure), and it is not a beat-inducing rhythm. It can be assumed that the processing of metric and non-metric sequences with varying levels of accent structure may apply an at least partly different strategy and as a result of this may employ a partly different set of neural networks. A recent neuroimaging study has

also confirmed that metric and non-metric rhythm processing can recruit partly different neural networks, and non-metrical representations lateralise to the right hemisphere (Sakai et al., 1999). However, it could be possible that different activation networks for rhythm with integer and non-integer ratio in the latter-mentioned study were influenced by the varying level of regularity of the perceptual accent structure (sense of metre). Therefore, during stimulus production, we controlled carefully their properties. In line with the aim of our study we used intervals related to non-integer ratio. It is well known that metric rhythm with regular accent structure is the most beat-inducing rhythm. However, studies have focused much less on the point of whether the regular accent structure alone is able to induce a beat, or whether subjective regularising phenomena related to non-metrical rhythm could provoke it. We therefore generated a non-metrical rhythm with irregular perceptual accent structure to avoid these disturbing effects. Furthermore, we used seven similarly structured but different sequences as a test condition in order to prevent participants from gaining any impression about the relationships between the intervals, because this may lead to the development of subjective regularising phenomena. Taking these together, we could examine non-metric rhythm processing itself. We assume that our right-lateralised fronto-temporal network takes part in a suprasegmental auditory sequence analysis as well. It has been well known that the primary auditory cortex is involved in early stages of processing signal parameters such as pitch, duration, intensity, and spatial location, whereas more complex feature extraction, including temporally distributed patterns of stimuli, is performed by the posterior region of secondary auditory cortices. Our stimuli represent temporally complex, non-metric sequences distributed in a long temporal integration window without sense of metre and any melodic aspects. We suggest that our activation in right posterior STG may reflect the slow changes of temporal structure of the stimuli used in our study. This result is in accordance with the AST (asymmetric sampling in time) hypothesis. This hypothesis proposes that acoustical processing of speech signal is elaborated asymmetrically in the time domain: left auditory areas preferentially extract information from short temporal integration windows, while the right hemisphere homologues preferentially extract information from long integration windows. It is proposed that the posterior portion of the auditory association cortex is the candidate region that accommodates this temporal processing. This localisation is in line with our results. Moreover, our findings may suggest that the right posterior STG is associated with not only coding the suprasegmental speech rhythm but also the slow temporal features of a non-metric rhythm. The other main region in which we found activation was the orbital part of right inferior frontal gyrus (BA 47). The frontal regions have also been known as a key structure for working memory (Courtney, Peti, Maisog, Ungerleider, & Haxby, 1998;

Courtney, Ungerleider, Keil, & Haxby, 1997) and monitoring of memorised information (Petrides, 1994, 2005). We assume that non-metric rhythm might require continuous monitoring and encoding of the different time intervals, as opposed to a metric rhythm, and this could be the cause of the observed activation in the right inferior frontal region. This assumption was confirmed by a previous imaging study on rhythm representation (Sakai et al., 1999), which found frontal activation only in the case of non-metric rhythm. The presence of activation in the right frontal region only in the case of non-metric rhythm, and our similar findings, could support the assumption that non-metric rhythm with irregularly changing time intervals may require a more explicit, continuous monitoring strategy than metric rhythm. We suggest that right inferior frontal cortex may participate in continuous mapping by temporal structures of changes in non-metric rhythm. Activation of this region has been reported in studies that were focused on processing of temporal coherence of music (Levitin & Menon, 2003; Poldrack et al., 1999). These argue that Brodmann area 47 is a brain area that organises structural units in the perceptual stream to create larger, meaningful representation. These approaches suggest that there is a cognitive system dedicated to the on-line monitoring of temporal structural pattern (Huettel, Mack, & McCarthy, 2002). Our findings might reflect the aspect of long-range structure of our stimuli and the sensitivity of pars orbitalis for temporal structural incongruity. Our results suggest that the right STG and the right IFG compose a network specifically associated with coding, continuous monitoring, and reconciliation of the irregularly changing time intervals in auditory sequences.

Furthermore, there is also a considerable amount of research that has associated the right anterior superior temporal cortex (right temporal pole, BA 38) with the representation of complex melodies and harmonies (Brown, Martinez, Hodges, Fox, & Parsons, 2004; Patterson, Uppenkamp, Johnsrude, & Griffiths, 2002) as well as in the perception of non-speech vocal sounds (Belin, Zatorre, & Ahad, 2002). We might argue that this region could also be involved in certain involuntary comparative processing while participants attend to setting the heard, atypical, non-metric auditory sequences against the implicit representation of the typical metric rhythmic features.

Three previous studies investigated the functional anatomy of auditory perception of Morse-coded text. In an early study before the modern neuroimaging era, Papcun, Krashen, Terbeek, Remington, and Harshman (1974) dichotically presented Morse code signals to Morse code operators and to naive participants. They showed that, if the stimuli were longer than seven elements, the naive participants showed left ear superiority (a presumed activation of the right hemisphere). These results are consistent with ours. In contrast to our study, Maier, Hartvig, Green, and Stodkilde-Jorgensen (2004)

reported that Morse code operators showed predominantly left-sided activation of the frontal and temporal perisylvian language areas and prefrontal cortex as well as premotor cortex during listening to Morse-coded auditory texts. The main difference between that study and the present work is that their participants were Morse operators—thus they knew Morse code and thus the stimulus had semantic components. This underlies the sensitivity of the left-sided perisylvian region to the semantic component of auditory stimuli. Recently, Schmidt-Wilcke, Rosengarth, Luerding, Bogdahn, and Greenlee (2010) have investigated the relationship between changes in neural activity pattern and changes in grey matter density associated with learning, in healthy participants who learned to resolve Morse code after Morse code training. Schmidt-Wilcke et al. have provided a clear evidence for neural plasticity associated with the newly acquired skill.

Summarising, our study suggests that perception of non-metric rhythm with irregular perceptual accent structure is confined to the right hemisphere. Furthermore, the extraction of the continuously altering temporal structure of non-metric rhythm takes place in the right lateralised fronto-temporal network.

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