

Hemispheric Lateralization Effects of Rhythm Implementation During Syllable Repetitions: a fMRI Study

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Abstract

Rhythm in terms of the modulation of syllable durations represents an information-bearing feature of verbal utterances contributing both to the meaning of a sentence (linguistic prosody) as well as a speaker's emotional expression (affective prosody). In order to delineate the neural structures subserving rhythmic shaping of speech production, functional magnetic resonance imaging (fMRI) was performed during (a) monotonous syllable repetitions and (b) production of syllable triplets with lengthening either of the initial or final unit. The latter pattern of syllable durations can be considered the prototypical rhythmic structure contributing both to linguistic and affective prosody. A cognitive subtraction approach (rhythmic versus monotonous iterations) revealed activation of right-sided perisylvian areas (superior temporal gyrus, Broca analogon and adjacent premotor cortex) as well as contralateral subcortical structures (putamen and thalamus). Presumably, these responses reflect a right-hemisphere rehearsal mechanism of rhythmic patterns and left-hemisphere monitoring of verbal output.

1. Introduction

In addition to organized sequences of speech sounds (phonemes), verbal utterances are characterized by a distinct speech melody contributing to the meaning of a sentence (linguistic prosody) as well as to a speaker's emotional expression (affective prosody). For example, sentences spoken in a happy tone exhibit, as a rule, larger pitch fluctuations than sentences spoken in a sad mood. Besides intonation, the temporal pattern of verbal utterances, i.e. their rhythmic structure, contributes to these prosodic aspects of acoustic communication [1, 2]. Perceived rhythm of spoken language mainly reflects the modulation of syllable durations. Prolongation of syllabic units may enhance the affective emphasis of an utterance (e.g., "How beautiful ...", the initial syllable being lengthened) and participates in the specification of word accent and sentence focus. For example, the items "descént" and "décent" predominantly differ in the relative length of the two syllables. Or, prolongation of the marked vowel /e/ in "She delivered the message to Jénny, not Charles" focuses on the recipient of the respective action. Thus, rhythmic patterning of verbal utterances "carries a heavy information load in ordinary connected speech" [3].

Based on a series of case studies, Ross assumed the right hemisphere (RH) to mediate processing of speech prosody [4]. In analogy to the classification of the various syndromes of aphasia bound to left-hemisphere (LH) damage, expressive (motor) and receptive (sensory) variants of aprosodia were assigned to predominant right-sided anterior or posterior perisylvian lesions. However, subsequent clinical investigations

yielded, both in the domains of linguistic and affective prosody, discrepant data with respect to the neural systems underlying prosody perception and production (for a review see [5, 6]). Conceivably, the various relevant acoustic cues such as fundamental frequency (F0, the acoustic correlate of pitch), sound intensity (loudness) and the temporal processing of language (rhythm) are encoded by differently lateralized cerebral networks. For example, Van Lancker and Sidtis found subjects with left-hemisphere (LH) as well as RH lesions to perform poorly as compared to a non-damaged control group when asked to identify the emotional tone of spoken phrases [5]. Further error analyses disclosed, that the RH subjects failed to make use of pitch information but rather relied on durational cues in order to recognize affective tone. The LH group, in contrast, showed the opposite pattern. Thus, the language-dominant hemisphere predominantly might encode the temporal structure (rhythm) of spoken sentences. Studies on music perception also suggest that distinct neural networks support the extraction of tonal (pitch) and temporal information inherent to melodies [7, 8].

As far as speech production is concerned, distorted rhythm of verbal utterances has been observed in aphasia [5] as well as in apraxia of speech [9], both syndromes being bound to damage to the left hemisphere. Apraxia of speech is considered a dysfunction of higher-order aspects of speech motor control in terms of disrupted programming or planning of articulatory gestures. Most presumably, this constellation reflects damage to the lower motor cortex [10] or the anterior insula [11]. The clinical findings of impaired speech rhythm in motor aphasia and apraxia of speech suggest that the language-dominant hemisphere might support the temporal coordination of the vocal tract musculature prerequisite to the adjustment of syllable durations. However, compromised rhythm both during spontaneous speech production and reading concomitant with an inability to track the rhythm of familiar songs also has been observed following an exclusive RH lesion encroaching on the lateral and superior surface of the temporal lobe [12]. Furthermore, recent perceptual and acoustic data obtained from patients with either a LH or RH lesion indicate that rhythmic disturbances of speech production may be associated with damage to either side [13]. Both cerebral cortices, thus, may participate in the implementation of speech rhythm mediating, conceivably, different components of this process. In order to further elucidate this suggestion, the present study measured hemodynamic activation during production of rhythmically structured syllable iterations by means of functional magnetic resonance imaging (fMRI). The test material consisted in three-syllable phrases comprising either a lengthened initial or final syllable as well as a monotonous syllable pattern with equivalent durations of

each syllable. These sequences represent prototypical rhythmic patterns contributing both to linguistic (e.g. word accent and sentence focus) and affective prosody [14, 15]. Previous fMRI investigations had documented bilateral responses of the central motor system, i.e. motor cortex, supplementary motor area (SMA) and cerebellum, during repetitive syllable productions [16, 17]. Calculation of the contrast between the hemodynamic responses elicited by monotonous and rhythmic performance, respectively, should cancel activation bound to speech execution but spare the network specifically supporting rhythm processing.

2. Materials and Methods

The present study recruited healthy native German subjects (six females and six males; mean age = 27.3 years, range 22-50 years). All participants were right-handed as determined by means of a standardized inventory. None of them reported a history of any neurological or psychiatric diseases.

During the activation phases of this experiment subjects were asked to produce aloud repetitions of the syllable sequence 'pa-pa-pa' in three different temporal patterns: (a) monotonous without prosodic modulation, (b) rhythmic with lengthening of the final syllable ('pa-pa-paa') or the initial syllable ('paa-pa-pa'). In the baseline condition, i.e. passive listening to the respective syllable sequences, subjects were simply instructed to pay close attention to the stimuli and to refrain from any responses. Prior to the experiment, subjects performed each task outside the scanner to get acquainted with the test materials. Repetitions were paced via earphones by naturally produced and recorded syllable trains with a frequency of 3 Hz and a duration of 3 seconds each. Subjects utterances were recorded by means of a microphone during functional imaging to determine the beginnings and the ends of speech production, as well as the frequency and the modulation of the respective syllable train. Each production of the item 'pa-pa-pa' counted for three syllables. The counterbalanced trial order of the activation conditions enclosing the various syllables 'pa-pa-pa' with monotonous and rhythmic modulation and the baseline conditions were randomized and jittered by interspersing gaps, so that the onset-to-onset intervals amounted between 12 to 24 s.

Subjects lay supine in a 1.5 T whole-body scanner (Siemens Vision), their heads being secured by means of foam rubber in order to minimize movement artifacts. Twenty-eight parallel axial slices (thickness 4mm, gap 1mm) were obtained across the complete brain volume using an echo planar imaging sequence [18] (64x64 matrix, FOV 192mm, TE 39ms, TR 3s, alpha 90 deg, each measurement period about 3s). High-resolution images obtained with a T1-weighted 3D turbo-flash sequence (MP range; 128 sagittal slices, thickness 1.5mm, 256x256 matrix, FOV 256mm, TE 4ms, TR 9.7ms) served as the anatomical reference for functional images. Signal analysis (slice timing, realignment of functional images, coregistration with structural data, spatial normalization, smoothing with a 10 mm Gaussian filter) and statistical analysis of an event-related reference function was performed with SPM99 (Wellcome Institute of Cognitive Neuroscience, London). The data obtained during the activation phases were compared to the respective perceptual baseline across all subjects separately for the monotonous and the rhythmic tasks. In order to test for significant activation differences between monotonous and rhythmic syllable patterns, all possible pairwise subtractions of hemodynamic responses were performed within an One-Way-ANOVA as a subtraction analysis. All steps of statistical analysis included correction for

multiple comparisons at voxel level with a height threshold of $T > 4.70$ and an extent threshold of $k > 36$ ($p < 0.05$, corr.). For anatomical localization of significantly activated areas, the fMRI maps were superimposed on structural MR images averaged across all subjects. MNI coordinates of significant activation maps were converted to Talairach space using a matrix provided by MRC Cognition and Brain Sciences Unit.

3. Results

Categorical analysis of group data, i.e. comparison of the repetition tasks with perceptual baseline, revealed significant bilateral hemodynamic responses of supplementary motor area (SMA), motor cortex, thalamus, insula and cerebellum during all task conditions (Table 1). Given the limits of topographic analysis on the basis of gyral anatomy, the activation clusters at the level of the motor cortex seem to encompass both the premotor area, i.e. lateral aspects of BA 6, as well as the primary motor area (BA 4). Significant bilateral activation of the putamen was restricted to the rhythmic task (Fig. 3, Table 1). Subtraction analysis of the two different rhythmic tasks (lengthening of the first versus lengthening of the final syllable and vice versa) did not reveal significant hemodynamic activation patterns. Therefore, a cognitive subtraction analysis within an One-Way-ANOVA was performed comparing all rhythmic versus monotonous tasks and vice versa. Computation of activation differences between rhythmic and monotonous tasks resulted in significant hemodynamic responses at the level of the left-sided putamen and thalamus, as well as the temporal plane (BA 41 and 42), posterior parts of the superior temporal gyrus (BA 22), Broca-analagon (BA 44) and premotor cortex (BA6; Fig. 3) of the non-dominant hemisphere. In contrast, subtraction analysis of monotonous vs. rhythmic syllable production did not reveal significant differences. These findings corroborate the notion that left subcortical as well as right cortical structures play an important role during rhythmic syllable production.

4. Discussion

The present study documented distinct LH and RH activation concomitant with rhythmic patterning of syllable sequences as compared to monotonous performance. RH responses bound to rhythm processing emerged at the level of the temporal plane (BA 41 and 42), posterior parts of the superior temporal gyrus (BA 22), Broca's area (BA 44) and adjacent premotor cortex (BA 6). Previous PET measurements suggest lateralization of a "pitch working memory" prerequisite to the temporary maintenance of tone sequences toward the right hemisphere [19, 20]. Conceivably, prototypical rhythmic patterns as investigated in this study also require transient storage within a RH rehearsal mechanism, supported by auditory areas and anterior perisylvian cortex, in order to become available to the speech motor control system.

Van Lancker and Sidtis found perception of the temporal organization of spoken utterances, albeit in the domain of affective prosody, to depend upon LH structures [5]. As concerns the language dominant hemisphere, unexpectedly, the cognitive subtraction approach yielded activation patterns restricted to subcortical structures, i.e. putamen and thalamus, sparing the cortical areas supporting motor aspects of speech production such as the supplementary motor area, the lower motor strip, the anterior insula or the cerebellum [21, 22]. Clinical and neuro-radiological studies, indeed, reported dysarthria subsequent to damage to the left periventricular white matter and basal ganglia

Table 1: fMRI activation during a monotonous and rhythmic syllable repetition task.

Region	Side	Monoton - Perceptual Baseline		Rhythmic - Perceptual Baseline	
		SPM coordinates	T and P values	SPM coordinates	T and P values
SMA	Medial	[-3 20 45]	5.89 (P = 0.001)	[0 29 46]	5.82 (P = 0.001)
Motor Cortex	Left	[-59 1 22]	6.51 (P = 0.000)	[-56 -5 25]	7.36 (P = 0.000)
	Right	[59 -4 22]	7.81 (P = 0.000)	[62 -2 25]	5.49 (P = 0.000)
Putamen	Left	-	-	[-30 1 11]	7.97 (P = 0.000)
	Right	-	-	[27 1 11]	6.22 (P = 0.000)
Thalamus	Left	[-9 -17 12]	6.10 (P = 0.001)	[-9 -17 12]	6.10 (P = 0.001)
	Right	[12 -21 10]	7.03 (P = 0.000)	[9 -20 12]	7.02 (P = 0.000)
STG [BA 22]	Left	#[-48 -43 16]	7.04 (P = 0.000)	#[-48 -31 15]	6.16 (P = 0.000)
	Right	#[51 -46 16]	5.25 (P = 0.011)	#[56 -34 16]	6.85 (P = 0.000)
DLPC [BA 44; 6]	Left	#[-54 12 10]	8.01 (P = 0.000)	#[-54 18 10]	8.95 (P = 0.000)
	Right	#[51 6 11]	6.33 (P = 0.000)	#[54 16 10]	6.31 (P = 0.000)
Insula	Left	[-27 18 2]	7.35 (P = 0.000)	[-30 18 2]	6.49 (P = 0.000)
	Right	[24 18 2]	5.89 (P = 0.000)	[33 20 2]	5.88 (P = 0.001)
Cerebellum	Left	[-30 -50 -31]	8.04 (P = 0.000)	[-30 -48 -31]	5.87 (P = 0.001)
	Right	[33 -50 -31]	7.28 (P = 0.000)	[30 -45 -31]	6.55 (P = 0.000)

T values and corresponding P values (corrected for multiple comparisons at voxel-level) represent activation maximum within each region. STG, superior temporal gyrus; DLPC, dorsolateral prefrontal cortex; # indicates activation clusters extending to different brain regions.

[23]. However, the lesion sites as documented by these previous investigations hardly fit into the observed pattern of language-dominant activation: Speech motor deficits predominantly seem to be bound to dysfunctions of the corticobulbar and corticopontocerebellar pathways. If at all, putaminal disorders give rise to hypophonia, a syndrome of reduced voice volume. Based on clinico-pathological data and the behavioral effects of electrical stimulation, Crosson proposed a cortico-striato-pallido-thalamo-cortical loop mediating response-release during speech production [24]. It is quite conceivable that rhythmically patterned syllable sequences pose higher demands on the control release of verbal output than monotonous repetitions. Since these mechanisms are upstream to speech motor execution, i.e. generation of an efferent pattern of nerve pulses, dysfunctions of the assumed release device must not result in perceived dysarthria.

In addition to pitch, timbre, and loudness, rhythm also represents a salient aspect of music performance. Admittedly, the available data do not yet provide a coherent model of cerebral asymmetry in this regard (see [25] and [26]). Nevertheless, clinical and functional imaging data reveal a similar cerebral organization of the processing of rhythms bound to music and speech production. Prior and coworkers found in LH patients significantly compromised discrimination of the durational values of musical notes as compared to controls and RH subjects [27]. Accordingly, a PET study measured significant hemodynamic responses only at the level of the left insula and inferior Broca's area during detection of irregularities of interval lengths embedded into tone sequences [28]. In contrast, both LH and RH dysfunctions seem to compromise tapping out of the rhythmic pattern of short musical pieces [27].

Previous fMRI studies documented bilateral activation of motor cortex, cerebellum and supplementary motor area during syllable repetitions [22, 17]. A similar pattern of hemodynamic responses emerged both during monotonous and rhythmic /pa/-sequences in comparison to the baseline condition. Besides motor aphasia and apraxia of speech, altered or impaired speech rhythm also has been observed with dysarthrias subsequent to bilateral dysfunction of the corticobulbar tracts or the cerebel-

lum. In these instances, most presumably, disrupted organization of syllable durations simply reflects slowness of articulatory gestures [29].

5. References

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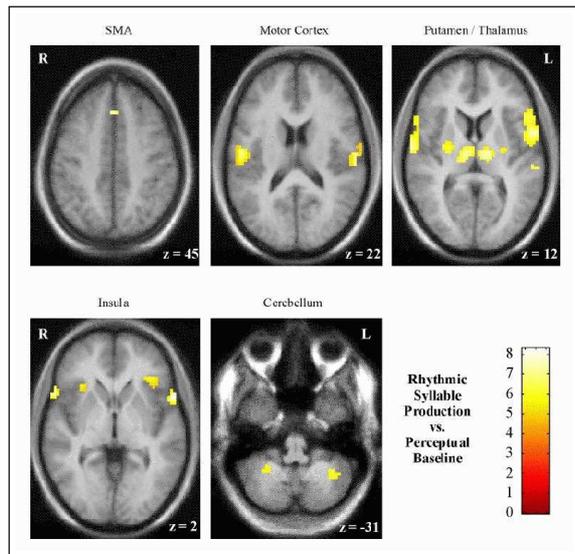


Figure 1: Activation patterns obtained within SMA, motor cortex, putamen, thalamus, STG, dorsolateral prefrontal cortex (DLPC), insula and cerebellum during rhythmic syllable production vs. perceptual baseline. Localization of the highest activated voxel within each cluster is displayed on transverse sections of the averaged anatomical reference images. The distance to the intercommisural plane is given in the right lower corner of each slice.

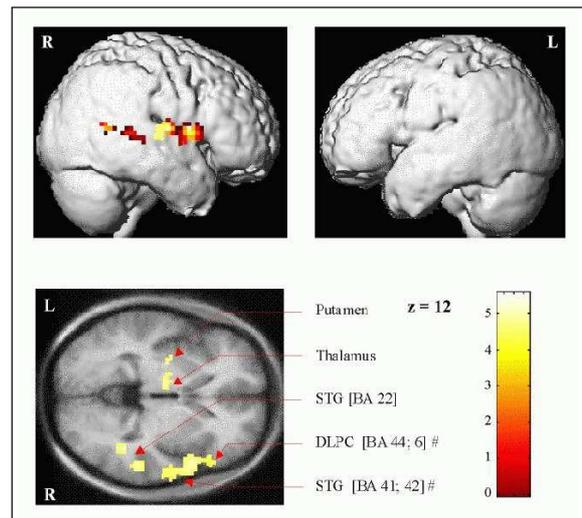


Figure 2: Subtraction analysis (One-Way-ANOVA) obtained during overt syllable repetition: rhythmic vs. monotonous task conditions. fMRI activation patterns within putamen, thalamus, STG and DLPC are displayed on surface-rendered and one transverse section of the anatomical reference images averaged across all 12 subjects; z , distance to the intercommisural plane; #, indicates activation clusters extending to different brain regions.

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