

Neural Substrates of Real and Imagined Sensorimotor Coordination

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Much debate in the behavioral literature focuses on the relative contribution of motor and perceptual processes in mediating coordinative stability. To a large degree, such debate has proceeded independently of what is going on in the brain. Here, using blood oxygen level-dependent measures of neural activation, we compare physically executed and imagined rhythmic coordination in order to better assess the relative contribution of hypothesized neuromusculoskeletal mechanisms in modulating behavioral stability. The executed tasks were to coordinate index finger to thumb opposition movements of the right hand with an auditory metronome in either a synchronized (on the beat) or syncopated (off the beat) pattern. Imagination involved the same tasks, except without physical movement. Thus, the sensory stimulus and coordination constraints were the same in both physical and imagination tasks, but the motoric requirements were not. Results showed that neural differences between executed synchronization and syncopation found in premotor cortex, supplementary motor area, basal ganglia and lateral cerebellum persist even when the coordinative patterns were only imagined. Neural indices reflecting behavioral stability were not abolished by the absence of overt movement suggesting that coordination phenomena are not exclusively rooted in purely motoric constraints. On the other hand, activity in the superior temporal gyrus was modulated by both the presence of movement and the nature of the coordination, attesting to the intimacy between perceptual and motoric processes in coordination dynamics.

Keywords: coordination dynamics, fMRI, imagery, perception–action, synchronization

Introduction

There is ongoing debate in the behavioral literature concerning the relative contribution of neuromuscular versus perceptual processes in determining the stability of uni- and bimanual coordination (Lee *et al.*, 2002; Swinnen, 2002; Oullier *et al.*, 2003; Carson, 2004; Mechsner, 2004). Advocates of the former view have argued that coordination phenomena are governed by physical (neuromusculoskeletal) limitations such as hand posture constraints (Carson *et al.*, 1999), the type of muscles recruited (Carson and Riek, 1998, 2001) and the tendency towards activation of homologous muscles (Riek *et al.*, 1992). According to this perspective, perceptual factors play little role. At the other extreme is the belief that the stability of coordination is completely arbitrary with respect to the physical properties of the individual components, depending instead only on the perceptual relationship between them (Mechsner *et al.*, 2001). Given the functional specialization of neural areas distinguishing between coordination modes (Mayville *et al.*, 2002; Jantzen *et al.*, 2004) in conjunction with recent behavioral studies favoring a context-dependent role of constraints on

coordination stability (Kelso *et al.*, 2001; Oullier *et al.*, 2003), it seems likely that such dichotomies may be enlightened by direct neurophysiological investigation rather than conclusions based largely upon behavioral manipulations and observations.

In this study, the specific contribution of motor processes in determining neural substrates underlying coordination stability is investigated using functional magnetic resonance imaging (fMRI). Participants were asked to syncopate or synchronize simple finger-thumb opposition movements with an auditory metronome (Kelso *et al.*, 1990). They were also required to imagine performing the same coordination tasks in the absence of overt movement. That is, instead of making the movements in time with the metronome, the subjects were required to imagine coordinating peak flexion either exactly on each metronome beat (imagined synchronization) or in between each metronome beat (imagined syncopation). In this way, the specific influence of the presence of efferent motor signals and resulting sensory afference were assessed.

Previous experiments using fMRI (Stephan *et al.*, 1999; Jantzen *et al.*, 2002, 2004; Mayville *et al.*, 2002), magnetoencephalography (MEG) (Kelso *et al.*, 1992; Fuchs *et al.*, 2000) and transcranial magnetic stimulation (TMS) (Meyer-Lindenberg *et al.*, 2002; Steyvers *et al.*, 2003) have shown that coordination patterns of differing behavioral stability (Kelso *et al.*, 1990; Kelso, 1995) are supported by different patterns of neural activity. If stability differences and underlying differences in neural activity (Yue *et al.*, 2000; Mayville *et al.*, 2002) are due only to neuromusculoskeletal factors, which are ultimately linked to cerebral processes through the production of motor output and the resulting feedback, these neural differences should be extinguished (or at least greatly diminished) during imagination conditions. However, if both perceptual and motor processes play a role in determining the stability of coordination (Kelso *et al.*, 2001), some aspects of the coordination-dependent differences observed between the two neural activation patterns should persist, even in the absence of overt movement. Additionally, manipulating the input and the output of the motor system might facilitate the identification of neural regions demonstrating both motor and coordination dependent modulation. Thus, specific loci of perception–action integration might be revealed, providing insight into the mechanism by which cognitive, perceptual and motor processes combine to influence behavioral stability.

The present paradigm differs from many studies of motor imagery (Annett, 1995; Jeannerod, 1995; Crammond, 1997) in that it compares two similar imagination conditions to each other and to their executed counterparts. Functional imaging studies have fostered enthusiasm for the perspective that imagination in general involves similar neural areas as actual

movement (Ehrsson *et al.*, 2003). However, to date, there has been little or no consideration of how faithfully imagination reproduces the more subtle neural differences between two similar tasks. In the present experiment, the metronome remains present during all conditions to allow for execution and imagination of both syncopated and synchronized coordination patterns. This is important since, while sharing basic sensorimotor components (identical motor behavior and identical stimulus input), the actual generation of these two coordination patterns results in distinct patterns of neural activity (Mayville *et al.*, 2002; Jantzen *et al.*, 2004). This allows us to assess whether, with respect to sensorimotor coordination, imagination reflects only the basic activation patterns associated with the motor aspects of the task (simple finger flexion), or whether the relative levels of neural activity distinguishing execution of the coordination modes are still present during imagination. Confirmation of the latter might suggest that imagination is constrained by many of the higher level cognitive processes, such as timing and planning, that are thought to result in observed hemodynamic differences between synchronization and syncopation.

Materials and Methods

Participants

All experimental procedures were approved by the Institutional Review Board of Florida Atlantic University and University MRI of Boca Raton, and conformed to NIH guidelines for research using human subjects. Fifteen participants, 10 males and five females, ranging in age from 22 to 53 years, gave full informed consent before participating in the experiment. All subjects reported being strongly right handed.

Tasks and Instructions

Subjects lay supine in the scanner with their head secured by a vacuum pad and a restraining strap. Two performance modes, execution (Ex) and imagination (Im), were fully crossed with two coordination modes, synchronization (Nize) and syncopation (Pate), resulting in a total of four experimental conditions. In the executed conditions, participants made finger-thumb opposition movements with their right hand that were either synchronized (peak flexion in time with each metronome beat, ExNize condition) or syncopated (peak flexion exactly between metronome beats, ExPate condition) with a rhythmic auditory stimulus (440 Hz, 60 ms duration). The stimulus was presented through headphones at a constant rate of 1.25 Hz, a frequency at which both coordination patterns can easily be performed (Kelso *et al.*, 1990; Engström *et al.*, 1996). In the imagination conditions, participants performed the same two coordination modes in the absence of overt movement; that is, instead of actually performing the movement, they imagined making either synchronized (ImNize) or syncopated (ImPate) movements in time with the metronome. Execution tasks were always performed first, followed by the corresponding imagination tasks. This order was chosen to ensure that subjects clearly knew what to imagine, i.e. that they were producing peak flexion of the finger on (or in between) the beats. This order manipulation seemed particularly important in light of recent evidence demonstrating differences between imagining actual execution of a movement versus visualizing themselves or someone else performing the task (Sirigu and Duhamel, 2001). The order of synchronization and syncopation trials was counterbalanced across participants.

Overt movements were monitored by pressure changes in a small air-filled pillow placed between the index finger and thumb of the right hand of each subject. Pressure values were converted into a voltage and recorded together with the metronome at a sampling rate of 500 Hz. Prior to analysis, movement data were bandpass filtered between 0.05 and 5 Hz. The measure of behavioral performance was the peak-to-peak relative phase, ϕ (Zanone and Kelso, 1992), between the metronome onset and the peak flexion defined as the point of maximum pillow

pressure. Stability of the performance was measured with the angular deviation of ϕ (Batschelet, 1981).

Neuroimaging

For each subject, a total of four functional scanning series were performed using a standard block design. Each run consisted of six alternated rest (metronome off, 30 s) and task (metronome on, 30 s) blocks for a total of 6 min per condition. Prior to each run, participants were instructed as to the coordination to perform in the presence of auditory tones. During periods of silence, subjects rested quietly. Subjects kept their eyes closed during the entire run.

Task-related changes in neural activity were determined by measuring local blood oxygenation (blood oxygen level-dependent or BOLD effect) using echo planar imaging on a 1.5 T GE Signa scanner equipped with real time fMRI capabilities (General Electric Medical Systems, Milwaukee, WI). Functional images were acquired using a single shot, gradient-echo, echo planar pulse sequence [echo time (T_E) = 40 ms, flip angle (FA) = 90°, field of view (FOV) = 24 cm, matrix size = 64 × 64]. Thirty-five axial 4-mm-thick contiguous slices were selected so as to provide coverage of the entire brain once every 3 s [time (T_R) = 3 s, voxel size = 3.75 × 3.75 × 4 mm]. Prior to functional imaging, high-resolution anatomical, spoiled gradient-recalled at steady state (SPGR) images (T_E = in phase, T_R = 325 ms, FA = 90°, FOV = 24 cm, 4 mm thickness, resolution = 256 × 256) were collected at the same slice locations as the functional images. These images were used to co-register the functional scans onto anatomical 3D SPGR axial images (T_E = 5 ms, T_R = 34 ms, FA = 45°, FOV = 26 cm, resolution = 256 × 256, thickness = 2 mm, no interslice gap) collected at the end of each experimental session.

Unless otherwise stated, all data analyses were performed using the AFNI software package (Cox, 1996; Cox and Hyde, 1997). Head movement during each recording run was quantified and corrected for using a Fourier method (Cox and Jesmanowicz, 1999). Time series were then spatially smoothed with a Gaussian kernel (full-width half-maximum = 4 mm) and temporally filtered (lowpass 0.1 Hz). Cross-correlations were computed comparing the functional time series of each voxel with a reference vector representing an ideal temporal activation pattern. In this case the reference was a boxcar function representing the pattern of consecutive on/off blocks convolved with a temporal basis function modelling the impulse response to a single stimulus presentation (hemodynamic response function). The maps of the resulting fit coefficients of each subject were then co-registered and re-sliced to match their individual anatomical images using SPM99 (Friston, 1995). All data were then transformed, using AFNI, into a common coordinate system as defined by the stereotaxic atlas of Talairach and Tournoux (1988).

Average activation maps were computed to fully characterize the BOLD signal patterns associated with each experimental condition. For each condition, the value at each voxel was averaged across subjects and one-sample *t*-tests were performed to determine a voxel level statistic. To correct for multiple comparisons (voxels) a combined probability threshold and clustering method was employed which allowed for the detection of significant clusters of activation (Goutte *et al.*, 1999). Any group of voxels exceeding an individual threshold of $P < 0.005$ that was spatially continuous across a volume of at least 618 μ l was considered significant with a volume corrected significance level of $P < 0.01$.

In order to detect differences between experimental conditions, several planned comparisons (paired *t*-tests) were performed. Executed syncopation was compared with executed synchronization (ExPate-ExNize) to determine whether differences in BOLD activity between these coordination patterns were similar to that reported previously (Mayville *et al.*, 2002; Jantzen *et al.*, 2002, 2004). A comparison was made between executed and imagined conditions (ExPate-ImPate and ExNize-ImNize) to isolate networks recruited exclusively during physical performance. Finally, imagined syncopation was compared with imagined synchronization (ImPate-ImNize) to ascertain if differences observed between these two coordination patterns during execution persisted when subjects only imagined making movements. Multiple comparisons were corrected by adopting a per voxel criterion threshold of $P < 0.005$ and a volume threshold of 564 μ l for an overall corrected error rate of $P < 0.05$. A final inclusive masking procedure was

performed in which a functional mask comprised of a combination of significant activity from all four conditions was applied to the results of both statistical comparisons. This procedure ensured that statistical comparisons between experimental conditions identified differences only within functionally relevant brain areas. That is, those brain areas that were found to participate in at least one of the four experimental tasks.

Results

Behavioral Performance

The circular mean and deviation of the relative phase between the onset of the metronome and the peak of the following movement were calculated for both execution conditions (ExPate and ExNize, Fig. 1). As shown in Figure 1 (left panel), on average, subjects were able to produce coordination patterns very close to those required by the task (ExNize: $10.3 \pm 14.8^\circ$; ExPate: $189.2 \pm 47.6^\circ$, mean \pm SD). Movements made in perfect synchrony or syncopation with the metronome would result in a relative phase of 0° and 180° respectively.

Not surprisingly, a Watson-Williams test for circular statistics (Batschelet, 1981) revealed that these differences in mean relative phase are statistically significant [$F(1,14) = 113.05$, $P < 0.001$], since they reflect the basic coordination requirements imposed. However, subjects displayed greater variability during the performance of the syncopation task with a between subject average angular deviation in relative phase of $46.2 \pm 13.7^\circ$ compared with a mean of $14.7 \pm 4.2^\circ$ for synchronization (Fig. 1, right panel). Quantitative analysis showed that these differences are significant [$F(1, 14) = 50.63$, $P < 0.001$] and are in line with previous studies (Kelso *et al.*, 1990; Engström *et al.*, 1996), showing that synchronization is a more stable coordination mode than syncopation.

Spontaneous switches from the less stable syncopated coordination pattern to the more stable synchronized pattern generally occur at higher movement rates (~ 2 Hz; Kelso *et al.*, 1990) than those employed in the current study. In accordance, no such phase transitions were observed here for the execution conditions (ExNize and ExPate). In previous studies, so-called

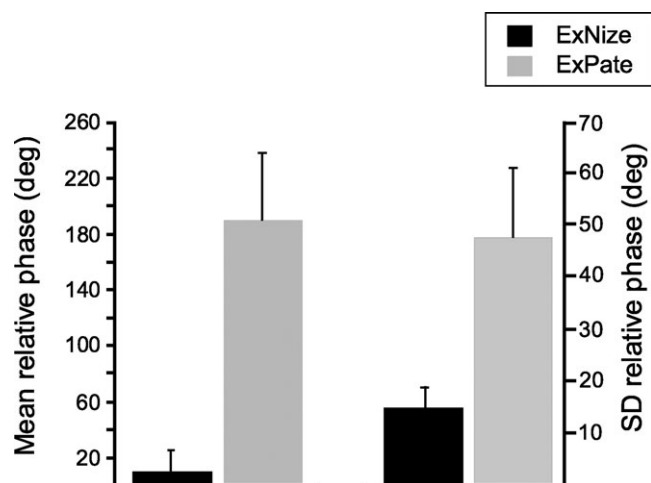


Figure 1. Behavioral results of the executed coordination modes: ExNize (black bars) and ExPate (gray bars). Left panel: circular mean of the relative-phase (in degrees) between the onset of the metronome and the peak flexion of the finger. Right panel: average circular deviation of the relative phase between the metronome and finger flexion (in degrees). Notice that, even at the low rate of 1.25 Hz, variability (stability) of syncopation is much greater than (less than) synchronization.

'imagined phase transitions' have been reported when subjects imagine making syncopated movements with a metronome that progressively increases in cycling frequency (Mayville *et al.*, 2000). These transitions attest on the ability of subjects to imagine different coordination patterns to an external event. To provide additional support for the assertion that participants were actually imagining the two different coordination patterns, we performed a similar behavioral study in which participants ($n = 7$) were asked to physically or mentally syncopate to an auditory metronome which pacing frequency increased (from 1 to 3 Hz, 0.25 Hz steps). The time at which participants reported experiencing imaginary transitions corresponded closely to the time at which physical transitions were observed, with no significant difference between them [$t(69) = 0.74$, $P > 0.05$]. This correspondence demonstrates the ability of subjects to imagine different coordination patterns and provides behavioral evidence that executed and imagined conditions share similar cognitive constraints.

Neuroimaging

Average activation maps from the four experimental conditions are shown in Figure 2. The coordinates of the center of mass of each activation cluster and the corresponding Brodmann's area

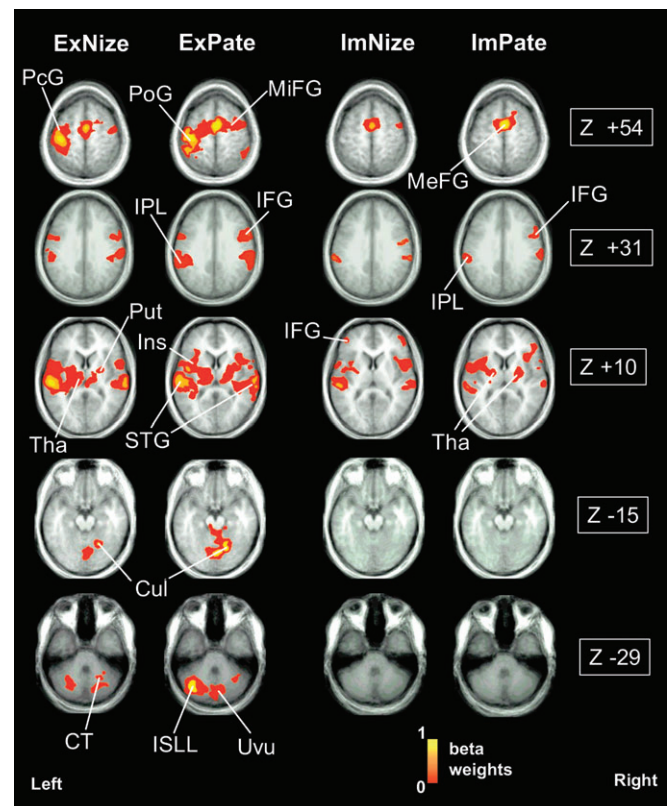


Figure 2. Average parametric maps across fifteen subjects from each of the four experimental conditions overlaid on five selected axial slices of an average anatomical scan. Each column represents a different condition. From left to right: ExNize, ExPate, ImNize and ImPate. Beta weights are expressed in arbitrary units and are shown in colors that range on a gradient from red (minimal activity) to yellow (peak activity). The Z-axis location shown gives the inferior-superior distance from the AC-PC line in Talairach space. PcG: precentral gyrus; PoG: postcentral gyrus; MiFG: middle frontal gyrus; MeFG: medial frontal gyrus; IPL: inferior parietal lobule; IFG: inferior frontal gyrus; STG: superior temporal gyrus; Ins: insula; Put: putamen; Tha: thalamus; Cul: culmen; CT: cerebellar tonsil; Uvu: uvula; ISLL: inferior semilunar lobule.

are listed in Table 1. Figure 2 is divided into four columns with the two columns on the left showing average activation patterns resulting from performance of the executed coordination conditions (ExNize and ExPate) and the two columns on the right showing averages from the imagination conditions (ImNize and ImPate). Significant areas of task-related BOLD increase are shown in color on selected slices of an average anatomical image. Significant clusters of activity were identified during ExNize in bilateral precentral gyrus (PcG) and medial frontal gyrus (MeFG) corresponding to primary sensorimotor cortex and supplementary motor area (SMA) (top row) respectively. Activity in the right inferior frontal gyrus (IFG) and bilateral inferior parietal lobules (IPL) was also observed (second row). In more inferior regions (third row) clusters were located bilaterally in superior temporal gyrus (STG, Heschl's gyrus), an area functionally identified as the primary auditory cortex. The large cluster of activity centered in left STG extends superiorly to include the inferior aspects of the PcG [Brodmann's area (BA) 44] and medially to the left thalamus (Tha), putamen (Put) and insula (Ins). Subcortical activity was also observed in the right Tha and Put (third row). Ipsilateral cerebellar activity was found in the declive (not shown), culmen (Cul), cerebellar tonsil (CT) and contralateral activity in the inferior semilunar lobule (ISLL; fourth and fifth row).

As expected, the network of activity identified during ExPate is more extended than that observed during ExNize (second column from the left in Fig. 2 and Table 1). In addition to areas identified during synchronization, activity was also observed bilaterally in the superior part of the middle frontal gyrus (MiFG; first row) and the right Ins (third row). In cerebellar regions additional activity was found centered in the right ISLL extending to the uvula (Uvu; fifth row).

A subset of the same networks recruited during execution was also active during imagination of the equivalent movements. As reported in Table 1, eight clusters were active during ImNize and 13 were active during ImPate. A selection of these clusters is illustrated in the right two columns of Figure 2. For ImNize, significant activity was found in SMA, bilateral middle

frontal gyrus (not shown on figure), ipsilateral inferior frontal gyrus (IFG), bilateral inferior parietal lobule (IPL; BA40) (second row) and bilateral STG extending to the Ins on the left side (not shown). In addition to the areas reported during ImNize, ImPate generated additional activity in bilateral Tha and Ins, as well as in contralateral Put (Fig. 2, third row fourth column). It is noteworthy that, at the chosen statistical threshold ($P < 0.01$), no activity was observed during imagination conditions in either primary sensorimotor cortex or cerebellum.

Syncopation versus Synchronization

Regions demonstrating significantly greater activity during ExPate than during ExNize are shown in red on Figure 3. The average BOLD amplitude of selected voxels located in these regions during the executed (black bars) and imagined (gray bars) conditions is also depicted. Talairach coordinates for the center of mass of each cluster are listed in the left column of Table 2. Increased activity for ExPate relative to ExNize was observed bilaterally in MeFG (pre-SMA), middle frontal gyrus (MiFG; premotor cortex, BA6) and IPL, as well as in bilateral (Cin; Fig. 3, top panel). In addition to these dorsal cortical areas, executed syncopated coordination also resulted in greater activity within right Ins, bilateral STG (not shown), Tha and right substantia nigra. Finally, in the cerebellum, greater activity was associated with ExPate in ipsilateral ISLL (not shown on figure), CT, contralateral Uvu, pyramis (Pyr) and ipsilateral Cul. No areas showed greater activity in executed synchronization than executed syncopation. These statistical results confirm observations based on visual inspection of the average activation maps shown in Figure 2. They also serve to replicate the findings of previous neuroimaging studies (Mayville *et al.*, 2002; Jantzen *et al.*, 2002, 2004) showing that, compared with synchronization, syncopation results in increased or additional activity across a broad cortical and subcortical network (see Fig. 3, black bar graphs).

The ImPate-ImNize comparison resulted in significant differences similar to those reported for the analogous comparison of the executed conditions (Table 2, right column, Fig. 3, green

Table 1

Talairach coordinates for the center of mass of significant clusters resulting from the average across 15 subjects in each condition.

Area	Hemisphere	ExNize				ExPate				ImNize				ImPate			
		x	y	z	BA	x	y	z	BA	x	y	z	BA	x	y	z	BA
Medial frontal gyrus	R/L	0	-4	58	6	0	-2	54	6	1	-2	58	6	2	-2	55	6
Precentral gyrus	L	-39	-21	53	4	-40	-18	54	4								
	R	51	-4	48	6	52	1	41	6								
Middle frontal gyrus	L									-38	-4	47	6	-37	-4	50	6
	R									44	0	51	6	40	9	45	6
Inferior frontal gyrus	R	51	6	28	9	52	8	33	9	53	7	31	9	55	5	34	9
Inferior parietal lobule	L	-53	-28	32	40	-56	-34	28	40	-60	-27	24	40	-60	-26	27	40
	R	58	-24	30	40	57	-32	29	40	62	-34	27	40	61	-26	30	40
Superior temporal gyrus	L	-54	-23	13	41	-56	-24	13	41	-58	-20	12	41	-55	-31	11	41
	R	63	-24	8	42	63	-24	13	41	60	-26	13	42	60	-26	10	42
Putamen	L	-25	-9	12	-	-24	-8	18	-					-22	-9	20	-
	R	21	-10	13	-	22	-2	15	-								
Insula	L	-44	-4	9	13	-35	12	10	13					-36	12	14	13
	R					36	17	8	13					39	19	9	13
Thalamus	L	-11	-21	8	-	-15	-13	12	-					-10	-19	6	-
	R	7	-18	12	-	18	-13	17	-					18	-16	6	-
Declive	R	8	-66	-20	-	10	-58	-13	-								
Culmen	R	24	-55	-23	-	24	-57	-21	-								
Inferior semilunar lobule	L	-31	-67	-38	-	-25	-69	-35	-								
	R					9	-76	-36	-								
Cerebellar tonsil	R	29	-61	-36	-	32	-51	-38	-								

L: left; R: right; BA: Brodmann's area; ExNize: executed synchronization; ExPate: executed syncopation; ImNize: imagined synchronization; ImPate: imagined syncopation.

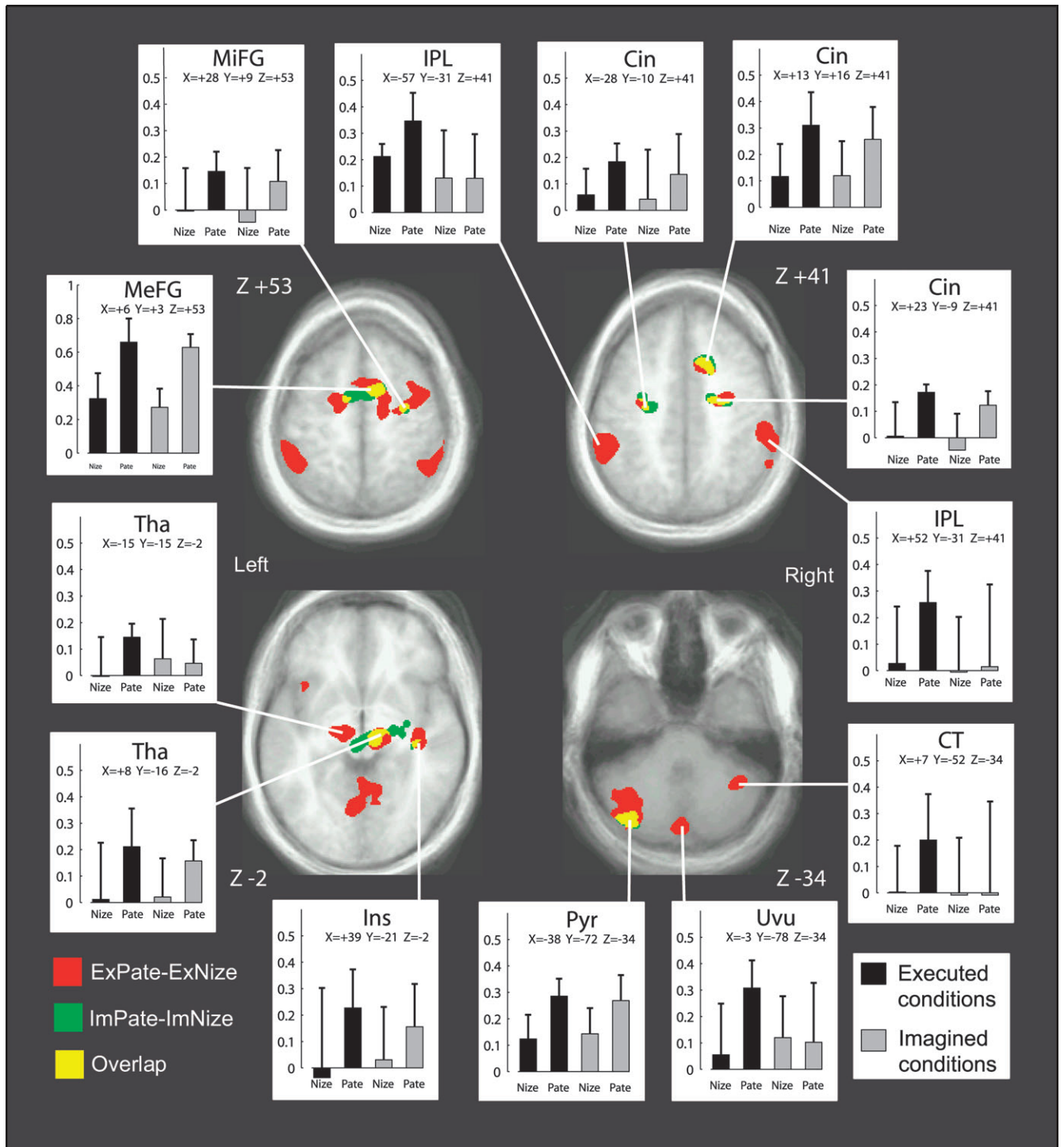


Figure 3. Comparisons between synchronization and syncope. Significant areas are overlaid on top of selected axial slices of an average anatomical scan. (The Z-axis location shown gives the inferior-superior distance from the AC-PC line in Talairach space.) Red overlays: brain areas that are significantly different between the execution of syncope and synchronization (ExPate compared with ExNize). Green overlays: brain areas that are significantly different between the imagination of syncope and synchronization (ImPate compared with ImNize). Yellow overlays: areas that are common to both comparisons (ExPate-ExNize and ImPate-ImNize). Bar graphs (black: executed conditions; gray: imagined conditions) illustrate the average BOLD amplitude (arbitrary units) of a single voxel located in a selected cluster of activity. The X, Y and Z values represent the coordinates of the voxel in Talairach space. Cin: cingulate; Pyr: pyramid. For other abbreviations, see Figure 2.

overlays). ImPate-ImNize resulted in differences bilaterally in MeFG, MiFG, Cin, right substantia nigra and right Ins, as well as bilateral Tha and left STG (STG cluster not shown in the figure). Investigation of the accompanying bar graphs (gray bars for imagination), when considered in conjunction with the activation

maps presented in Figure 2 and Table 1, makes it apparent that differences between imagined coordination modes arise due to a large positive BOLD signal during imagination of syncope compared with either no activation or significantly smaller positive activation during imagination of synchronization.

Table 2

Talairach coordinates for the center of mass of significant clusters resulting from the comparison of syncopation and synchronization

Area	Hemisphere	ExPate-ExNize				ImPate-ImNize				
		x	y	z	BA	x	y	z	BA	
Medial frontal gyrus	R	8	5	58	6	9	4	57	6	
Middle frontal gyrus	L	-29	-11	40	6	-24	-10	43	6	
	R	43	2	38	6	28	36	21	9	
Inferior parietal lobule	L	-53	-41	44	40					
	R	55	-34	43	40					
Cingulate gyrus	L	-26	-7	34	24	-23	-24	33	31	
	R	2	2	25	24	13	17	40	32	
	R	23	-23	27	13					
Superior temporal gyrus	L	-52	-31	12	41	-35	-42	11	41	
	R	38	-39	11	41					
Insula	R	39	-18	-4	13	40	-20	-3	13	
Thalamus	L	-9	-17	0	-	-13	-8	5	-	
	R	13	-17	3	-	23	-25	11	-	
Substantia nigra	R	11	-21	-6	-	10	-20	-6	-	
Inferior semilunar lobule	R	4	-72	-42	-					
Culmen	R	3	-54	-2	-					
Uvula	L	-36	-64	-26	-					
Cerebellar tonsil	R	40	-52	-32	-	-39	-57	-45	-	
Pyramis	L	-2	-78	-24	-	-35	-75	-34	-	

Abbreviations as for Table 1.

In spite of the noticeable absence of cerebellar activity for the imagination conditions (Fig. 2 and Table 1), differences were found in the right CT (not shown in figure) and the left pyramis (Pyr) when ImPate was compared with ImNize (Fig. 3). This discrepancy likely resulted from the use of a less stringent statistical threshold for the statistical comparisons ($P < 0.05$; Table 2) compared with the average activation maps ($P < 0.01$; Table 1). To verify this assumption, average activation maps of ImNize and ImPate were recalculated at a reduced statistical threshold of $P < 0.05$. BOLD signal amplitude was observed within lateral cerebellum for both imagined conditions (e.g. BOLD amplitude of the pyramis in Fig. 3, gray bar graphs) indicating that the statistical difference between them reflects task-related modulation in a functionally relevant brain area.

With few exceptions, differences between imagination conditions (ImPate-ImNize) largely overlapped with those observed during execution. Overlap between the two contrasts (ExPate-ExNize and ImPate-ImNize) is shown in yellow in Figure 3 and illustrates the close concordance between imagination and execution. Taken together, these data confirm previous research showing that syncopation, compared with synchronization, requires increased activity within a distributed neural network (Mayville *et al.*, 2002). They also demonstrate that at least portions of this extended network are also required when one simply imagines syncopation. It is noteworthy that activity in the auditory cortex is always higher for the syncopated pattern in both the executed (ExPate) and the imagined case (ImPate) (see Table 2 and Fig. 4).

Execution versus Imagination

Comparisons between the executed conditions and their imagined counterparts (Fig. 4 and Table 3) were made in order to determine brain regions associated with the purely motoric aspects of the task. The comparison between executed and imagined synchronization (ExNize-ImNize, green overlays and black bars in Fig. 4) revealed significant greater activity during execution in left pre- and postcentral gyri (PoG), bilateral IPL, left precuneus (PreCu; BA39) and STG, as well as across broad regions of the cerebellum with clusters centered in the right Cul and left ISLL (not shown). Additional clusters were noted in

right parahippocampal gyrus (not shown) and left Ins. Again, the bar graphs are useful in demonstrating that these statistical differences result from increased motor related activity in task relevant areas and do not result from subthreshold positive BOLD signal changes in motor conditions and subthreshold negative BOLD signal changes in imagination conditions.

Comparison between execution and imagination of the syncopated pattern (ExPate-ImPate, red overlay in Fig. 4) resulted in a distribution of clusters similar to those seen when comparing synchronized conditions. Executed syncopation resulted in significantly greater activity primarily within contralateral pre- and postcentral and superior temporal gyri, bilaterally in the IPL, and across broad regions of the cerebellum with clusters centered in the left declive (not shown), tuber and ISLL (not shown), and right parahippocampal gyrus (not shown) and Cul. Additional clusters were also noted in right inferior frontal gyrus (IFG), left precuneus (not shown) and Ins and right anterior cingulate gyrus (Cin).

The comparison between execution and imagination revealed areas showing increased activity during execution regardless of the coordination mode employed (i.e. common to both comparisons). These areas are colored yellow in Figure 4. The most prominent of these regions are well known for their role in motor execution and processing of sensory feedback and include large portions of the contralateral pre- and postcentral gyri as well as bilateral IPL, left Ins and large portions of the Cul and cerebellar declive (Dec).

For both comparisons (ExPate-ImPate and ExNize-ImNize) no area exhibited significantly greater activity during imagination compared with execution. Ideation of a motor task has been reported to activate imagination-specific brain activity including premotor, prefrontal, and parietal areas (Gerardin *et al.*, 2000). For instance, the role of parietal cortex in motor imagery has been extensively discussed in the literature especially in situations involving mental visualization of a task (Sirigu *et al.*, 1996; Deiber *et al.*, 1998). Here, however, we specifically designed the experiment and tailored the instructions to encourage subjects to explicitly imagine the execution of coordination patterns as opposed to externally visualizing themselves performing the task (Sirigu and Duhamel, 2001).

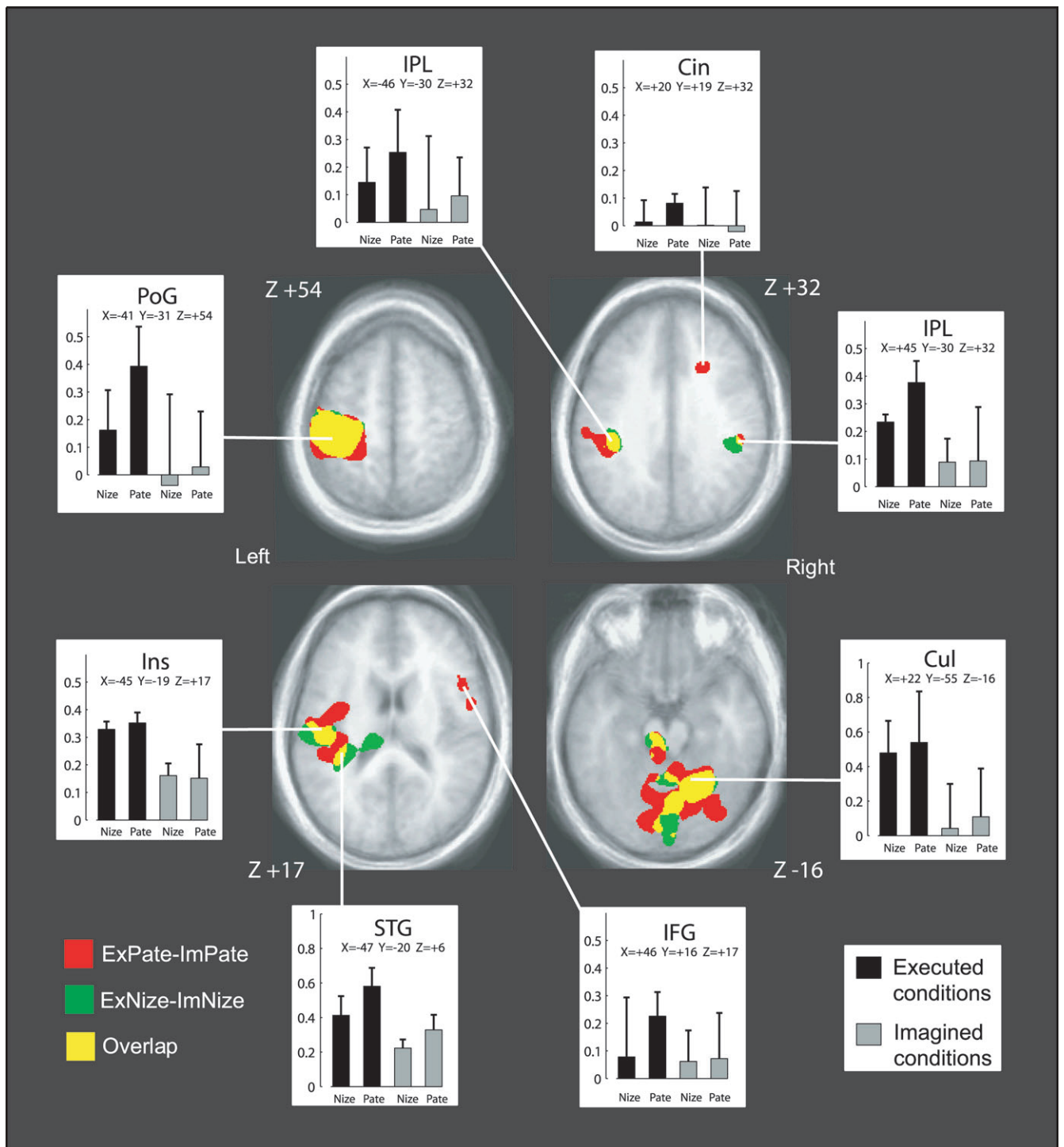


Figure 4. Comparison of executed and imagined coordination. Significant areas are overlaid on top of selected axial slices of an average anatomical scan. (The Z-axis location shown gives the inferior-superior distance from the AC-PC line in Talairach space.) Red overlays: brain areas that are significantly different between the execution and the imagination of the syncopated mode (ExPate compared with ImPate). Green overlays: brain areas that are significantly different between the execution and the imagination of the synchronization mode (ExNize compared with ImNize). Yellow overlays: areas common to both comparisons (ExPate-ImPate and ExNize-ImNize). Bar graphs (black: executed conditions; gray: imagined conditions) illustrate the average BOLD amplitude (arbitrary units) of a single voxel located in a selected cluster of activity. The X, Y and Z values represent the coordinates of the voxel in Talairach space. For abbreviations, see Figure 2.

The fact that no additional brain areas were recruited to perform imagination suggests that subjects were performing the imagination task as requested by not engaging additional cognitive processes specific to certain imagination strategies.

Finally, one additional region demonstrating greater activity during execution compared with imagination is of particular

interest. For both syncopation and synchronization, the STG (in the region of Heschl's gyrus) was significantly more active when subjects were executing compared with imagining the coordination pattern. This difference occurred despite the fact that the auditory metronome was present and identical for all the conditions. In addition, we reported earlier that activity in

Table 3

Talairach coordinates for the center of mass of significant clusters resulting from comparison the executed and imagined coordination modes

Area	Hemisphere	ExNize-ImNize				ExPate-ImPate				
		x	y	z	BA	x	y	z	BA	
Precentral gyrus	L	-38	-20	51	4	-38	-21	53	4	
Postcentral gyrus	L	-36	-35	58	2	-48	-26	41	2	
Inferior frontal gyrus	R					54	3	23	9	
Precuneus	L	-22	-53	30	39	-25	-57	33	39	
Inferior parietal lobule	L	-39	-29	28	40	-39	-30	25	40	
	R	42	-33	31	40	46	-35	45	40	
Cingulate gyrus	R					22	20	32	32	
Insula	L	-34	-34	21	13	-37	-5	16	13	
Superior temporal gyrus	L	-58	-22	7	41	-36	-29	16	41	
Parahippocampal gyrus	R	39	-16	-20	20	35	-22	-18	36	
Declive	L					-18	-61	-23	-	
Culmen	R	22	-55	-18	-	24	-52	-23	-	
Tuber	L					-36	-80	-29	-	
Inferior semilunar lobule	L	-32	-61	-45	-	-24	-64	-57	-	

Abbreviations as for Table 1.

the same regions was sensitive to coordination mode, demonstrating greater activity for syncopation than synchronization. The STG activity was therefore modulated both by the nature of the coordination mode (Table 2) and by the presence of physical movement (Table 3). The STG bar graphs shown in Figure 4 represent this interaction, demonstrating clearly that regardless of the presence of movement, activity within STG was always higher when syncopating compared with synchronizing. Similarly, regardless of coordination mode, activity was always higher when movements were executed than imagined.

Discussion

In this study, a motor imagery paradigm (Annett, 1995; Jeannerod, 1995) was employed in order to investigate the role of efferent motor signals and associated afferent feedback in a sensorimotor coordination task. Two new findings were revealed through the application of this paradigm. First was the demonstration that similar networks of brain areas support both the performance and imagination of rhythmic coordination tasks. Like actual performance, imagination of the synchronized and syncopated coordination modes resulted in activity within SMA, premotor cortex, inferior parietal lobe, STG, inferior frontal gyrus and basal ganglia. Previous neuroimaging work has demonstrated that execution and imagination, broadly defined as the mental simulation of a motor act (Crammond, 1997), activate a similar network of brain areas (Roth *et al.*, 1996; Deiber *et al.*, 1998; Hanakawa *et al.*, 2003; Nair *et al.*, 2003). This finding covers a broad set of imagined tasks ranging from simple finger flexion (Gerardin *et al.*, 2000) and joystick manipulation (Stephan *et al.*, 1995), to complex reaching and grasping movements (Decety *et al.*, 1994; Grèzes and Decety, 2001). Motor imagery consistently involves a network comprising SMA, premotor and parietal cortices as well as basal ganglia (Decety *et al.*, 1994; Stephan *et al.*, 1995; Grafton *et al.*, 1996). Such findings support the popular notion that executed and imagined movements share a common neural substrate, the latter differing only in the lack (or suppression) of a final efferent motor command (Crammond, 1997; Jeannerod, 1999). Our results extend this existing motor imagery literature by showing that imagination of two basic forms of sensorimotor coordination, synchronization and syncopation also engages networks that largely overlap with their executed counterparts.

While sharing basic motor processes, syncopation and synchronization have differing coordinative constraints and are subject to different cognitive demands. This leads to the second important finding emerging from the present study, namely that well-established neural differences between synchronized and syncopated coordination modes (Mayville *et al.*, 2002; Jantzen *et al.*, 2002, 2004; see also Chen *et al.*, 2003) persist in the absence of overt movement. Syncopation still results in greater activity within a specific cortical and subcortical network even when subjects are only imagining making movements between beats. Remarkable overlap was seen when comparing differences between the executed conditions and between the imagined ones, with common clusters located in pre-SMA, cingulate, dorsal premotor cortex, insula, superior temporal gyrus, thalamus and lateral portions of the cerebellum.

The significant increase in the BOLD signal observed during syncopation, even in the absence of movement, leads to two conclusions. First, many of the differences in neural activity reported previously (Mayville *et al.*, 2002; Jantzen *et al.*, 2004) are related to cognitive factors such as planning and preparation as opposed to direct motor factors. This conclusion is corroborated by recent PET and TMS evidence demonstrating that activity within a network composed of SMA, bilateral premotor cortex, vermis and left parietal cortex is directly related to bimanual coordinative stability and not to overt changes in motor constraints such as movement rate (Meyer-Lindenberg *et al.*, 2002). Second, such cognitive processes are still involved to a greater degree for imagined syncopation compared with imagined synchronization. The implications for the perceptual versus motor debate in coordination dynamics is that the relative stability between coordination modes, as indexed by differences in underlying brain activity (Kelso *et al.*, 1992; Mayville *et al.*, 2002; Meyer-Lindenberg *et al.*, 2002), is still maintained in the absence of movement. Moreover, apart from the generation of efferent commands and resulting afferent feedback, imagination of the syncopated pattern imposes similar constraints to actual performance. The latter idea is supported by extensive behavioral and neuroimaging work showing that not only do imagined and executed movements result in the activation of similar neural areas (Stephan *et al.*, 1995; Porro *et al.*, 1996; Roth *et al.*, 1996; Lotze *et al.*, 1999; Jancke *et al.*, 2001), they also appear to share the same timing constraints (Decety, 1996; Crammond, 1997; Papaxanthis *et al.*, 2002). For instance, the fastest speed at which subjects can imagine making paced finger thumb

opposition movements is very similar to their actual physical limit (Sirigu *et al.*, 1995, 1996). Unpaced movements take about the same amount of time to complete regardless of whether they are overtly performed or imagined. In addition, the well-known speed-accuracy trade-off described by Fitts' law (Fitts, 1954; Kelso, 1992) applies even if pointing movements are only imagined (Decety and Jeannerod, 1995; Sirigu *et al.*, 1995, 1996). Recent fMRI evidence demonstrates a somatotopic organization of different body parts for imagined as well as real movements (Ehrsson *et al.*, 2003). Body-part specific activity in motor and premotor (mesial and lateral BA6) areas was maintained for imagined hand, foot and tongue movements. In the context of the coordination task presented here, there is initial MEG and behavioral evidence that imagination of syncopation to a metronome that increases in presentation rate results in the occurrence of a transition to imagined synchronization (Mayville *et al.*, 2000). Behaviorally, subjects reported undergoing imagined transitions from syncopation to synchronization at the same movement rate as during actual performance. Neurally, greater event-related desynchronization was observed in the beta range (15–30 Hz) over sensorimotor cortical areas for syncopation (whether imagined or executed) than synchronization. For both real and imagined coordination, this difference disappeared at the transition from syncopation to synchronization.

Despite the compelling similarities in neural activity for executed and imagined coordination patterns, the present study also identified several areas that are specific to motor execution. When compared with the imagination conditions, execution of both coordination modes resulted in increased activity within a network comprising pre- and postcentral gyrus (M1/S1), inferior parietal lobe, cingulate and areas of the cerebellum concentrated within the vermis. Although some debate surrounds the issue, there is growing evidence, including this study, that imagination does not activate the primary motor and sensory cortices located within anterior and posterior walls of the central sulcus (Parsons *et al.*, 1995; Stephan *et al.*, 1995; Deiber *et al.*, 1998; Gerardin *et al.*, 2000; Hanakawa *et al.*, 2003, but see Ehrsson *et al.*, 2003). Similarly, differences between overt and imagined conditions found in the cerebellum likely reflect a lack of afferent input from peripheral receptors or efferent input from cortical regions. Comparison of the executed conditions revealed greater activity in large cerebellar clusters centered in areas near the vermis. This result is compatible with previous reports showing that medial portions of the cerebellum are more involved in motor execution and integration than timing *per se* (Ivry *et al.*, 1988; Rao *et al.*, 2001). Comparison between syncopated and synchronized conditions, on the other hand, revealed greater activity for syncopation in lateral cerebellar regions, consistent with the notion that these areas are important in timing (Ivry *et al.*, 1988).

Taken together, neuroimaging and neuropsychological data support the role of cortical and subcortical mechanisms in mediating the stability of coordination patterns. Here the afferent and efferent motor constraints were removed when participants imagined performing each pattern. Nonetheless, key components of the neural network supporting the intrinsically less stable coordination mode persisted. This suggests that motor system constraints such as hand posture or muscle recruitment are not singularly responsible for determining coordinative stability and instability (Carson *et al.*, 1999). Rather, the evidence suggests that biomechanical and neuromuscular constraints work together with central neural cognitive and

perceptual processes to modulate intrinsic patterns of coordinative stability (Kelso *et al.*, 2001; Carson and Kelso, 2004).

Surprisingly, activity in STG was modulated both by the coordination mode and by the presence of overt movement. In addition to being significantly greater during syncopation compared with synchronization, STG also demonstrated a greater BOLD response during executed versus imagined conditions. Modulation of primary auditory processing areas occurred despite the fact that an identical auditory stimulus was present across all conditions and was presumably used in the same way to guide coordination, regardless of whether it was imagined or executed. Although we find this result provocative it must be interpreted with caution since there are a number of reasons why such modulation may occur. For instance, behavioral findings report that the generation of off-the-beat patterns are more attention demanding than on-the-beat ones (Monno *et al.*, 2002). When taken together with recent imaging work demonstrating attentional modulation of activity in auditory cortex (Sevostianov *et al.*, 2002; Hugdahl *et al.*, 2003; Specht and Reul, 2003), such results suggest that attention may play a key role in modulating STG activity when a syncopated rather than synchronized pattern is adopted. Increased activity in auditory cortex in the presence of movement, on the other hand, may reflect processes other than attention, possibly providing an initial glimpse into ways in which perceptual and motor systems can interact to influence coordinative stability. Interestingly, a similar sensorimotor interaction within auditory cortex has been shown during both speech (Paus *et al.*, 1996) and object manipulation (Foxe *et al.*, 2002), opening up the possibility that perceptual-motor integration may occur at a very early processing stage. Such integration may provide a putative mechanism by which movement can shape perceptual events via modulation of neural activity generated by sensory (here auditory) input.

The insula may also provide an anatomical substrate through which motor activity, in the form of efferent signals or afferent feedback, may influence auditory processing. The insular cortex is well known for its role in auditory processing (Bamiou *et al.*, 2003) and has reciprocal connections with a number of sensorimotor processing areas, including precentral gyrus, secondary somatosensory cortex, the medial aspect of the middle frontal gyrus and lateral premotor cortex (Augustine, 1996). Functionally, Ins has been shown to respond to stimuli presented across multiple modalities (Downer *et al.*, 2000) and has been implicated as playing an important role in multimodal integration (Calvert *et al.*, 2001). The influence by both coordination mode and motor execution on activity in primary auditory cortex suggests the Ins as a possible site through which behavior may exert an influence on coordinative stability. Such a finding also questions the thesis that behavioral (in)stability is exclusively due to purely perceptual processes (Mechsner *et al.*, 2001; Mechsner, 2004) independent of motor constraints.

Conclusions

Until now, dichotomous debates contrasting 'purely' motoric and perceptual accounts of sensorimotor coordination have proceeded based largely on behavioral findings, unconstrained by neural evidence. In this study, we used fMRI to investigate the neural correlates of overt and imagined sensorimotor coordination. We identified a network of brain regions common to the execution and the imagination of rhythmic coordination.

The existence of this network — composed of SMA, right inferior frontal gyrus, bilateral inferior parietal lobe and STG — attests to the similarity in neural mechanisms underlying the execution and imagination of coordination. Previously established neural differences between executed synchronization and syncopation found in premotor cortex, SMA, basal ganglia and lateral cerebellum were shown to persist when the coordination patterns are only imagined. This finding suggests that neural indices reflecting behavioral (in)stability are not tied directly to the presence of overt movement and supports the hypothesis that coordination phenomena are not exclusively rooted in purely motoric constraints. Finally, activity in the primary auditory cortex was modulated both by coordination pattern and the presence (or absence) of overt movement indicating that interactions between perceptual and motor influences may occur at a relatively early processing stage. Taken together, our neuroimaging results shed new light on behavioural studies addressing the origins of coordinative (in)stability by attesting to the intimacy between perceptual and motoric processes.

Notes

Research supported by NIMH Grants MH42900 and MH01386. The authors would like to thank Dr Dinesh Nair for helpful comments on earlier versions of the manuscript.

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