Practice-dependent modulation of neural activity during human sensorimotor coordination: a functional Magnetic Resonance Imaging study

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Abstract

We investigated the degree to which differences in the pattern of blood oxygen level dependent activity (BOLD) between syncopated and synchronized coordination patterns are altered by practice. Baseline levels of BOLD activity were obtained from eight subjects while they syncopated or synchronized with an auditory metronome at 1.25 Hz. Subjects then practiced syncopation at the same rate for four consecutive sessions. Post practice scans of the two coordination patterns were then performed. Before practice, baseline syncopation activated a much broader network of both cortical and subcortical regions than synchronization that included Supplementary Motor Area (SMA), bilateral putamen, left thalamus, bilateral superior temporal gyrus as well as the vermis. This pattern of activity is hypothesized to reflect the extra timing and attention requirements of syncopation. After practice, activity in superior temporal gyrus and vermis were no longer observed during syncopation reflecting a reduction in the need for attention and the use of sensory feedback for guiding behavior. Surprisingly, post practice synchronization resulted in additional significant activations in SMA, inferior frontal gyrus and superior temporal gyrus as well as small activations in bilateral putamen. Practice with the more difficult syncopation task thus had a dual effect of decreasing the number of active regions during syncopation and increasing the number of active regions during synchronization. Since overt syncopation performance did not change significantly as a result of practice, these observed neural changes appear to be due to context- and history-dependent factors, rather than behavioral learning per se. © 2002 Elsevier Science Ireland Ltd. All rights reserved.

Keywords: fMRI (functional Magnetic Resonance Imaging); Blood oxygen level dependent activity; Coordination; Practice; Behavioral context

Within the last decade, investigations of human brain function have successfully demonstrated that intrinsic differences in stability between various sensorimotor coordination patterns, already known to exist at the behavioral level [8], are also observed in the time domain [2,3,7,10], frequency domain [4,11] and in spatially distributed patterns of neural activity [12]. Recent functional Magnetic Resonance Imaging (fMRI) data have revealed that syncopation (moving off the beat) engages a distributed network of cortical and subcortical areas compared to synchronization (moving on the beat) [12]. Most notable among these were several cortical and subcortical areas involved in motor planning, timing and monitoring. These included premotor cortex, basal ganglia, superior temporal gyrus and the cerebellum.

There is now mounting behavioral evidence that the dynamical properties of coordinated behavior such as syncopation and synchronization can be altered through learning and practice [9,16,18,20,21]. In some cases training has the dual effect of increasing stability of a practiced pattern and decreasing the stability of a previously stable, but unpracticed pattern [20]. Such findings attest to the role of context, in the form of behavioral history and pre-existing ability, in determining how practice shapes behavior toward a target pattern (see also ref. [17]). Although there is evidence for neuromagnetic changes associated with behavioral improvement during sensorimotor coordination [4], the degree to which alterations in neural activation are simply a function of practice or depend on behavioral improvement alone remains unknown.

The process of learning a specific motor behavior is

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complex and can involve multiple cognitive and behavioral processes including attention, practice, memory, response selection, consolidation and behavioral improvement. Although several studies have demonstrated changes in cortical activation associated with behavioral improvement, few have addressed the role that simple repeated exposure to a task may play in altering neural activity. In the current study we use fMRI to investigate how short-term behavioral practice alone affects intrinsic differences in neural activity between synchronized and syncopated coordination modes. On the basis of previous work demonstrating behavioral and neural consequences of practice of a syncopation task [4],we hypothesized that practice by itself, in the absence of knowledge of results, may decrease activity in the distributed neural network underlying syncopation. At the same time, we were curious to see how exposure to a quite difficult timing task (syncopation) affects the neural structures supporting an easier but unpracticed task (synchronization). A large body of literature concerning adaptation, orienting and priming suggests that context plays an important role in the cognitive processes involved in any task (see ref. [14] for a discussion).

Eight healthy, right-handed, neurologically normal subjects (seven males; one female age range 23–46) gave informed consent before participating in the study. Changes in neural activity were determined by measurement of changes in local blood oxygenation (BOLD effect) using echo planar imaging on a 1.5 Tesla Signa Scanner (General Electric Medical Systems, Milwaukee, WI) equipped with real time fMRI capabilities. Echo-planar images were collected using a single shot, gradient-echo, echo planar pulse sequence (echo time (TE) = 60 ms, flip angle (FA) = 90°, field of view (FOV) = 24 cm, in plane resolution = 64 × 64). Twenty axial 5 mm thick slices spaced 2.5 mm apart were selected so as to provide coverage of the entire brain (voxel size = 3.75 × 3.75 × 7.5 mm). Prior to functional imaging, high resolution anatomical spoiled gradient-recalled at steady state (SPGR) images (TE = in phase, TR = 325 ms, FA = 90°, FOV = 24 cm, 5 mm thickness, 2.5 mm spacing, number of excitations = 2) were collected at the same slice locations as the functional images. These images served as the background onto which the functional information was displayed and were also used to co-register the functional scans onto anatomical 3D SPGR axial images (TE = 5 ms; TR = 34 ms; FA = 45°, FOV = 24 or 26 cm; resolution = 256 × 256; thickness = 2 mm) which were collected at the end of each experimental session.

Data were acquired using a block design with ten images in the 'off' block (30 s; TR = 3000 ms) followed by ten images in the 'on' block. A single session consisted of four consecutive off/on blocks. During the 'on' block subjects were required to coordinate flexion movements of the right index finger and thumb (by squeezing an air filled pillow) to an auditory metronome (1000 Hz, 60 ms duration) presented at a constant rate of 1.25 Hz (24 tones per on

block) through plastic tubes attached to a set of headphones. This low movement rate was chosen to both allow for direct comparison with previous work [12] and to ensure that all subjects can perform the syncopated pattern without showing transitions into synchronization. During the 'off' block subjects rested. The subject's eyes remained closed during all sessions. During the pre-practice phase subjects performed one session of syncopation and one session of synchronization. During synchronization subjects were asked to time the peak of finger-thumb flexion to coincide with the sound of the metronome. During syncopation they were required to time the peak of flexion exactly between metronome beats. The Practice phase consisted of four consecutive syncopation sessions. These were then followed by a post-practice phase in which single syncopation and synchronization sessions were performed. In order to maximize the uninterrupted exposure to the practiced task, syncopation sessions were always presented consecutively as the second to seventh session while synchronization was always performed as the first and eighth session.
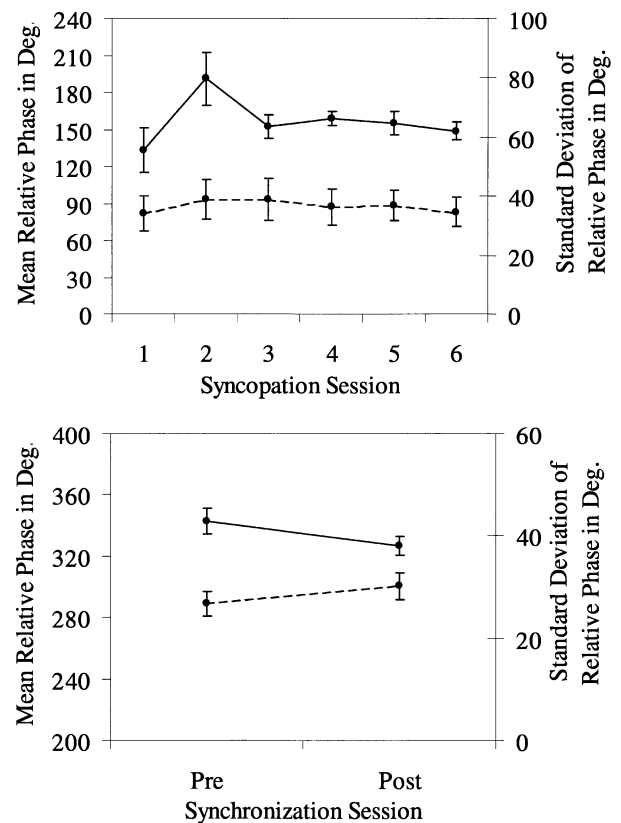

Fig. 1. Behavioral performance during syncopation sessions (top) and synchronization sessions (bottom) averaged across all subjects. The solid line shows the mean relative phase between the auditory metronome and the time of peak flexion of the following response (left axis). Perfect syncopation is 180°, perfect synchronization is 360°. The dotted line shows the standard deviation of the relative phase (right axis). On average no performance changes occurred as a function of syncopation practice. Error bars show the between subject standard error.

All processing and analysis procedures were performed using the MCW-AFNI software package [1] running under Linux on a PC. Data from each scanning session were first corrected for any head motion before being spatially smoothed (Gaussian kernel full width at half maximum (FWHM) = 4 mm) and temporally filtered with a lowpass of 0.1 Hz. In order to fully characterize all areas involved in each task, functional images were constructed by comparing the BOLD signal intensity during the coordination period with that measured during rest. This was done by correlating the time series of each voxel with a reference vector representing an ideal temporal activation pattern. In this case a boxcar function representing the pattern of consecutive on/off blocks was convolved with a temporal basis function modeling the impulse response to a single stimulus presentation (hemodynamic response function). The percent signal change was determined for each voxel and these data were then coregistered with each subject's own anatomical scan to facilitate transformation into the standardized space defined by Talairach and Tournoux [19]. After transformation into Talairach space, the percent signal change of each voxel was averaged across subjects and T-tests were performed to determine a final voxel level statistic. In order to correct for multiple comparisons (voxels) a combined probability threshold and clustering method was employed that allows for the detection of significant clusters of activation. Any group of voxels exceeding an individual threshold of $T > 5.32$ ($P < 0.0001$) that was spatially continuous across a volume of at least 527 mm^3 were considered to be significantly active across the population studied (corrected $P < 0.02$).

On average, practice did not result in significant changes in syncopation performance. The average and standard deviation of the relative phase (with respect to the metronome beat) on each session are shown in Fig. 1. A six level (syncopation session) one-way analysis of variance on both the mean relative phase ($F_{(5,42)} = 2.01$, $P = 0.096$) and the standard deviation ($F_{(5,42)} = 0.1$, $P = 0.98$) did not reveal any significant differences between performance on any session. Interestingly there was a modest, yet significant, alteration in synchronization performance following the practice sessions. The synchronization mean across subjects significantly decreased from the pre-practice phase of $-17.5° \pm 26.7°$ to a post-practice phase of $-33.4° \pm 30.2°$ ($P = 0.039$; paired two tailed T-test). The variability, on the other hand, showed a slight, but significant increase (pre: $26.72° \pm 7.0°$; post: $30.15° \pm 7.33°$; $P = 0.015$, paired two tailed T-test).

Inspection of the pre-practice average activation maps for the two coordination conditions (Fig. 2 left column; see also Table 1) revealed functional differences similar to those previously reported when comparing synchronized and syncopated coordination [12]. Synchronization resulted in significant average activations within contralateral precentral gyrus (GCp, corresponding to M1), the left insula (in the region of the planum temporale) and right superior temporal

gyrus (GTs, Brodmann's area 41). Syncopation, on the other hand resulted in a much broader network of both cortical and subcortical origin. In the cortex these included contralateral GCp, a single cluster in bilateral medial frontal gyrus (Gfmed) extending from left SMA to right pre-SMA, left posterior insula (planum temporale), right GTs and inferior frontal gyrus (GFi) (Fig. 2, Table 1). Subcortical structures showing increased BOLD activity included bilateral puta-
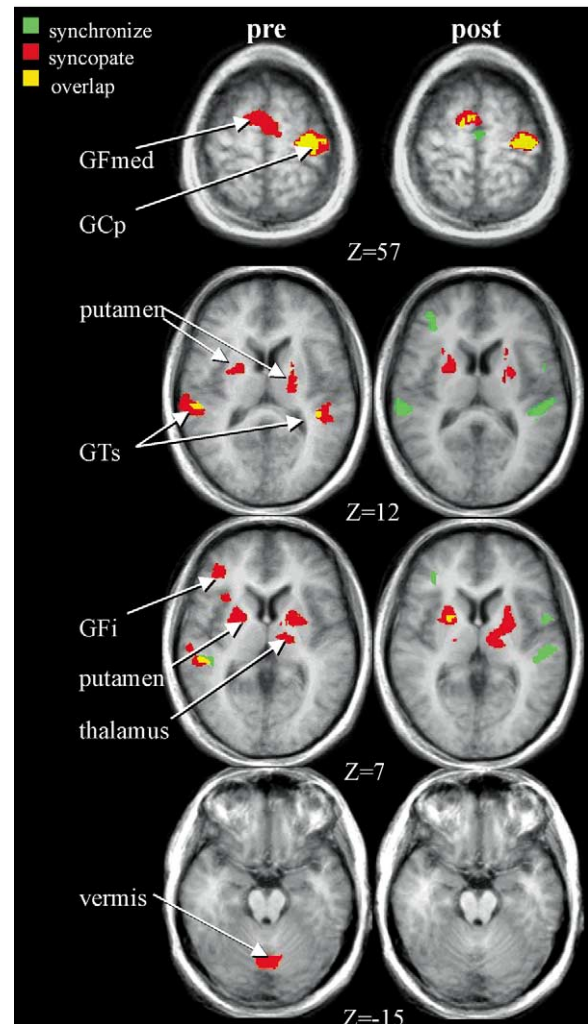

Fig. 2. Statistical parametric maps for the pre-practice (left column) and post-practice (right column) conditions displayed on an averaged anatomical scan. Significant areas of activation observed during synchronization (green), syncopation (red) as well as common areas (yellow) are displayed on four axial slices. Prior to practice the more automated task of synchronization activated only the motor cortex (GCp) and auditory cortex (GTs). Syncopation resulted in a larger network of activity including additional clusters in SMA (medial frontal gyrus; GFmed), inferior frontal gyrus (GFi) bilateral putamen, the thalamus and the vermis of the cerebellum. Practice resulted in a significant reduction of activity during syncopation in GTs, GFi and cerebellum and additional activity during synchronization in SMA, putamen, GFi and GTs. Abbreviations: GCp, post central gyrus; GTs, superior temporal gyrus; GFi inferior frontal gyrus; and GFmed, medial frontal gyrus.

Table 1
Location of clusters of activation for all experimental conditions

	Talairach Coordinates			
	X	Y	Z	Volume (μl)
Pre practice syncopation				
Precentral gyrus (L)	− 34	− 17	56	7724
Medial frontal gyrus	3	− 1	60	4430
Superior temporal gyrus (BA41) (R)	59	− 27	12	1051
Inferior frontal gyrus (R)	58	6	10	478
Inferior frontal gyrus (R)	37	38	7	451
Insula (BA13) (L)	− 45	− 29	19	2472
Insula (L)	32	20	5	563
Putamen (R)	23	3	7	1274
Putamen (L)	− 22	6	2	2520
Thalamus (VLN) (L)	− 11	− 13	5	870
Vermis	4	− 69	− 16	641
Pre practice synchronization				
Precentral gyrus (L)	− 33	− 17	58	5151
Superior temporal gyrus (BA41) (R)	51	− 28	10	620
Insula (L)	− 41	− 29	19	1230
Post practice syncopate				
Precentral gyrus (L)	− 36	− 16	56	3655
Medial frontal gyrus (R)	7	2	58	1859
Putamen (L)	− 22	1	6	2648
Putamen (R)	23	6	8	2481
Thalamus (VLN) (L)	− 12	− 12	5	1324
Post practice synchronize				
Precentral gyrus (L)	− 33	− 17	55	3012
Medial frontal gyrus (R)	9	− 1	62	1185
Superior temporal gyrus (R)	59	− 28	15	1269
Superior temporal gyrus (BA41) (L)	− 46	− 29	14	2735
Middle frontal gyrus (R)	35	38	9	547
Putamen (L)	− 22	7	1	1485
Putamen (R)	24	9	2	597

men, the left ventral lateral nucleus (VLN) of the thalamus and the vermis of the cerebellum. Pre-practice differences between coordination modes were restricted to regions involved primarily in motor planning, timing and monitoring (cerebellum, SMA, VLN, basal ganglia), and were not observed in primary motor cortex, an area serving a mainly executive role.

After behavioral practice changes in the pattern of activation were apparent for both syncopation and synchronization. A reduced number of significant activations was observed during syncopation (Fig. 2 right column and Table 1). Regions of activation were restricted to contralateral M1, right pre-SMA, bilateral putamen and left VLN. The activations observed during the initial syncopation session in bilateral temporal cortex, insula and ipsilateral cerebellum as well as the left SMA were no longer present following practice. For later synchronization there were several areas of significant activation in addition to those observed before practice. In addition to a significant signal

increase in contralateral GPc further activations were observed in the right SMA (medial frontal gyrus), bilateral superior temporal gyrus, middle frontal gyrus and bilateral putamen (Fig. 2 and Table 1). Furthermore, the activations observed in the auditory regions were larger than during pre-practice.

In general, constant physical rehearsal of a difficult sensorimotor coordination task (syncopation) had two main effects. The first was a decrease in specific cortical networks active during the practiced syncopation task. The second was an increase in activity within related networks during a previously stable but unpracticed synchronization task. These effects occurred in the absence of significant performance improvement; due presumably to the lack of explicit knowledge about timing error, suggesting they are related to changes in variables such as expectation, automaticity and novelty as opposed to learning, per se. For instance, increases in automaticity, and the associated decrease in attention required to perform a task, have been shown to result in decreases in the amount of widespread neural activity (see ref. [5]). The basal ganglia together with the thalamus and SMA form a network involved in the precise timing of motor behavior [13,15]. Prior to practice, activation in this network was observed only during syncopation. This is consistent with the separate timing demands of the two coordination modes: during synchronization timing information is provided by the external stimulus whereas syncopation imposes the additional requirement of making movements based on determination of the time between successive stimuli. Following practice, no changes in this network were observed during syncopation. However, small activations in bilateral putamen and SMA were observed during synchronization, apparently a carry-over effect of syncopation practice. These activation increases suggest that the degree to which the various task-related subsystems are engaged is influenced by contextual factors, including recent behavioral history.

It has been proposed that, during auditory-motor coordination, activation of primary auditory areas and anterior insula reflect perception and internal generation of auditory signals [13]. Reductions in these areas following continued exposure to the syncopation task may reflect a decrease in attention to auditory stimulation. Similarly, cerebellum has been shown to be active during sensorily guided movements [6] and is thought to use sensory feedback to update and optimize behavior [5]. In the current experiment, the increased activity within primary auditory cortex and vermis during syncopation compared to synchronization may reflect an increased awareness of, or need for sensory feedback. Post practice reductions in these areas, coupled with unchanged behavioral performance, suggest that syncopation rehearsal reduces the need to continually monitor behavior in order to maintain a specific performance level. This effect may be an indication of behavioral automaticity, a state in which accurate performance can be achieved with a relatively small demand on attentional

resources. Paradoxically, post rehearsal synchronization resulted in a slight increase in the amount of activity in auditory cortex and a similar increase in behavioral variability, perhaps reflecting increases in attention. Such an interpretation is consistent with recent results showing covariance between attentional load and coordination stability [22].

The present research has demonstrated practice-related modulation of activity within specific functional brain networks involved in sensorimotor coordination. The specific nature of the systems involved suggests that even short-term exposure to a task can reduce the amount of attention and feedback required without necessarily changing overt measures of behavioral performance. This in itself is an intriguing result since lack of measurable change in overt behavior does not necessarily translate into consistency in neural activity. In addition, we demonstrated that continuous rehearsal of one timing task might also alter activation within similar areas for a non-practiced, but related timing task. These dynamic effects in the brain appear to reflect a type of context dependence in which the neural activity that underlies a specific behavior is dependent not only on current task demands, but also on previous exposure to related tasks. Similar behavioral outcomes can thus be supported by varying neural activity patterns that evidently depend on previous task history and current context.

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