Task-Relevance and Temporal Synchrony Between Tactile and Visual Stimuli Modulates Cortical Activity and Motor Performance During Sensory-Guided Movement

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Abstract: Sensory-guided movements require the analysis and integration of task-relevant sensory inputs from multiple modalities. This article sought to: (1) assess effects of intermodal temporal synchrony upon modulation of primary somatosensory cortex (S1) during continuous sensorimotor transformations, (2) identify cortical areas sensitive to temporal synchrony, and (3) provide further insight into the reduction of S1 activity during continuous vibrotactile tracking previously observed by our group (Meehan and Staines [2007]: *Brain Res* 1138:148–158). Functional MRI was acquired while participants received simultaneous bimodal (visuospatial/vibrotactile) stimulation and continuously tracked random changes in one modality, by applying graded force to a force-sensing resistor. Effects of intermodal synchrony were investigated, unbeknownst to the participants, by varying temporal synchrony so that sensorimotor transformations dictated by the distracter modality either conflicted (low synchrony) or supplemented (high synchrony) those of the target modality. Temporal synchrony differentially influenced tracking performance dependent upon tracking modality. Physiologically, synchrony did not influence S1 activation; however, the insula and superior temporal gyrus were influenced regardless of tracking modality. The left temporal-parietal junction demonstrated increased activation during high synchrony specific to vibrotactile tracking. The superior parietal lobe and superior temporal gyrus demonstrated increased activation during low synchrony specific to visuospatial tracking. As previously reported, vibrotactile tracking resulted in decreased S1 activation relative to when it was task-irrelevant. We conclude that while temporal synchrony is represented at higher levels than S1, interactions between inter- and intramodal mechanisms determines sensory processing at the level of S1. *Hum Brain Mapp* 30:484–496, 2009. © 2007 Wiley-Liss, Inc.

Key words: multimodal integration; sensorimotor integration; somatosensory; visuospatial; vibrotactile

Contract grant sponsors: Natural Sciences and Engineering Research Council of Canada, Canada Foundation for Innovation, Ontario Research Fund.

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Received for publication 25 July 2007; Revised 17 October 2007; Accepted 26 October 2007

DOI: 10.1002/hbm.20520

Published online 19 December 2007 in Wiley InterScience (www.interscience.wiley.com).

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INTRODUCTION

Sensory-guided movements require the analysis and integration of task-relevant sensory inputs from one or multiple modalities. Recent perceptual research has shown that multiple modalities representing the same sensory event are integrated along a hierarchical processing stream. These inputs initially arrive and are processed at very distant, distinct modality-specific cortical regions before being integrated at later heteromodal processing sites [Stein et al., 2002]. However, growing evidence suggests that multisensory effects may even be present within

traditionally viewed modality-specific cortices governed by feedback projections from the traditional heteromodal areas [Macaluso and Driver, 2005] as well as more direct, shorter latency projections between the modality-specific cortices [Foxe and Schroeder, 2005].

It has been suggested that modulation of modality-specific cortex is contingent upon the temporal synchrony and/or spatial relationship between the two sensory modalities [Macaluso and Driver, 2005]. In contrast, evidence from auditory-tactile multisensory interactions suggests that they can occur along a diverse range of spatio-temporal alignments at very short processing latencies [Murray et al., 2005]. However, despite the benefits, both behavioral and physiological, of integrating sensory inputs across modalities [Murray et al., 2005] failure to extract task-relevant from irrelevant information can have adverse effects on behavior. The most common examples of this failure are the ventriloquist (where concurrent auditory stimuli are mislocalized to visual stimuli) and the McGurk (alteration of speech perception by concurrent yet conflicting lip movements) effects. It has been suggested that the extraction of task-relevant sensory information occurs through a system that weights stimulus representations through facilitation of the relevant and a relative suppression of the irrelevant sensory inputs [Gazzaley et al., 2005; Staines et al., 2002] and it is the failure to properly weight the simultaneous sensory cues, largely due to the spatial/temporal synchrony, that results in these perceptual deficits [McGurk and MacDonald, 1976; Radeau and Bertelson, 1974].

Investigations of intermodal selective attention, like those of multisensory integration, have demonstrated task-dependent modulation of modality-specific sensory cortex primarily during perceptual detection tasks. Recent imaging studies of both sustained and transient shifts of intermodal selective attention have shown not only increased activation of the modality-specific sensory cortex of the relevant modality but also a concomitant decrease in activation within the sensory representation of the irrelevant modality [Johnson and Zatorre, 2005, 2006; Shomstein and Yantis, 2004]. Converging evidence is also provided by event-related potential (ERP) studies of visual-tactile divided attention that demonstrate a reduction in the amplitude of sensory-specific perceptual somatosensory ERP components in addition to later heteromodal somatosensory ERP components compared to selective attention conditions [Kida et al., 2004]. Further, studies investigating the spatial/temporal factors have shown that the suppression within the sensory cortex of the task-irrelevant modality can depend upon its spatial/temporal relationship with the facilitated target modality during perceptual detection tasks [Eimer and van Velzen, 2005; Kida et al., 2007; Macaluso and Driver, 2001; Macaluso et al., 2002a, 2002b, 2003, 2005]. However, intermodal selective attention is not universally associated with modulation of modality-specific cortex with effects localized solely to higher order heteromodal areas [Downar et al., 2001].

Two interesting questions arise from the reviewed literature. Does changing task-demands, by introducing a continuous tracking requirement, result not only in changes in sensory-specific cortices but also in primary sensory cortex? If so, are task-demands attributed to intermodal properties such as the spatial relationship/temporal synchrony between task-relevant and irrelevant modalities reflected at this level? It is possible that the presence of intermodal effects or lack thereof in the reviewed literature may be attributable to differences in the demands associated with the various tasks, such as differences in sensory-sensory interactions or the required response, that determine where in the sensory processing stream intermodal effects manifest.

Recently, our group investigated intermodal selective attention during continuous sensorimotor transformations in the presence of simultaneous conflicting vibrotactile and visuospatial stimulation [Meehan and Staines, 2007]. In contrast to previous unimodal [Gazzaley et al., 2005; Staines et al., 2002] and bimodal [Johnson and Zatorre, 2005; 2006; Shomstein and Yantis, 2004] perceptual studies, the introduction of the continuous motor response resulted in a decrease in S1 activation contralateral to the finger of stimulation, when the vibrotactile stimulus was task-relevant relative to visuospatial tracking where the vibrotactile stimulus was irrelevant. Further, these changes in S1 activation were insensitive to the spatial relationship between the simultaneously presented modalities. However, whether modulation of S1 is sensitive to task-demands associated with the temporal synchrony between two simultaneously presented stimuli, a factor that may have a stronger influence upon multisensory processing, during a continuous tracking task is unknown.

The purpose of the current article was threefold: (1) to assess the influence of temporal synchrony upon task-relevant modulation of S1 during continuous sensory-guided movements in the presence of bimodal stimulation, (2) to identify potential modulators involved with the extraction of task-relevant information, and (3) to replicate and provide further insight into the reduction of activity in S1 during continuous vibrotactile tracking observed previously by Meehan and Staines [2007]. Functional MRI (fMRI) and behavioral measures were acquired while participants applied graded force to a force-sensing resistor according to the intensity of a continuous vibrotactile stimulus or the spatial position of a simultaneously presented continuous visual stimulus. Unbeknownst to the participants, we varied the temporal synchrony between the simultaneously presented target and distracter modalities by driving the continuous fluctuations in the vibrotactile and visuospatial stimuli with distinct or identical waveforms. Synchrony was manipulated without prior knowledge of the participant to avoid biasing the participants to a particular modality regardless of its task-relevance. In the case of low temporal synchrony, the motor response dictated by the tracking target and distracter were distinct and tracking the task-irrelevant distracter modality resulted in poor

tracking performance. However in the high temporal synchrony case, there was no such penalty to tracking the distracter, reducing sensorimotor conflict between the modalities. In all cases, participants did not receive feedback as to their tracking accuracy. To address the purposes stated above we tested four hypotheses. (1) Tracking performance would benefit when the sensory-guided responses required by the target and distracter were not in conflict (high temporal synchrony) relative to when the simultaneous inputs conflicted in the required motor response (low temporal synchrony). (2) The increase in temporal synchrony would modulate S1 activation. (3) Reducing distraction by increasing temporal synchrony would be associated with increased activation in heteromodal areas such as the superior temporal sulcus, inferior parietal lobe, and insula that have been previously implicated in detecting intermodal stimulus synchrony. (4) A comparison of the vibrotactile versus visuospatial tracking under low temporal synchrony would replicate our previous findings that S1 activity would be lower in the vibrotactile-tracking task [Meehan and Staines, 2007].

MATERIALS AND METHODS

Participants

Ten healthy volunteers (4 male, 6 female, age range 22–53) were recruited. All participants gave their written informed consent to participate in the study. The experimental procedures were approved by the Sunnybrook Health Sciences Centre Ethics Committee and the Office of Research Ethics at the University of Waterloo.

Experimental Tasks

For each of the 10 participants, fMRI was performed in the presence of simultaneous binocular visuospatial and unilateral right vibrotactile stimulation (details below). Independent bimodal stimulation was delivered in a blocked design (10 s stimulation/20 s no stimulation, 10 repetitions). Prior to the start of each collection block, participants were instructed to either track the intensity/position of one modality (target) while ignoring position/intensity of the other modality (distracter). Tracking was carried out by applying graded force to a force-sensing resistor mounted on a rigid plastic tube under the thumb of their left hand. In all cases, participants did not receive any feedback as to their tracking performance.

During the vibrotactile tracking conditions, participants were instructed to apply graded force that followed the intensity of the tactile stimulation so that as the intensity of the tactile stimulation increased, force applied to the resistor increased and as tactile intensity decreased the force applied decreased (Track Vibrotactile) (Fig. 1A). During the visual tracking conditions, participants were instructed to apply graded force in such a fashion that a needle position equivalent to seven o'clock represented minimal force,

five o'clock represented maximal force, and twelve o'clock represented intermediate force (Track Visuospatial) (Fig. 1A).

In addition to tracking the target modality, the temporal synchrony between the tracking target and distracter modalities was also manipulated. In one set of conditions, the waveforms driving the target and distracter were distinct, such that changes in the spatial position of the needle in the dial and the vibrotactile stimulus required different motor responses (low synchrony) (Fig. 1B). In a second set of conditions the waveforms driving the target and distracter were identical, such that changes in the spatial position of the needle and the intensity of the vibrotactile stimulation were linked and associated with the same motor output at any given point in time (high synchrony) (Fig. 1C). Manipulations of temporal synchrony were done without the prior knowledge of the subject, to prevent them from being biased to one specific modality over the other.

The experiment consisted of a 2 (Tracking Modality: Vibrotactile, Visuospatial) $\times$ 2 (Temporal Synchrony: Low, High) repeated measures design with four conditions in all: (1) track vibrotactile, low synchrony, (2) track vibrotactile, high synchrony, (3) track visuospatial, low synchrony, and (4) track visuospatial, high synchrony. Each condition was performed during a separate scan for a total of four functional scans per subject each 5 min in duration.

Somatosensory Stimulation

Somatosensory stimuli were presented via a custom-made MRI-compatible vibrotactile device [Graham et al., 2001]. The vibrotactile device consisted of a plastic tube with a wooden dowel (1 cm diameter) extending from the body such that the index finger, when extended, rested over the dowel's surface. The wooden dowel was controlled to vibrate at varying forces by passing fluctuating current through coils within the body of the vibrotactile device according to a 25-Hz sine wave with random intensity fluctuations. Vibrotactile stimulation was controlled by digitally generating waveforms that were converted to an analog signal at a rate of 100 Hz (DAQCard 6024E, National Instruments, Austin, TX) and then amplified (Bryston 2B-LP, Peterborough, Ontario, Canada). Variation in amplitude of the driving voltage at a given frequency (25 Hz) led to proportionate increases in force applied by the dowel onto the finger. The vibrotactile waveform varied in average frequency from 0.10 to 0.50 Hz superimposed upon the underlying 25 Hz vibrations and was generated as a random combination of four sinusoid waveforms of varying amplitude and frequency using Labview software (version 7.1, National Instruments, Austin, TX). Output from the computer was routed through a penetration panel to the magnet room using a filtered 9-pin D subconnector and shielded cable to ensure that no perceptible torque was produced by currents induced by radio-

Figure 1.

(A) Example of the experimental design. Subjects were presented with a vibrotactile stimulus on their right index finger and a bilateral visuospatial stimulus, simultaneously. On any given scan subjects tracked either the intensity of the vibrotactile stimulus or the spatial position of the needle of the dial by applying graded force to a force sensing resistor in their right hand. In the case of track visuospatial, movement of the needle to the right was a sign for subjects to apply greater force to the FSR while movement to

the left required less force to be applied. Prior to the start of the scan subjects were instructed to track one of the modalities and ignore the other. (B) An example of the stimulus waveforms and the motor output required for the track tactile and track visual conditions in the presence of low temporal synchrony (see text for details). (C) An example of the stimulus waveforms and the motor output required for the vibrotactile and visuospatial tracking conditions in the presence of high temporal synchrony (see text for details).

frequency transmit pulses or time-varying magnetic field gradients during imaging.

Visual Stimulation

The visuospatial stimulus was back projected (BoxLight 6000) onto a white screen placed at the bore of the magnet, in spatial alignment with the vibrotactile device and viewable to the subject via an angled mirror placed within the head coil. The visuospatial stimulus consisted of a white dial presented against a black background. Within the dial was a yellow needle that moved back and forth (with a maximum range of five to seven o'clock, via twelve o'clock) according to a randomly generated composite sine wave. The position of the needle was controlled by computer using the same Labview software as the vibrotactile device with an average frequency between 0.10 and 0.5 Hz.

Data Acquisition

Functional and anatomical imaging was performed at Sunnybrook Health Sciences Centre on a 3 T clinical whole body MRI scanner (GE HealthCare, Milwaukee, WI) using a standard birdcage head coil with the head immobilized. Blood oxygenation level dependent (BOLD) images were acquired axially using gradient echo imaging with single-shot spiral in-out readout (TR = 2000 ms, TE = 30 ms, flip angle $\theta = 70^\circ$, FOV = 20, 26 slices, 5 mm slice thickness). Prior to acquisition of the functional data, subjects underwent a high-resolution anatomical scan (TR = 12.4 ms, TE = 5.4 ms, flip angle $\theta = 35^\circ$, FOV = 20×16.5 , 124 slices, 1.4 mm slice thickness) for later coregistration with the functional maps. Total scan time was ~40 min.

fMRI Data Analyses

For each scan, a time series consisting of 154 images per slice location was generated by offline gridding and reconstruction of the raw data. The reconstructed time courses were analyzed using BrainVoyager QX 1.8 software (Brain Innovation, Maastricht, The Netherlands). Prior to further analysis, the first four volumes at each slice location were excluded to prevent artifact from transient signal changes as the brain reached a steady magnetized state. The following preprocessing steps were performed prior to coregistration: linear trend removal, temporal high pass filtering to remove nonlinear low-frequency drift of three cycles or less per second, and three-dimensional motion correction (using trilinear interpolation) to detect and correct for small head movements during the scan by spatially realigning all subsequent volumes to the fifth volume acquired. Estimated translation and rotation measures were visually inspected and never exceeded 1 mm and 1° , respectively. The functional data sets were transformed into Talairach space [Talairach and Tournoux, 1988] through coregistration with spatially transformed 3D anatomical data sets for each individual subject. The resulting

volume time courses were filtered using an 8-mm Gaussian kernel at full width half maximum.

To statistically evaluate the relative differences across the four experimental conditions, a multiple regression approach was employed using four predictors: (1) track vibrotactile, low synchrony, (2) track vibrotactile, high synchrony, (3) track visuospatial, low synchrony, and (4) track visuospatial, high synchrony, with the 20 s of no stimulation serving as a baseline. Four stimulation protocols using dummy-predictors (for those predictors not included in a given scan) were adopted and convolved with a boxcar haemodynamic response function [Boynton et al., 1996] to account for the expected shape and temporal delays of the physiological response. The resulting reference functions served as the model for the response time course functions used in the general linear model.

To assess task-related modulations, a two-step approach was employed. First, a region of interest (ROI) analysis was employed to assess the relative effects of the experimental manipulations on S1. This is consistent with previous studies investigating attentional modulation of S1 that demonstrate an insensitivity of voxel-based approaches to early attentional modulations within this area [Johansen-Berg et al., 2000]. Second, a voxel-based approach was then employed to determine additional areas that demonstrated task-related modulation.

For the ROI analysis, a fixed effects general linear model was employed for each individual subject, scan and ROI. Anatomical markers were used to create separate masks for both the left (contralateral to the vibrotactile stimulation) and right (ipsilateral to the vibrotactile stimulation) S1 as defined in each individual according to the following landmarks: the central sulcus anteriorly, the medial wall of the "hand knob" medially, and the most lateral edge of the postcentral gyrus [Nelson et al., 2004]. Any significant voxels that exceeded the Bonferroni corrected value of $P < 0.05$ were included in ROI analyses. Task-related changes were then quantified as changes in the intensity and volume of individual voxels relative to rest. For the intensity measurements, the individual time course data for all significantly activated voxels within a cluster were extracted and averaged across each individual subject and condition. This resulted in one time series per subject per condition representing signal changes for the tracking relative to the rest blocks for a given scan. BOLD signal changes were expressed as a percentage relative to the baseline rest. For the volume measurements, the total number of voxels that met the outlined criteria was represented as a percentage of the total number of voxels in the anatomical region defined using the landmarks stated.

Both the volume and intensity measures were analyzed using a 2 (Hemisphere: Ipsilateral, Contralateral) $\times$ 2 (Tracking Modality: Vibrotactile, Visuospatial) $\times$ 2 (Temporal Synchrony: Low, High) repeated measures analysis of variance (ANOVA) to assess any potential interactions between hemisphere, tracking modality, and temporal synchrony. Significant results were interpreted using a priori

contrasts (where applicable) and statistical significance was defined as $P < 0.05$.

For the voxel-based analysis, the same predictors outlined above in the ROI analyses were used. A separate subjects model was employed in which one predictor per condition per subject was generated and subjected to a 2 (Tracking Modality: Vibrotactile, Visuospatial) $\times$ 2 (Temporal Synchrony: Low, High) repeated measures ANOVA. Voxels were deemed significant if the threshold exceeded a corrected value of $P < 0.05$ with a cluster threshold of eight contiguous voxels [Forman et al., 1995]. The center of gravity, volume, and absolute t -statistics for each significant cluster for the main effect of temporal synchrony and the Tracking Modality $\times$ Temporal Synchrony interaction were then extracted. Areas demonstrating main effect of tracking modality, having previously been reported Meehan and Staines [2007] were not of interest in the current article and these analyses are not included. Contrasts were then computed for areas demonstrating significant changes in activation for the main effect of temporal synchrony or for the Tracking Modality $\times$ Temporal Synchrony interaction to interpret changes observed.

Behavioral Data Analysis

Tracking performance for each condition was quantified by calculating the root mean square error (RMSE) of the difference waveform derived from the graded motor response and that driving the task-relevant target. Average RMSE was calculated according to the following. First, the amplitude of the task-relevant waveform was normalized to that of the motor response. Second, the first second of tracking and last second of tracking for each block during the scan was then excluded to avoid artificial increases in RMSE associated with initial lags in participant responses. Third, the remaining motor output waveform was then subtracted from the task-relevant sensory input at each data point, yielding a difference waveform. Finally, the RMSE of the difference waveform was computed and averaged for each condition across subjects. Therefore, a decrease in the RMSE implies a decrease in the difference between the motor output generated and the sensory task-relevant target supplied, or an increase in tracking performance. In contrast, an increased RMSE implies that the difference between the motor output and sensory target increased, or tracking performance decreased.

Behavioral performance was assessed with a 2 (Tracking Modality: Vibrotactile, Visuospatial) $\times$ 2 (Temporal Synchrony: Low, High) repeated measures ANOVA using RMSE as the dependent variable. Because of technical difficulties with the force-sensing resistors during collection, the behavioral data from three subjects was dropped from the tracking performance analyses. To address issues related to sample size and power due to the loss of behavioral data, three additional participants not included in the original functional imaging data set were placed into the scanner under identical conditions to those faced by

Figure 2.

A plot of the average normalized RMS values for the tracking modality and temporal synchrony. * denotes $P < 0.05$. See text for details on calculation of average RMS.

the original participants. No fMRI data was acquired and the additional participants ran through an abbreviated block design (20 s stimulation/5 s no stimulation, 4 repetitions).

RESULTS

Behavioral Tracking Data

The means for each of the four experimental conditions are shown in Figure 2. A 2 (Tracking Modality: Track Tactile/Track Visual) $\times$ 2 (Temporal Synchrony: High/Low) ANOVA revealed a significant interaction between tracking modality and temporal synchrony [$F(1,9) = 7.77, P < 0.02$]. An inspection of Figure 2 reveals that the interaction is due to an increase in tracking performance during visual tracking in the high synchrony condition relative to the low synchrony condition (contrast; $P < 0.02$) and a slight, nonsignificant decrease in tracking performance in the high synchrony condition compared to the low synchrony condition during vibrotactile tracking. An ANOVA on the original seven participants whose behavioral data was collected during fMRI acquisition revealed a trend for an interaction [$F(1,6) = 3.70, P < 0.1$] that was identical to the pattern of results observed with the three additional participants suggesting that this interaction was present in the original group.

fMRI Data—S1 ROI Analyses

The contralateral S1 (relative to the vibrotactile sensory stimulus) anatomical ROI analyses revealed a region of increased blood flow, relative to rest, lateral to the “hand knob” of the central sulcus (average center of gravity Talairach x, y, z coordinates (SD across subjects): $-51 (6), -28 (7), 44 (5)$). The ipsilateral S1 (relative to the vibrotactile sensory stimulus) ROI analyses revealed a region of increased blood flow, relative to rest, encompassing both the medial and lateral aspects of the hand knob of the cen-

Figure 3.

(A) Plot showing the means for the percent volume of activation for the significant Hemisphere (relative to the vibrotactile stimulus) $\times$ Tracking Modality interaction. Volume is defined as the percentage of significantly active voxels relative to the total volume of the anatomically defined primary somatosensory cortex (see text for details). (B) Plot showing the means for the percent signal change for the hemisphere (relative to the vibrotactile stimulus) and tracking modality main effects. Signal change is defined as the percent signal change relative to the baseline signal for the significantly activated cluster within the anatomically defined primary somatosensory cortex (see text for details). * denotes $P < 0.05$.

tral sulcus (average center of gravity: 40 (2), -27 (3), 49 (3)).

A three-way ANOVA on the mean volume of activation, expressed as a percentage of the total volume of the original S1 anatomical ROI, revealed a significant Hemisphere $\times$ Tracking Modality interaction [$F(1,9) = 5.09$, $P < 0.05$] as well as main effects of hemisphere [$F(1,9) = 58.60$, $P < 0.00003$] and tracking modality [$F(1,9) = 14.53$, $P < 0.004$]. Contrasts revealed that the mean percent volume of activation was reduced during vibrotactile tracking compared to visuospatial tracking for both the contralateral and ipsilateral S1 ROIs (both contrasts, $P < 0.01$); however, this reduction was greater for ipsilateral S1 (Fig. 3A).

A three-way ANOVA on the mean percent signal change, relative to rest, revealed significant main effects of hemisphere [$F(1,9) = 20.34$, $P < 0.001$] and tracking modality [$F(1,9) = 20.54$, $P < 0.001$]. The main effect of Hemisphere can be attributed to a greater percent signal change within ipsilateral S1 compared to contralateral S1 (Fig. 3B). The main effect of tracking modality can be attributed to a greater percent signal change during visuospatial tracking compared to vibrotactile tracking for both the contralateral and ipsilateral S1 (Fig. 3B).

fMRI Data—Whole Brain Analyses

Main effect of temporal synchrony—Task-related changes regardless of tracking modality

Figure 4 shows the statistical contrast maps for the main effect of temporal synchrony (low synchrony vs. high synchrony regardless of modality tracked). The network of areas that demonstrated increased activation in the low synchrony relative to high synchrony conditions are shown in Figure 4A. The center of gravity and t -statistics are shown in Table I. These areas included a number of frontal areas, as well as bilateral insula (BA 13), bilateral superior temporal gyrus (BA 22) and areas of the primary and secondary visual cortices.

In addition, another network of cortical areas demonstrated greater activation in the high synchrony relative to low synchrony conditions. This left-hemisphere dominated network (contralateral to the vibrotactile stimulation) is shown in Figure 4B while the center of gravity and t -statistics are shown in Table I. These areas included the superior and medial frontal gyri (BA 8 and 10), as well as the middle temporal gyrus (BA 39) and the fusiform gyrus (BA 37).

Interaction effects: Tracking Modality $\times$ Temporal Synchrony

The interaction between tracking modality and temporal synchrony refers to those areas that demonstrated differential modality specific modulation between high temporal synchrony and low temporal synchrony. Those areas that demonstrated a significant interaction between tracking modality and temporal synchrony are shown in Figure 5. The center of gravity and t -statistics are shown in Table II.

Contrasts revealed that the interaction near the TPJ centered on the middle temporal gyrus (BA 19, extending into BA 39) could be attributed to an increase in activation during vibrotactile tracking under high temporal synchrony (relative to low temporal synchrony) but no change during visuospatial tracking. In contrast, the significant interactions observed in the left postcentral gyrus (BA 40) and inferior parietal lobule (BA 40) could be attributed to increased activation during vibrotactile tracking under low temporal synchrony.

Figure 4.

Map for areas demonstrating a main effect of temporal synchrony split according to direction of significant effect. **(A)** Map of areas demonstrating greater activation during low temporal synchrony relative to high temporal synchrony. Note, left medial frontal gyrus and right superior frontal gyrus not visible. **(B)** Map of areas demonstrating greater activation during high tem-

poral synchrony relative to low temporal synchrony. Note: medial frontal gyrus not visible. The maps are overlaid on an individual's inflated cortex and the colour scale reflects *t*-values. CS—central sulcus, IFG—inferior frontal gyrus, STG—superior temporal gyrus, ITG—inferior temporal gyrus, LG—lingual gyrus, and IOG—inferior occipital gyrus.

Figure 5.

Map for areas demonstrating a significant Tracking Modality $\times$ Temporal Synchrony interaction, see text and Table II for interpretation. The color scale reflects *t*-values. CS—central sulcus, PoCG/SPL—postcentral gyrus/superior parietal lobule, IPL—inferior parietal lobule, STG—superior temporal gyrus, MTG—middle temporal gyrus.

TABLE I. Activated clusters from areas demonstrating a main effect of temporal synchrony

Condition	Anatomical (Brodmann) area	<i>x</i>	<i>y</i>	<i>z</i>	<i>t</i> -statistic
Main effect: Temporal synchrony					
Areas demonstrating greater activation during low synchrony relative to high synchrony	Lt. medial frontal gyrus (BA 6)	-7	-7	62	4.70
	Rt. inferior frontal gyrus (BA 9)	48	12	23	4.57
	Bil. insula (BA 13)	-31/30	25/26	6/5	5.22/5.83
	Bil. superior temporal gyrus (BA 22)	-65/59	-37/-35	10/14	5.06/5.61
	Rt. superior frontal gyrus (BA 10)	34	49	24	4.78
	Rt. inferior occipital gyrus (BA 17)	17	-89	-7	4.89
	Lt. lingual gyrus (BA 18)	-23	-69	-13	4.95
	Rt. inferior temporal gyrus (BA 20)	50	-25	-15	5.94
	Rt. cerebellum—posterior lobe, tuber	37	-66	-25	4.99
	Rt. cerebellum—posterior lobe, cerebellar tonsil	27	-41	-36	4.54
	Lt. cerebellum—posterior lobe, semi-lunar lobule	-35	-63	-36	4.93
	Rt. cerebellum—anterior lobe, culmen	18	-54	-18	4.55
Areas demonstrating greater activation during high synchrony relative to low synchrony	Lt. superior frontal gyrus (BA 8)	-16	33	45	5.04
	Lt. medial frontal gyrus (BA 10)	-2	68	13	4.62
	Lt. middle temporal gyrus (BA 39)	-46	-70	20	5.58
	Lt. fusiform gyrus (BA 37)	-43	-51	-13	5.05

Areas are separated according to direction of significant effect.

The interaction effect observed in the left superior temporal gyrus can be attributed to an increase in activation during visuospatial tracking under high temporal synchrony (relative to low synchrony) but no change during vibrotactile tracking. In contrast, the significant interactions observed in the right postcentral gyrus (BA 5), right superior parietal lobe (BA 7), and right superior temporal gyrus (BA 22) can be attributed to an increase in activation dur-

ing visuospatial tracking under low temporal synchrony but no change during vibrotactile tracking.

DISCUSSION

The present study assessed the effect of temporal synchrony between simultaneously presented vibrotactile/

TABLE II. Activated clusters from areas demonstrating a tracking modality × temporal synchrony interaction effect

Condition	Anatomical (Brodmann) area	<i>x</i>	<i>y</i>	<i>z</i>	<i>t</i> -statistic
Interaction: Modality × Synchrony					
Areas demonstrating increased activation during high synchrony relative to low synchrony during vibrotactile tracking only	Lt. middle temporal gyrus (BA 19)	-43	-59	15	4.94
Areas demonstrating increased activation during low synchrony relative to high synchrony during vibrotactile tracking only	Lt. post-central gyrus (BA 40)	-64	-18	16	5.83
	Lt. inferior parietal lobule (BA 40)	-53	-31	34	4.99
Areas demonstrating increased activation during high synchrony relative to low synchrony during visuospatial tracking only	Lt. Superior Temporal Gyrus (BA 22)	-62	3	-5	5.56
Areas demonstrating increased activation during low synchrony relative to high synchrony during visuospatial tracking only	Rt. post-central gyrus (BA 5)	25	-40	64	4.77
	Rt. precuneus (BA 7)	13	-57	61	4.63
	Rt. superior temporal gyrus (BA 22)	52	-45	16	5.11

Areas are separated according to effects driving interaction as revealed by contrasts.

visual stimuli upon task-relevant modulation of tracking performance and cortical activation (including S1) during continuous sensory-guided movement. Functional MRI was acquired when participants tracked changes in the target modality while ignoring those in an irrelevant distracter modality. Temporal synchrony was manipulated by changing the stimulus-response relationships between the simultaneously presented target and distracter modalities. The specific hypotheses were partially supported. As hypothesized, tracking performance increased during visuospatial tracking during high temporal synchrony compared to low synchrony; however, this was not the case during vibrotactile tracking. Changes in temporal synchrony were not reflected at the level of S1 as tracking performance and S1 activation were dissociated. Instead changes in temporal synchrony were observed in networks of higher order heteromodal areas including networks sensitive to temporal synchrony regardless of the modality to be tracked, networks sensitive to temporal synchrony specific to vibrotactile tracking and those sensitive to temporal synchrony specific to visuospatial tracking. Finally, as hypothesized S1 activation was reduced during continuous vibrotactile tracking relative to during continuous visuospatial tracking in the presence of an irrelevant vibrotactile stimulus.

Participants tracked both the vibrotactile and visuospatial stimuli equally well and as hypothesized visuospatial tracking benefited from a nonconflicting temporally synchronous distracter modality. It was thought altered task-demands associated with increased temporal synchrony would result in increased tracking performance due to decreased feed-forward competition between the representations of each modality. There are two possible explanations for this benefit. First, intermodal selective attention was more effective at extracting the target modality due to a change in distracter salience when it was in temporal synchrony (required the same motor response) as the visuospatial target. Alternatively, it is possible that the task-irrelevant representation of the nonconflicting vibrotactile distracter simply fed forward along the hierarchical model and was integrated involuntarily into the motor response due to the spatial and temporal relationship between the target and distracter modalities resulting in a benefit to tracking performance [Murray et al., 2005], similar to the ventriloquist and McGurk effects without the detriment to performance [Macaluso et al., 2004]. In contrast to the visuospatial task, vibrotactile-tracking performance was not altered by the temporal synchrony between the vibrotactile target and visuospatial distracter. During stimulus onset asynchrony visual-tactile congruency effects are larger when the visual stimulus precedes a tactile stimulus [Shore et al., 2006]. Therefore, it is possible that the differential effect of temporal synchrony may be explained by differences in task-demands associated with the nature of the information extracted from a vibrotactile versus visuospatial stimulus.

A key finding in this study was that S1 activation volume was not influenced by the temporal synchrony

between the target and distracter modalities. This is consistent with our previous work [Meehan and Staines, 2007] and others [Murray et al., 2005] demonstrating insensitivity of S1/early cortical activity to the spatial relationship between simultaneously presented intermodal stimuli despite behavioral task performance differences. Previously we offered two alternate hypotheses to explain the lack of spatial interaction at the level of S1, (1) that there was a lack of explicit value associated with spatial location to the tracking task and/or (2) there was a lack of higher level feedback to S1. Similar to the manipulation of spatial location temporal synchrony does not appear to mediate primary cortical activity beyond that already associated with tracking modality. This would suggest that intermodal selective attention works at the level of S1 to extract task-relevant information (possibly through low-level pathways) but works at subsequent processing levels to extract other features (via top-down feedback from heteromodal areas). This notion is supported by previous work demonstrating excitatory changes in primary visual cortex during somatosensory processing but inhibitory changes in secondary and subsequent visual areas [Merabet et al., 2007]. Alternatively, it is possible that the temporal synchrony manipulation was not strong enough to elicit any differences although this seems unlikely due to the behavioral interaction observed.

The decrease in S1 activation volume, contralateral to the vibrotactile stimulus, during vibrotactile tracking compared to visuospatial tracking was similar to that which we previously observed [Meehan and Staines, 2007]. This result was novel as previous studies investigating intermodal selective attention [Johnson and Zatorre, 2005, 2006; Shomstein and Yantis, 2004] are generally associated with increased activation over modality-specific cortices of the relevant modality. In the current study, we also observed a decrease in the intensity of activation (% signal change) within the same contralateral S1 that mirrored the volume changes, a change not observed in our previous work. In addition, we also report similar changes in S1 activation, ipsilateral to the vibrotactile stimulus (but contralateral to the motor response). These additional results offer further insight into potential explanations originally offered [Meehan and Staines, 2007] for this novel result. Although the decrease in volume of activation of contralateral S1 supports surround inhibition [Drevets et al., 1995] associated with vibrotactile tracking the concomitant decrease in signal intensity within contralateral S1 make it unlikely as one would expect to see either no change or an increase in signal intensity associated with a facilitation of the neuronal activity of the core set of relevant neurons. Of the two remaining explanations, the role of low-level influences [Cappe and Barone, 2005; Foxe et al., 2000] and/or interhemispheric cortical-cortical interactions [Hlushchuk and Hari, 2006; Hoshiyama and Kakigi, 1999; Seyal et al., 2005], the most plausible is that the decreased S1 activation is due to an interaction between interhemispheric and intermodal selective attention mechanisms brought about by

the presence of functionally relevant somatosensory information in S1 ipsilateral to the vibrotactile stimulus but contralateral to the sensory feedback from the continuous movement.

Interhemispheric interactions have been demonstrated using cooling of ipsilateral S1 [Clarey et al., 1996] and repetitive TMS over ipsilateral M1 [Seyal et al., 2005]. Cooling of ipsilateral S1 results in an increase in the receptive field of contralateral S1, thought to be mediated by the removal of tonic inhibition from the cooled ipsilateral S1 while repetitive TMS over ipsilateral primary motor cortex can reduce the amplitude of early SEP potentials in S1 as well as perceptual threshold. However, interhemispheric interactions are generally associated with a negative correlation between the hemispheres. Yet in the current study, both contralateral and ipsilateral S1 demonstrate identical patterns of excitability changes, both demonstrating reduced excitability during vibrotactile tracking. Alternatively, the influence of low-level connections between the two modalities cannot be ruled out as it has been demonstrated that during tactile sensory processing, primary visual cortex demonstrates increased activity despite decreased activity in secondary visual cortices [Merabet et al., 2007]. Therefore, it is possible that the increase in S1 activation may be attributable to coactivation during visuospatial tracking. However, under this explanation one might expect no difference in S1 activation during visuospatial and vibrotactile tracking. Therefore, it is possible that the reduction in S1 activation may be attributable to an interaction between these mechanisms associated with the different task demands imposed by the continuous tracking requirement use currently and perceptual tasks used previously. We suggest that participants may employ a task-switching strategy, in order to perform the tracking task correctly, due to the need to simultaneously extract the vibrotactile sensory stimulus and monitor proprioceptive feedback from the motor effector that recruits intramodal selective attention mechanisms due to the competition between the two relevant somatosensory inputs. This mechanism results in a competitive disadvantage within S1 of both hemispheres that is not present during visuospatial tracking because the contralateral vibrotactile sensory inputs are irrelevant returning ipsilateral activation to baseline. However, intermodal mechanisms result in contralateral S1 activation associated during visuospatial tracking. Under this hypothesis, one would expect a relative decrease in both ipsilateral and contralateral S1 during vibrotactile tracking relative to visuospatial tracking with the interaction between the two mechanisms resulting in parallel changes in activation with S1 of both hemispheres.

In addition to investigating changes in S1, we observed additional areas that were sensitive to the temporal synchrony between the target and distracter regardless of tracking modality. Areas that demonstrated increased activation during tracking under high synchrony compared to low temporal synchrony included an area of the middle temporal gyrus (BA 39) near the temporal-parietal junction,

the fusiform gyrus (BA 37), superior frontal gyrus (BA 8), and medial frontal gyrus (BA 10). In particular, the superior frontal gyrus (BA 8) has been suggested to be part of a network, including the superior colliculus, involved in cross-modal integration of synchronous sensory inputs [Calvert et al., 2001]. This area as well as those around the middle temporal (BA 39) and inferior frontal/fusiform gyri (BA 37) have also been implicated in the detection and extraction of task relevant information, presumably the detection, extraction, and integration of the irrelevant modality during cases of high temporal synchrony.

In addition, a large network of areas demonstrated increased activity during tracking under low temporal relative to high temporal synchrony (Table I, bottom). The increased activation in these areas likely reflects the increased task demands associated with extracting the relevant information and the subsequent sensorimotor transformations under low temporal synchrony. In particular, left insular activation (BA 13) has been associated with extraction of task-relevant information in the presence of cross-modal irrelevant distracters [Downar et al., 2001]. The superior temporal gyrus (BA 22) is often associated with multisensory integration, however, the associated activation is generally reported in the posterior portions of the gyrus compared to the more anterior activation reported here, perhaps reflecting consciousness-related binding [Bischoff et al., 2007]. Other areas including the medial frontal gyrus (BA 6) in the area of the SMA and the inferior frontal gyrus (BA 9) also known as the dorso-lateral prefrontal cortex have been implicated with selective attention and the extraction of task-relevant information [Staines et al., 2002], demands that are more prevalent during tracking under low temporal synchrony.

In addition to areas that were influenced by temporal synchrony regardless of tracking modality, there were a number of areas that demonstrated differential effects dependent upon the tracking modality and the irrelevant distracter modality (Table II). Only an area of the TPJ (middle temporal gyrus, BA 19/39) demonstrated increased activation during high temporal synchrony but only during vibrotactile tracking. This heteromodal area has been implicated in the extraction of task-relevant as well as multisensory integration [Matsushashi et al., 2004] and may reflect the detection/extraction of potentially task-relevant information from the distracter modality due to the high temporal synchrony and resulting convergence of the vibrotactile and visuospatial representations. This is supported by the change in tracking performance. In contrast, areas of the inferior parietal lobule and postcentral gyrus (BA 40) sensitive to low temporal synchrony specific to vibrotactile tracking supports evidence of their role in somatosensory processing [Johansen-Berg and Lloyd, 2000] and likely reflects task-relevant facilitation during situations where extraction of task-relevant somatosensory information is critical to task performance [Staines et al., 2002].

For the interaction between temporal synchrony of competing sensory targets and the specific task-relevant

modality, only the middle to anterior portion of the left superior temporal gyrus (BA 22) demonstrated increased activation under high temporal synchrony specific to visuospatial tracking. Again, this area may reflect consciousness-related binding [Bischoff et al., 2007] and may be associated with increased tracking performance in this condition. In contrast a number of areas demonstrated increased activation during low temporal synchrony relative to high temporal synchrony that was specific to visuospatial tracking. This specific sensitivity can likely be attributed to the change in task demands associated with the visuospatial stimulus. In particular, increased activation in the right superior parietal lobe (BA 5) during visuospatial tracking under low synchrony could be attributed to the increased demand on these areas during visuomotor transformations, including reference frame transformations [Buneo and Andersen, 2006].

In conclusion, this study demonstrated that temporal synchrony between a visuospatial and vibrotactile stimulus is not reflected at the level of S1 despite previous evidence to suggest that it is reflected at the level of modality-specific cortex. Instead, it appears that areas of the TPJ, superior temporal gyrus, and anterior insula may mediate detection of temporal synchrony and task-relevance. In contrast to temporal synchrony, the relevance of the vibrotactile stimulus does appear to be reflected at the level of S1 when it is presented with a concurrent visuospatial stimulus regardless of temporal synchrony. Further, this relevance representation in S1, manifested as a decrease in activation when the vibrotactile stimulus is task-relevant, appears to be the result of interhemispheric influences between sensorimotor cortex associated with the continuous tracking aspect of the current task, not present during visuospatial tracking, that may interact with the traditional facilitatory intermodal selective attention mechanisms. This suggests that sensorimotor requirements may have an important modulatory role in modulating feed-forward activation within primary somatosensory cortex compared to top-down effects from heteromodal areas. This could have implications for the efficacy of rehabilitative strategies in functional recovery after sensorimotor damage.

ACKNOWLEDGMENTS

The authors thank Amaya Singh and Gary Detzler for technical assistance. This work was supported by a research grant to WRS from the Natural Sciences and Engineering Research Council of Canada.

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