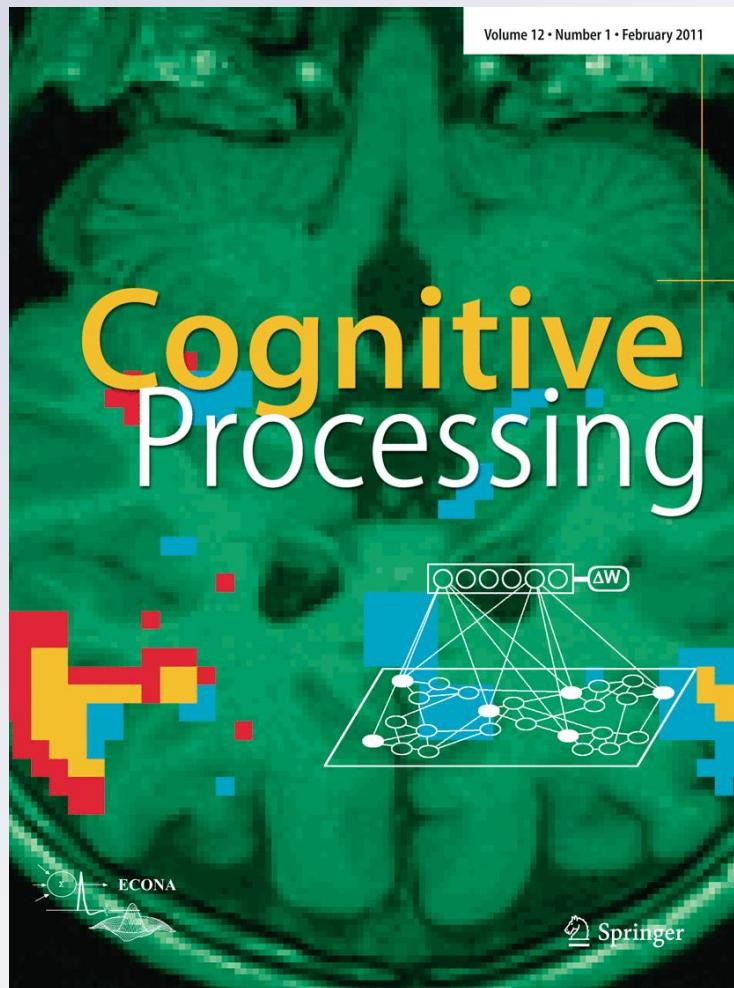


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Effects of feedback from active and passive body parts on spatial and temporal parameters in sensorimotor synchronization

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Abstract Previous research on sensorimotor synchronization has manipulated the somatosensory information received from the tapping finger to investigate how feedback from an active effector affects temporal coordination. The current study explored the role of feedback from passive body parts in the regulation of spatiotemporal motor control parameters by employing a task that required finger tapping on one's own skin at anatomical locations of varying tactile sensitivity. A motion capture system recorded participants' movements as they synchronized with an auditory pacing signal by tapping with the right index finger on either their left index fingertip (Finger/Finger) or forearm (Finger/Forearm). Results indicated that tap timing was more variable, and movement amplitude was larger and more variable, when tapping on the finger than when tapping on the less sensitive forearm. Finger/Finger tapping may be impaired relative to Finger/Forearm tapping due to ambiguity arising through overlap in neural activity associated with tactile feedback from the active and the passive limb in the former. To compensate, the control system may strengthen the assignment of tap-related feedback to the active finger by generating correlated noise in movement kinematics and tap dynamics.

Keywords Sensorimotor synchronization · Sensory feedback · Timing · Kinematics · Intra-active touch

Introduction

The coordination of one's actions with external events in space and time is a fundamental human skill. The mechanisms underlying temporal coordination are often investigated with sensorimotor synchronization paradigms that require participants to tap a finger in time with an isochronous sequence of clicks (see Repp 2005, for a review). In the current study, we employ a motion capture system to record spatial as well as temporal features of tapping movements while sensory feedback is manipulated in a novel manner that involves tapping on different locations of one's own body. The main aim of the study is to test whether feedback from these 'passive' body parts plays a role in the spatiotemporal control of movement during sensorimotor synchronization.

In conventional studies addressing temporal aspects of sensorimotor synchronization, it is typically found that taps precede clicks by several tens of milliseconds. This *negative mean asynchrony* has been taken to indicate that subjective synchrony is established at a central 'representational' level via anticipatory timing mechanisms that function to ensure that the arrival of (relatively slow) somatosensory feedback from finger taps coincides with (faster) auditory feedback from pacing sequence clicks (see Aschersleben 2002).

Studies testing this sensory feedback-based account have manipulated (1) whether or not taps produce sounds, and, if so, the temporal displacement between taps and feedback sounds (Aschersleben and Prinz 1995, 1997; Mates and Aschersleben 2000), (2) the force with which taps are made on a solid surface (Aschersleben et al. 2004), and (3) whether taps are made on a solid surface or in the air (Aschersleben et al. 2001). Additional approaches have involved applying local anesthetic to participants' fingers

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(Aschersleben et al. 2001) and comparing the performances of deafferented patients (with complete loss of somatosensory feedback below the neck) and healthy controls (Stenneken et al. 2006). The general outcome of these studies is that mean asynchrony decreases with increasing availability of feedback.

Less is known about the effects of sensory feedback on *timing variability* during synchronization. Stenneken et al. (2006) found that the variability of asynchronies was higher for one deafferented patient than for controls, while a second patient was less variable than controls. Another study demonstrated that anesthetizing healthy fingers does not increase variability (Aschersleben et al. 2001). However, work on other forms of coordination has shown that supplementary auditory feedback can facilitate temporal stability in antiphase (off-beat) tapping (Keller and Repp 2008). Furthermore, in studies of the bimanual advantage in self-paced tapping, the increased feedback provided when tapping synchronously with two hands decreases the variability of inter-tap intervals relative to unimanual tapping (Drewing and Aschersleben 2003; cf. Drewing et al. 2004).

Models that address the role of feedback in sensorimotor synchronization typically assume that sensory information from different sources—usually separate modalities—is integrated to form central representations that guide movement timing (e.g., Aschersleben 2002; Aschersleben et al. 2004). Related work on multisensory integration suggests that information from each source would be weighted according to its reliability in such representations (see Ernst and Bülthoff 2004). If one source of feedback is eliminated or rendered ambiguous or unreliable (e.g., due to degradation or masking), then the actor may compensate by increasing feedback on another dimension. Evidence for such compensation has been observed in a recent motion capture study that required musicians to produce temporally regular sequences of finger taps on multiple keys of a response device (Keller et al., in press). The amplitudes of finger movements were found to be larger in experimental conditions where taps did not trigger tones than in conditions where taps did trigger tones. Keller et al. (in press) interpreted this increase in movement amplitude to reflect an attempt to enhance tactile feedback by increasing the force with which keys were struck in the absence of auditory feedback. According to this account, a spatial motor control parameter (movement amplitude) was modulated in order to regulate sensory feedback in the service of precise temporal control (cf. Aschersleben et al. 2004; Goebl and Palmer 2009).

The research described above addresses the role of sensory feedback associated with an *active* effector (the moving finger). The aim of the current study was to test whether ancillary feedback from *passive* body parts affects spatiotemporal coordination during sensorimotor

synchronization. Active and passive sources of feedback are simultaneously present during ‘*intra-active*’ touch, i.e., when an individual touches his or her own body, as when cleansing, grooming, or using the body as a percussive instrument (e.g., palmas in Flamenco music).

Work on intra-active touch has shown that the contribution of the passive component to overall sensation depends on the body region that is touched. For example, a magnitude estimation study that required steel balls to be rolled by an active index finger upon either a passive thumb or a passive forearm (in addition to various control conditions) found that perceived size was determined by feedback from the passive component in the thumb condition and feedback from the active component in the forearm condition (Bolanowski et al. 2004). Bolanowski et al. proposed that different mechanisms are engaged when active and passive regions are similar in tactile sensitivity than when these regions differ in sensitivity.

It is known from psychophysical and physiological studies that tactile sensitivity is greater for the glabrous skin of the fingers than for the hairy skin of the forearm, in part because glabrous skin is relatively high in mechanoreceptor density and is represented by large areas of somatosensory cortex (Bolanowski et al. 1988). In a classic study, Weinstein (1968) found that, although the index fingertip and forearm do not differ reliably in pressure sensitivity, they do differ massively in two-point discrimination sensitivity and point localization thresholds (which were measured by requiring participants to judge whether a stimulation point differed from a previously stimulated reference point). Furthermore, research on vibration detection has revealed that differences in the anatomical and physiological organization of tactile channels in glabrous and hairy skin can affect temporal processing (Gescheider et al. 2004). Specifically, vibrotactile thresholds for the finger are determined primarily by the Pacinian channel, where receptors are most sensitive to frequencies higher than 40 Hz, while thresholds for the forearm are determined mainly by non-Pacinian channels, where receptors are most sensitive to lower frequencies extending down to 2 or 0.4 Hz, depending on the channel (Morioka et al. 2008).

The current study, which is exploratory in nature, employed an intra-active sensorimotor synchronization paradigm to investigate how the timing and kinematics of the active finger are affected by tactile feedback from passive body parts that vary in sensitivity. In each of three experiments, a motion capture system recorded participants’ movements as they synchronized with a 2-Hz auditory pacing signal by tapping with the right index finger on either their own left index finger or forearm. Several additional conditions—in which participants tapped on others’ bodies, soft rubber surfaces, or hard wooden surfaces—were also included across the experiments.

However, the current empirical report focuses on the effects of correspondence between active and passive parts of one's own body (Finger/Finger vs. Finger/Forearm) upon synchronization accuracy and movement amplitude. We expected that synchronization accuracy would be higher when tapping on the passive finger than the forearm due to the finger's relatively high tactile receptor density and fine temporal sensitivity. We were also interested in whether movement amplitude would be modulated to compensate for this effect of tap target location on synchronization accuracy.

Methods

Participants

A total of 75 right-handed, healthy adults participated in the three experiments (with different individuals in each experiment). Forty-five participants were female, median age was 24 years (range 19–33 years), and median years of musical training was 7 (range 0–24).

Materials and procedures

Each experiment utilized a repeated measures design in which participants synchronized with an auditory pacing signal by tapping with the right index finger on several different surfaces. All experiments included conditions where participants tapped on the palmar surface of the distal phalanx of their own left index fingers (Finger/Finger) and the volar surface of their forearms, one-third of the forearm's length distal to the crease of the elbow (Finger/Forearm). In addition, participants tapped—in separate experiments—on (a) two wooden surfaces, i.e., a tabletop and a block of wood of similar height and breadth to an average forearm (Experiment 1), (b) other same-gender participants' left fingers and forearms (Experiments 2 and 3), and (c) rubber surfaces with firmness that matched average fingers and forearms (based on measurements from a representative sample) (Experiment 3). Condition order was counterbalanced across participants in each experiment.

Participants were tested individually while sitting on a height adjustable chair at a table. They wore headphones and a 'marker' (an infrared light-emitting diode) attached to the fingernail of the right index finger. Two different arm positions were adopted across experiments for the Finger/Finger and Finger/Forearm conditions. In one arrangement (used in Experiments 1 and 2), the left forearm rested on the table with the palm facing up in both conditions. The right hand rested palm down in a position that facilitated tapping on the left index fingertip in the Finger/Finger

condition (where the left finger was extended, resting on the table, and the other fingers were flexed), while the right hand was supported by a foam wedge that raised it to a comfortable height for tapping on the left forearm in the Finger/Forearm condition. The second arrangement (used in Experiment 3) required participants to rest their left and right arms on separate adjustable splints positioned on the table. The splints were arranged for each participant in such a way that the position of the right arm was held constant across conditions, while the position of the left arm was adjusted to bring the left finger or forearm target region into contact with the right finger. The location of the various surfaces used in the other conditions allowed the right hand to tap in a similar manner to when participants tapped on their own fingers and forearms.

Each condition was run in two separate blocks of 1 practice plus 10 test trials. The pacing signal in each trial consisted of 48 clicks (1,000 Hz, with 20 ms duration) separated by 500 ms inter-onset intervals and delivered at a comfortable loudness level over the headphones. Click timing was controlled by Presentation software (Neurobehavioral Systems) running on a Windows PC. Each trial was initiated by the experimenter pressing the spacebar on the computer keyboard when the participant indicated readiness.

Participants were instructed to start tapping with the fifth click in each trial and to move only the right index finger when tapping. It was emphasized that they should synchronize as accurately as possible under all conditions. Text on the computer screen reminded participants of the tap target region prior to each trial. In addition, a laser pointer mounted above the apparatus was illuminated between trials to indicate the precise tap target location. Participants were instructed to maintain visual fixation on this location during the trial.

The three-dimensional position of the marker attached to the right index finger was tracked by an Optotak Certus motion capture system (Northern Digital Inc.) with 250-Hz sampling frequency. Information about marker position was relayed by the Optotak System Control Unit to a second PC for storage. This PC also stored information about click onset times and codes identifying each condition and trial by recording digital signals that issued from the parallel port of the Presentation PC to the System Control Unit via an Optotak Data Acquisition Unit II. Motion data and events controlled by Presentation were thus recorded at the same frequency.

Dependent measures

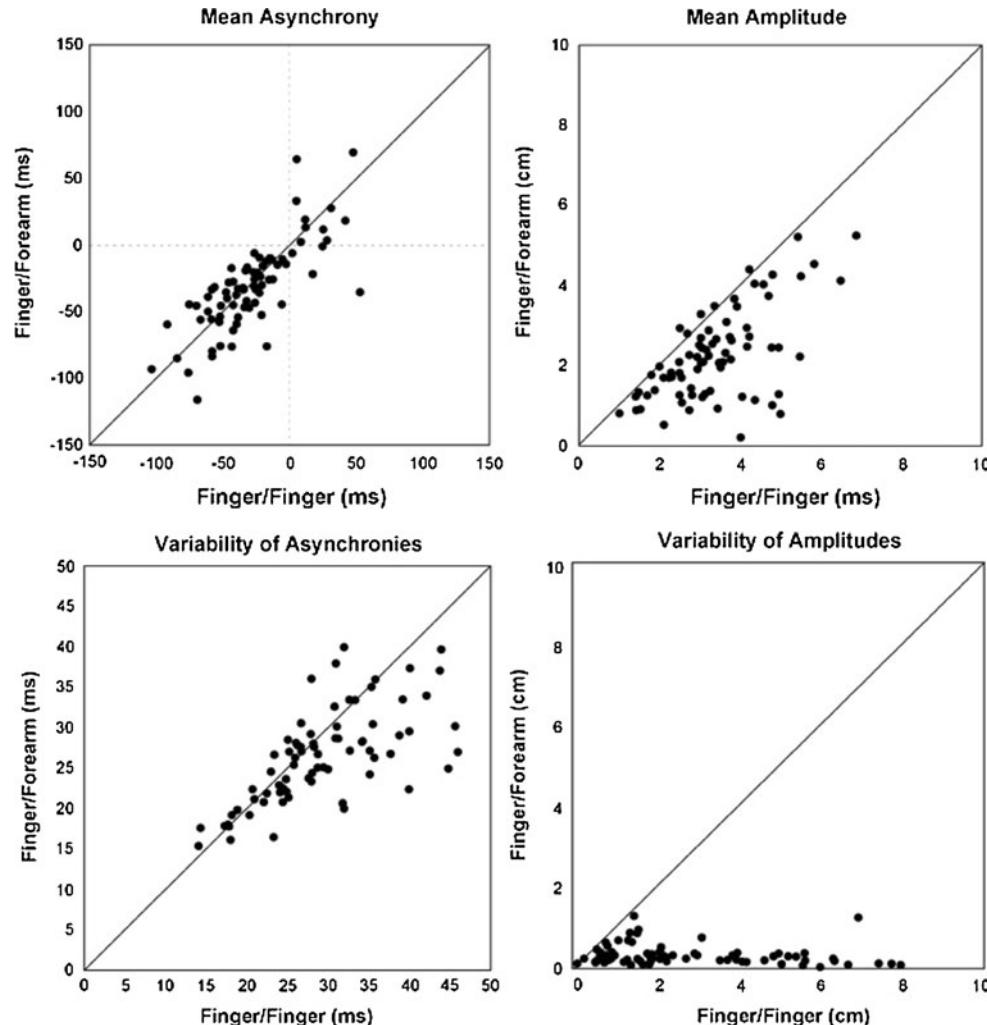
Measures of movement timing and spatial kinematics were computed offline from the finger motion data. For the timing measures, information about tap contact times was

extracted from the finger trajectories (by finding local minima in vertical position), and the asynchrony between each click and the nearest tap was computed (tap time minus click time). Two indices of synchronization accuracy were then calculated for each participant in each condition: *mean asynchrony* and *variability of asynchronies* (i.e., the average within-trial standard deviation of asynchronies). For spatial kinematics, movement amplitude for each tap was measured by calculating the difference between the maximum and minimum vertical position of the finger. *Mean amplitude* and *variability of amplitudes* (average within-trial standard deviation of amplitudes) were subsequently computed for each participant in each condition. For all measures, only taps made in relation to the final 36 pacing clicks were analyzed.

Results

This report focuses on results from the Finger/Finger and Finger/Forearm conditions, pooled across experiments.

Fig. 1 Individual participants' average data for *mean asynchrony*, *variability (SD) of asynchronies*, *mean amplitude*, and *variability (SD) of amplitudes* in Finger/Finger and Finger/Forearm conditions



Data from these conditions are shown for each of the four dependent measures in a separate scatter plot in Fig. 1. Here, it can be seen that there was a positive correlation between performance in Finger/Finger and Finger/Forearm conditions for *mean asynchrony* ($r = 0.77$), *variability of asynchronies* ($r = 0.68$), and *mean amplitude* ($r = 0.62$) ($P < 0.01$), whereas this was not the case for *variability of amplitudes* ($r = -0.17$). It can also be seen that most participants' average scores are higher in the Finger/Finger condition than in the Finger/Forearm for *variability of asynchronies*, *mean amplitude*, and *variability of amplitudes* (i.e., scores fall below the diagonal, most clearly for *variability of amplitudes*), but not for *mean asynchrony*.

One-way repeated measures ANOVAs performed separately on data for each dependent measure confirmed the reliability of the above pattern of results. For the timing measures, there was no statistically significant difference in *mean asynchrony* between Finger/Finger (-28.17 ms) and Finger/Forearm (-31.38 ms) conditions [$F(1, 74) = 1.55$, $P = 0.22$], while there was a significant difference in *variability of asynchronies* between Finger/Finger (29.16 ms)

and Finger/Forearm (26.34 ms) conditions [$F(1, 74) = 18.88, P < 0.01$].

For spatial kinematics, significant differences were found between Finger/Finger and Finger/Forearm conditions for both *mean amplitude* [$F(1, 74) = 91.78, P < 0.01$] and *variability of amplitudes* [$F(1, 74) = 98.50, P < 0.01$], indicating that movement amplitude (3.40 cm) and variability (2.78 cm) for Finger/Finger tapping were larger than amplitude (2.27 cm) and variability (0.34 cm) for Finger/Forearm tapping. In an additional analysis, coefficients of variation were calculated by dividing each participant's *variability of amplitudes* score by his/her *mean amplitude* score, and the resulting values were fed into an ANOVA. This analysis revealed a significant difference between Finger/Finger (0.83 cm) and Finger/Forearm (0.16 cm) conditions [$F(1, 74) = 119.10, P < 0.01$], replicating the result that variability was highest in the former. This finding suggests that—although variability and mean amplitude were positively correlated in Finger/Finger ($r = 0.34, P < 0.01$) and Finger/Forearm ($r = 0.55, P < 0.01$) conditions—the effect of passive body region on the variability of movement amplitude was not a trivial side effect of differences in mean amplitude when tapping at the two regions.

The results for additional experimental conditions that required tapping on wooden and rubber surfaces, and on others' fingers and forearms, are shown in Table 1. Here, it can be seen that, regardless of the type of surface (wood, rubber, or another's skin), little evidence was found for differences in performance across the two target regions that served as surrogate fingers and forearms. The single exception was *variability of asynchronies* when tapping on another person's body: Timing variability was reliably higher when tapping on another person's finger than when tapping on their forearm.

Discussion

The results of the present study suggest that the timing and spatial kinematics of the active finger are affected by the identity of the passive body part upon which one taps during intra-active sensorimotor synchronization. The results were not entirely as expected, however. Tap timing was more variable, and movement amplitude was both larger and more variable, when tapping on the finger than when tapping on the forearm. Mean asynchrony did not differ across these locations. The results in control conditions that required tapping on surfaces that were not on one's own body bore little resemblance to results in the Finger/Finger and Finger/Forearm conditions, suggesting that the above effects are not attributable to the position of

Table 1 Average data for *mean asynchrony* (M Async.), *variability of asynchronies* (SD Async.), *mean amplitude* (M Amp.), and *variability of amplitudes* (SD Amp.) in conditions that required tapping on various surfaces that served as surrogates for participants' own fingers and forearms: wooden surfaces, i.e., tabletop vs. block (Experiment 1), others' fingers and forearms (Experiments 2 and 3), and rubber surfaces varying in relative firmness (Experiment 3)

Measure	Surrogate	Surrogate	<i>F</i>	<i>P</i>	
	finger	forearm			
	Table	Block			
Experiment 1					
M Async.	−28.70 (31.41)	−25.25 (33.59)	0.79	0.40	
SD Async.	27.22 (8.37)	29.01 (8.95)	1.15	0.31	
M Amp.	1.66 (0.71)	1.33 (0.57)	2.36	0.15	
SD Amp.	0.22 (0.08)	0.21 (0.16)	0.02	0.88	
	Other finger		Other arm		
Experiments 2 and 3					
M Async.	−33.01 (27.42)	−34.90 (31.81)	0.40	0.53	
SD Async.	28.15 (7.05)	25.87 (5.85)	15.98	<0.01	
M Amp.	2.09 (1.15)	2.03 (1.04)	0.63	0.43	
SD Amp.	0.31 (0.20)	0.39 (0.56)	1.28	0.26	
	Firm rubber		Infirm rubber		
Experiment 3					
M Async.	−24.73 (40.57)	−21.08 (38.30)	2.22	0.15	
SD Async.	27.65 (6.78)	28.44 (8.23)	1.20	0.28	
M Amp.	3.38 (1.27)	3.34 (1.25)	0.54	0.47	
SD Amp.	0.43 (0.24)	0.48 (0.32)	0.87	0.36	

Asynchrony data are in ms and amplitude data are in cm. The sample standard deviation is shown below each mean value in parentheses. *F*-values, *P*-values, and degrees of freedom (*df*) for surrogate finger vs. forearm comparisons are shown in the two rightmost columns

Note that Table and Block amplitude data for nine participants from Experiment 1 could not be analyzed due to equipment failure. Specifically, four reference markers fixed to the tabletop ceased operating midway through Experiment 1, though the experimenters did not become aware of this fact until the completion of the experiment. Amplitude data were processed using a computer program that required position information from these reference markers. (Timing data were analyzed using a program that did not rely upon information from these markers)

the right hand in the apparatus or to differences between finger and forearm firmness or size.

There was, however, an intriguing tendency for *variability of asynchronies* to be higher when tapping on another person's finger than when tapping on their forearm. A potential explanation for this finding is related to the fact that the secondary somatosensory cortex is activated when individuals are touched and when they observe someone else being touched (see Keysers et al. 2004). The tapper may thus 'empathically' experience to some degree the feeling that the passive participant gets when being touched (cf. Singer et al. 2004). In any case, the fact that corresponding differences in movement amplitude were not observed (see Table 1) suggests that the Finger/Forearm effect found on one's own body is not merely indicative of differences in morphology or compliance between fingers and forearms.

Our main finding—that is, tap timing was more variable, and movement amplitude was both larger and more variable, in the Finger/Finger than the Finger/Forearm condition (on one's own body)—may appear somewhat puzzling. One might have expected (as we did) that Finger/Finger tapping should be more efficient and stable than Finger/Forearm tapping because sensory feedback provided by passive fingers should be more precise and reliable than feedback from less sensitive passive forearms due to the difference in tactile receptor density. Since our findings suggest the contrary, other factors must be at work.

Potentially relevant differences between the two conditions relate to spatial and temporal overlap in neural activity associated with tap contact. In the Finger/Finger condition, there is presumably spatial overlap in regions of somatosensory cortex for the active and the passive finger (despite being on opposite sides of the body; see Hari et al. 1993; Sutherland and Tang 2006; Urbano et al. 1996), whereas such overlap is less likely for Finger/Forearm tapping. Temporal overlap may also differ for the Finger/Forearm and the Finger/Finger condition due to the involvement of different tactile channels and slightly shorter nerve conduction time for tactile feedback from the forearm than the finger.

Rather than being helpful, overlap in brain activation may create ambiguity in the assignment of tap-related feedback to fingers (active vs. passive), which may in turn be detrimental to motor control of the active finger. This is because the timing of upcoming taps requires that feedback from completed taps is unambiguously attributed to the active finger and its control system. Ambiguity concerning the source of feedback would introduce uncertainty into the process of determining the current state of the system. It has been argued that state estimation, which is necessary for accurate motor control, involves comparing actual

sensory feedback with predicted feedback generated by an internal forward model (Wolpert and Ghahramani 2000; Wolpert et al. 1998). This process may be compromised when the required assignment to the active finger competes with the passive finger in the Finger/Finger condition.

When confronted by such competition, one possible measure that the control system may take to strengthen the linkage between the active finger's movements and ensuing tactile feedback is to generate noise on a movement-related dimension that leads to correlated noise on a tap-related dimension. For instance, the control system may boost the variability of movement amplitudes, effectively causing taps to differ in force and pressure (Aschersleben et al. 2001; Billon et al. 1996). Since amplitudes have a lower bound (at zero), increasing their variability will require some increase in their mean, too. The primary effect thus resides in the observed (large) increase in amplitude variability, whereas the (smaller) increase in mean amplitudes is secondary.¹ This measure would create a correlation between kinematic features of finger movements and dynamic features (force and pressure) of ensuing taps—a correlation that could act to strengthen the assignment of taps to the active finger and, hence, the integration of tap-related information into the operation of the control system that guides movement timing.

According to the informal model described above, the control system for the active finger exploits the correlation between movement kinematics and tap dynamics to disambiguate feedback that arrives at a common brain region from different peripheral sources. This can be seen as an instance where spatial aspects of movement are modulated in order to assist in achieving specific temporal goals (cf. Keller et al., in press). Although the current account remains speculative at this stage, the robustness of our results suggests that intra-active sensorimotor synchronization provides a promising paradigm for future explorations of the role of feedback from active and passive body parts in spatiotemporal movement coordination. A next step could involve the comparison of intra-active tapping across a wide range of body parts (including the toes, legs, shoulders, and face) in order to investigate more systematically the effects of relations between active and passive regions in terms of somatotopic representation, nerve conduction time, and the anatomical and physiological organization of tactile channels. Ultimately, studies of intra-active sensorimotor synchronization have the potential to further our understanding of how spatiotemporal information associated with (actively) touching and

¹ Note that sensory attenuation associated with self-touch is unlikely to provide a full explanation of our results because it has been found not to vary with the intensity of self-generated input (Bays and Wolpert 2007).

(passively) being touched is jointly represented in the human nervous system.

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