RESEARCH ARTICLE

Response requirements modulate tactile spatial congruency effects

**Alberto Gallace · Salvador Soto-Faraco · Polly Dalton ·
Bas Kreukniet · Charles Spence**

Abstract Several recent studies have provided support
for the view that tactile stimuli/events are remapped into an
abstract spatial frame of reference beyond the initial soma-
totopic representation present in the primary somatosensory
cortex. Here, we demonstrate for the first time that the
extent to which this remapping of tactile stimuli takes place
is dependent upon the particular demands imposed by the
task that participants have to perform. Participants in the
present study responded to either the elevation (up vs.
down) or to the anatomical location (finger vs. thumb) of
vibrotactile targets presented to one hand, while trying to
ignore distractors presented simultaneously to the other
hand. The magnitude and direction of the target–distractor
congruency effect was measured as participants adopted
one of two different postures with each hand (palm-up or
palm-down). When the participants used footpedal
responses (toe vs. heel; Experiment 1), congruency effects
were determined by the relative elevation of the stimuli in
external coordinates (same vs. different elevation), regardless
of whether the relevant response feature was defined
externally or anatomically. Even when participants
responded verbally (Experiment 2), the influence of the rel-
ative elevation of the stimuli in external space, albeit atten-
uated, was still observed. However, when the task involved
responding with the stimulated finger (four-alternative
forced choice; Experiment 3), congruency effects were vir-
tually eliminated. These findings support the view that tac-
tile events can be remapped according to an abstract frame
of reference resulting from multisensory integration, but
that the frame of reference that is used while performing a
particular task may depend to a large extent on the nature of
the task demands.

Keywords Somatosensation · Touch · Multisensory ·
Response requirements · Frame of reference

A. Gallace · P. Dalton · B. Kreukniet · C. Spence
Department of Experimental Psychology,
University of Oxford, Oxford, England

S. Soto-Faraco
ICREA and Parc Científic de Barcelona,
Universitat de Barcelona, Barcelona, Spain

B. Kreukniet
Graduate School Life Sciences, Utrecht University,
Utrecht, The Netherlands

A. Gallace (✉)
Department of Psychology,
Università degli Studi di Milano-Bicocca,
P.zza dell'Ateneo Nuovo 1, 20126 Milan, Italy
e-mail: alberto.gallace1@unimib.it; albertogallace@hotmail.com

Response requirements modulate spatial congruency effects in tactile perception

The primary somatosensory area of the human brain (SI),
lying along the post-central gyrus (anterior parietal cortex),
is neatly arranged to correspond topographically with the
body surface (the classic homunculus first described by
Penfield and Rasmussen 1950; see also Narici et al. 1991).
Neural activity in SI signals the location of tactile stimuli in
terms of a somatotopically based spatial representation.
However, in order for people to localize and act upon sen-
sory inputs in the environment, most of their somatosen-
sory experience must be referred to spatial locations
defined according to other frames of reference (e.g.,
Holmes and Spence 2005, 2006; Paillard 1999; Pick 1974;
Polanyi 1962). For example, given that the body can adopt
a variety of different postures, a tactile sensation arising

from the hand can potentially originate from anywhere within reachable space (see also Spearman 1907, for an early discussion of this topic). The ability to rapidly localize a tactile stimulus is critical if one is to take rapid evasive or defensive action based on that information (e.g., Graziano et al. 2004).

Many researchers have suggested that the brain computes the location of tactile events in terms of abstract spatial reference frames that take into account information regarding the current posture of the body (i.e., Azañón and Soto-Faraco 2008; Botvinick and Cohen 1998; Driver and Grossenbacher 1996; Eimer et al. 2001; Gallace and Spence 2008; Lloyd et al. 2003; Pavani et al. 2000; Soto-Faraco et al. 2004; though see Zampini et al. 2005). These representations of tactile location can only be constructed through the combination of somatosensory inputs with other sources of sensory information concerning body posture, such as proprioception and/or vision (and possibly audition, on some occasions). One interesting implication of this type of result is that these multisensory binding processes occur in a fairly automatic and obligatory manner. Consistent with this view, it has been argued, perhaps somewhat counterintuitively, that the "conscious sensation of touch takes place in space rather than on the skin. That is, conscious sensation of touch is first localized in space to where the hand (and thus the particular part of the skin) is placed, before it is finally localized to the skin." (Kitazawa 2002; p 476). This preattentive conceptualization of the binding between somatosensory and postural information (conveyed proprioceptively and/or visually) implies that tactile events are consciously localized according to an abstract frame of reference (be it external or body-part centered), beyond the initial somatotopic maps found in the primary somatosensory cortex (Azañón and Soto-Faraco 2008). Moreover, this abstract frame of reference might provide the basis for the coordination of spatial information arising from different sensory modalities, such as from vision and touch (e.g., Austen et al. 2004; Driver and Grossenbacher 1996; Pavani et al. 2000; cf. Gallace and Spence 2008).

These predictions have received empirical support from several different studies (e.g., Driver and Grossenbacher 1996; Lakatos and Shepard 1997; Soto-Faraco et al. 2004). For example, Soto-Faraco and his colleagues demonstrated that people's ability to select a tactile target presented to one hand depends on the distance at which the other hand, receiving a distracting vibrotactile stimulus, is placed in external space (see also Driver and Grossenbacher 1996; Shore et al. 2005). Similarly, when selective attention is deployed in a multisensory context (i.e., to selectively respond to tactile targets while trying to ignore visual distractors), the interfering effect of distractors has been shown to be determined by their position in external spatial coordi-

nates rather than by their initial hemispheric projections (see Spence et al. 2000; Eimer and Driver 2000, for electrophysiological evidence; Làdavas and Farnè 2004; Moscovitch and Behrmann 1994, for neuropsychological evidence; though see also Spence et al. 2001c). Findings from animal electrophysiology are consistent with the existence of such multisensory representations of peripersonal space in several brain areas (i.e., Cohen and Andersen 2004; Graziano et al. 2004): for example, a number of the neurons in the ventral premotor cortex have tactile as well as visual receptive fields centered on a monkey's hand and arm, and their visual receptive fields often appear to shift in line with the hand as it moves through space (e.g., Graziano and Gross 1998).

One critical, but as yet still unresolved, issue regarding the nature of tactile representations of space is how flexible they are in terms of the behavioral context and current task goals (see Millar 1994; Millar and Al-Attar 2003). On the one hand, as discussed above, previous results suggest that the spatial selection of tactile events seems to operate within an abstract spatial frame of reference (e.g., see Driver and Grossenbacher 1996; Moscovitch and Behrmann 1994; Soto-Faraco et al. 2004; Spence 2002), which, according to such results, would appear to be constructed automatically. On the other hand, however, it is well known that selective attention can operate at multiple different levels of representation, depending on the relevant feature, object, or action that the task involves (e.g., Desimone and Duncan 1995; Kanwisher et al. 1995; Kennett et al. 2002). For example, neural competition, thought to reflect attentional processes in vision, can take place at various different stages in the hierarchy of visual processing (e.g., Desimone and Duncan 1995; Motter 1993) depending on the particular feature that is currently relevant for selection. In humans, the behavioral goal (or relevant selection feature) can form the basis for dissociations between different types of spatial hemineglect in neurological patients (e.g., Baylis et al. 1993; di Pellegrino et al. 2005; see also Rapp and Hendel 2003).

The possibility therefore arises that the nature of the behavioral tasks used in previous studies of tactile information processing may have determined the type of spatial coding that was used by participants in these studies. Several results in the literature on tactile selective attention also suggest that under certain circumstances, a somatotopically based frame of reference might prevail over an external representation of space (i.e., Azañón and Soto-Faraco 2008; Evans and Craig 1991; Evans et al. 1992; Röder et al. 2002; Zampini et al. 2005). For example, a recent study by Azañón and Soto-Faraco showed that the frame of reference in which tactile distractors influence the processing of visual targets changes with time, from an initial short-lived representation in a somatotopic code to a later, more stable,
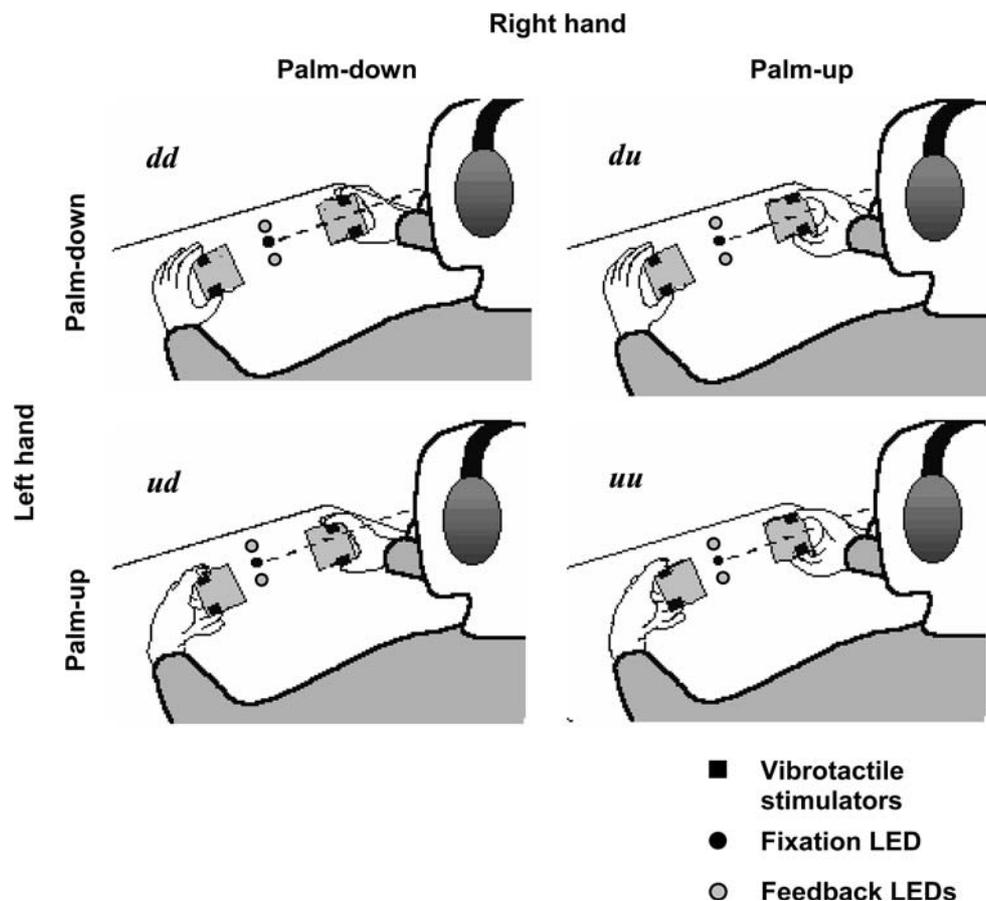
representation based on external coordinates. Therefore, one important issue currently regards the question of whether the abstract spatial frame of reference that is often reported in studies of tactile processing reflects the adaptability of the system to the requirements of the task, or else, results from the mandatory remapping of tactile spatial information as has been suggested by certain researchers (e.g., Kitazawa 2002; Soto-Faraco et al. 2004; Yamamoto and Kitazawa 2001).

We addressed this crucial question in the present study by using an elevation judgment task that has previously been used to study tactile and crossmodal spatial congruency effects (see Soto-Faraco et al. 2004; Spence and Walton 2005; Spence et al. 2000, 2004a, b). Participants had to make speeded elevation judgments in response to targets (brief continuous vibrations) presented to either the top or bottom of one of two foam cubes that they held between the thumbs and index fingers of both hands (see Fig. 1). At the same time that the target was presented to one hand, the other hand received a distractor (pulsed vibration), which was presented at an elevation that was either congruent or incongruent with respect to the elevation of the target. The typical result reported by Soto-Faraco and his colleagues was that responses to targets

paired with an incongruent distractor were, on average, significantly slower and less accurate than responses to targets that were paired with a congruent distractor. This congruency effect has been interpreted as showing a failure to filter out effectively irrelevant information across the hands.

One of the most interesting findings to emerge from the experiments reported by Soto-Faraco et al. (2004) was that this congruency relationship depended on the external location of the tactile events, and not on the anatomical location (i.e., on the particular digits) where the target and distractor events were presented. This was revealed when the participants' hands were placed in different orientations as, for example, when the participants held one cube with the right hand palm down and the other cube was held by the left hand in a palm-up posture. Under such conditions, a distractor delivered to the top of the right cube (i.e., to the index finger) would be incongruent with a target delivered to the top of the left cube (i.e., to the thumb) in terms of its somatotopic representation, but would be congruent in terms of the external spatial coordinates of the stimuli. Thus, contrary to the situation when both of a participant's hands are placed in the same orientation, the congruency effects predicted on the basis of somatotopic

Fig. 1 Schematic outline of (**a**) the experimental set-up, and (**b**) the different postures adopted by participants in Experiments 1 and 2. Responses were made via footpedals placed beneath the table (not shown). Each *panel* is labeled according to the nomenclature used in the text to describe the various different hand posture conditions (*dd*, *du*, *ud*, and *uu*). Note that in the *palm-up* posture, the thumb rested on the top of the foam cube, while the index finger rested on the bottom of the cube. The opposite was true for the *palm-down* posture

representations were opposite to those based on more abstract (i.e., externally or body-part centered) representations. Soto-Faraco et al.'s results therefore supported an interpretation based on an abstract reference frame (such as one coding space in external coordinates). That is, regardless of the particular combination of hand postures that were adopted by participants, distractors presented from the *top* (spatially) of one cube always facilitated the processing of targets presented from the *top* (spatially) of the other cube.

In the experiments reported by Soto-Faraco et al. (2004), as well as in many other previous studies that have investigated the nature of the spatial representation of tactile stimuli (i.e., Maravita et al. 2002; Pavani et al. 2000; Spence et al. 2000, 2001a, c; see also Gallace and Spence 2008; Spence et al. 2004b, for recent reviews), the participants were instructed to respond on the basis of the external location from which the target was presented (i.e., they had to respond in terms of the elevation of the targets; top vs. bottom). Therefore, while these results are illustrative of the possibility of remapping the location of tactile events into a more abstract frame of reference according to the particular requirements of the task at hand, it is still unclear whether the type of spatial code that the task affords mediates this remapping process. In the present study, we introduced a number of manipulations of the task whereby the participants either had to localize the tactile events in terms of their external location (i.e., top vs. bottom), or in terms of their anatomical location (i.e., finger vs. thumb). The response effectors were also varied (footpedal responses, Experiment 1 vs. verbal responses, Experiment 2) in an attempt to evaluate the role played by the spatial or nonspatial nature of the action required by the response. We also replaced the elevation judgment task with a four-alternative manual forced choice (4-AFC) task (Experiment 3) to assess the importance of target–distractor spatial compatibility at the level of response selection.

If the spatial representation underlying the perception of tactile stimuli is flexible and adapts as a function of the behavioral context, then one would expect to find that spatial congruency effects depend on absolute spatial position when the task requires a judgment based on external location (elevation), but on somatotopic location when the judgment is based on the anatomical body part (i.e., digit) stimulated. By contrast, if tactile spatial representations are mandatorily remapped as a function of any changes in body posture, then congruency effects should follow external space regardless of the task demands, posture adopted, or response effector utilized. Of course, there is also the possibility of an intermediate result, whereby neither of these two spatial frames of reference is completely dominant.

Experiment 1

Methods

Participants

Sixteen participants (10 women, age range 19–33 years, $M = 24$ years) took part in this study. They were all naïve as to the purpose of the experiment, right-handed by self-report, and had normal tactile sensitivity and normal or corrected-to-normal vision. The participants were given a five pound (UK Sterling) gift-voucher in return for their participation. All of the experiments reported here were noninvasive and had ethical approval from the Department of Experimental Psychology, University of Oxford, and were performed in accordance with the ethical standards laid down in the 1991 Declaration of Helsinki.

Apparatus and materials

The participants sat at a table in a completely dark sound-proof booth, holding two foam cubes (with 9 cm of side), one between the fingers and thumb of either hand. A green fixation light was placed midway between the two cubes, and two additional red LEDs, one placed directly above and another placed directly below the fixation LED, were used to provide feedback whenever participants made an erroneous response. The cubes were attached to the table by means of Velcro placed between the tabletop and the lower rear edge of each cube (to ensure a constant positioning of the cubes, regardless of the posture adopted), separated by 45 cm, and placed approximately 45 cm from the participant's chest. Vibrotactile stimulators (Oticon bone-conducting vibrators, p/n BC-461-1 100) were mounted on the top and bottom surfaces of each foam cube (see Fig. 1a). The target consisted of a continuous suprathreshold vibration (200 Hz sine wave) presented for 300 ms, while the distractor consisted of three 50 ms bursts (200 Hz sine wave) each separated by a 50 ms interstimulus interval. The participants wore a pair of closed ear headphones to mask any noises associated with the operation of the vibrotactile stimulators. White noise was presented at 65 dB (A) from a pair of loudspeaker cones, one located just behind each cube. Responses were collected via two footpedals placed on the floor, beneath the table.

Design

The design included one between-participants factor, namely task (respond-to-elevation vs. respond-to-digit). Each participant performed only one of the two tasks ($N = 8$ participants in each group) to avoid any confusion that might potentially have been associated with participants

switching task mid-experiment. Each participant was tested in four different hand orientations in separate blocks of experimental trials (both palms down, both palms up, left palm down and right palm up, or left palm up and right palm down; these postures will be referred as *dd*, *uu*, *du*, or *ud*, respectively; see Fig. 1). Within each block of trials, target position (left or right) and distractor congruency (congruent or incongruent) were chosen at random on a trial-by-trial basis.

Procedure

The participants were instructed to keep their eyes fixed on the central fixation light and to hold the two foam cubes between the index finger and thumb of each hand (the left cube with the left hand, and the right cube with the right hand). The fingers/thumbs were placed in contact with the vibrotactile stimulators, and the participants were asked to keep the footpedals depressed throughout the experiment, except when making a response. The experimental session consisted of eight blocks of 64 trials, giving rise to a total of 512 trials. Prior to the start of each block of trials, the participants were instructed to adopt one of the four postures (*dd*, *uu*, *ud*, or *du*). When a participant's hand was placed in the palm-down hand orientation, their index finger rested on the top vibrator and their thumb rested on the bottom vibrator, while the reverse was true for the palm-up hand orientation. Each combination of hand orientations (i.e., each posture) was tested in two blocks of trials for each participant, with the order of postures in successive blocks counterbalanced across participants according to a Latin square design.

In each trial, participants received a target (a continuous vibration) from either the top or bottom vibrator on one of the two cubes, while the distractor (a pulsed vibration) was presented to the top or bottom vibrator of the other cube. The cube (left or right) and elevation (top vs. bottom) of the target and the spatial congruency of the distractor (congruent vs. incongruent) were determined at random on every trial and were equiprobable throughout each block of trials, with the sole restriction that the target and distractor were always presented to different hands on each trial. The instructions given to participants varied according to the condition they were assigned to at the start of the experiment.

The participants in Experiment 1 made their responses by means of two footpedals placed under the toes and heel of their dominant foot. In the *respond-to-elevation* condition, the participants were instructed to judge whether the vibrotactile target had been presented to the upper vs. lower part of the cube (lift the toes vs. heel, respectively), regardless of whether the target had been presented to their thumb or index finger. By contrast, in the *respond-to-digit* condition, the participants were instructed to respond according

to the digit that had been stimulated (finger vs. thumb; lift the toes vs. heel, respectively), regardless of the elevation from which the target had been presented. Response latency from target onset and response accuracy were registered by means of a custom computer program. No feedback was given following a correct response. In the case of an erroneous response, the fixation and feedback LEDs flickered on (for 90 ms) and off (for 30 ms) eight times. If no response was given within 3,000 ms of target onset, both feedback LEDs flashed, while the green fixation LED was illuminated continuously.

Each participant completed two blocks of 20 practice trials prior to the main experimental session. In the first practice block, vibrotactile targets were presented randomly from either elevation to either hand in the absence of any distractor stimuli. In the second practice block, the targets were all presented to the participant's right hand, while the distractors were all presented to their left hand. The data from these two practice blocks (which were presented simply in order to acquaint the participant with the task) were not analyzed. The whole experimental session took approximately 40 min to complete.

Results

For consistency with the task requirements, we chose to define congruency according to the relevant response dimension. Thus, in the *respond-to-elevation* group of participants, congruency was defined in terms of the spatial relationship (i.e., relative elevation) between the target and distractor (top–top and bottom–bottom were coded as congruent, and top–bottom and bottom–top were coded as incongruent). For the *respond-to-digit* group, congruency was defined in terms of the anatomical site of stimulation (index–index and thumb–thumb were coded as congruent, while index–thumb and thumb–index were coded as incongruent).

The RT and accuracy data were submitted to separate analysis of variance (ANOVA), with task (*respond-to-digit* vs. *respond-to-elevation*) as a between-participants factor and with congruency (congruent vs. incongruent) and posture (*dd*, *uu*, *du*, and *ud*) as the within-participants factors. The analysis of the RT data revealed significant main effects of task [$F(1,33) = 5.17$; $P = 0.029$], posture [$F(3,99) = 5,25$; $P = 0.002$], and congruency [$F(1,33) = 13.86$; $P < 0.001$]. The interactions between task and posture [$F(3,99) = 10.02$; $P < 0.0001$], posture and congruency $F(3,99) = 17.75$; $P < 0.0001$], and the three-way interaction were also significant [$F(3,99) = 13.93$; $P < 0.0001$].

A similar analysis of the accuracy data revealed significant main effects of task [$F(1,33) = 25.02$; $P < 0.0001$] and congruency [$F(1,33) = 12.18$; $P = 0.001$]. The interactions

between task and congruency [$F(1,33) = 6.96$; $P = 0.01$], posture and congruency $F(3,99) = 9.88$; $P < 0.0001$], and the three-way interaction were also significant [$F(3,99) = 7.76$; $P = 0.0001$].

Given the significant three-way interactions observed in both analyses, the RT and accuracy data from each group of participants (those who completed the *response-to-elevation* task and those who completed the *response-to-digit* task) were submitted to two separate two-way ANOVAs, with congruency (congruent vs. incongruent) and posture (*dd*, *uu*, *du*, and *ud*) as the within-participants factors. Significance values were Greenhouse–Geisser-corrected where appropriate. Those trials in which no response was made and those trials in which the participants responded in under 200 ms or with a latency of greater than 2,500 ms were excluded from the RT analyses (less than 1% of trials across Experiments 1–3).

In the *respond-to-elevation* condition (see Fig. 2), analysis of the RT data revealed a significant main effect of Congruency [$F(1,7) = 11.4$, $P = 0.01$], with participants responding more rapidly on the congruent trials ($M = 577$ ms) than on the incongruent trials ($M = 750$ ms) overall. Neither Posture [$F(3,21) = 2.8$, $P = 0.106$], nor the interaction between Posture and Congruency were significant ($F < 1$). The analysis of the error data revealed a similar pattern of results. That is, there was a significant main

effect of Congruency [$F(1,7) = 35.9$, $P < 0.001$], with participants responding more accurately on congruent trials ($M = 3.9\%$ errors) than on incongruent trials ($M = 26.8\%$ errors) overall. There was no main effect of Posture [$F(3,21) = 2.3$, $P = 0.153$] nor any interaction between Posture and Congruency ($F < 1$).

In the *respond-to-digit* condition (see Fig. 3), the analysis of the RT data revealed a significant main effect of Congruency [$F(1,7) = 24,0$, $P = 0.002$], with the participants responding more rapidly on the congruent trials ($M = 752$ ms) than on the incongruent trials ($M = 807$ ms) overall. There was also a significant main effect of Posture [$F(3,7) = 3.7$, $P \leq 0.05$], with faster responses being observed in those blocks of trials where both of the participant's hands were placed in the same orientation (729 ms for *dd*, and 763 ms *uu*) than when they were placed in different orientations (810 ms for *ud* and 814 ms for *du*). However, none of the paired comparison *t* tests reached statistical significance after Bonferroni correction (all $P > 0.1$). Interestingly, there was a robust interaction between Posture and Congruency [$F(3,21) = 28.7$, $P < 0.001$]. Upon detailed analysis, this interaction revealed a significant difference in the congruency effect (RT difference between congruent and incongruent trials) as a function of the posture adopted by participants. In particular, when both of the participant's hands were placed in the same orientation, responses were

Fig. 2 Results of the *respond-to-elevation* group of Experiment 1 (*bars* represent mean RTs and *lines* represent mean percentages of errors) averaged over participants (*error bars* represent the standard errors of the means). The results are shown separately for each of the four postures adopted (see the *inset conditions labels* in each *graph*). Congruency is shown as a function of *external* location (i.e., in terms of the task-relevant dimension)
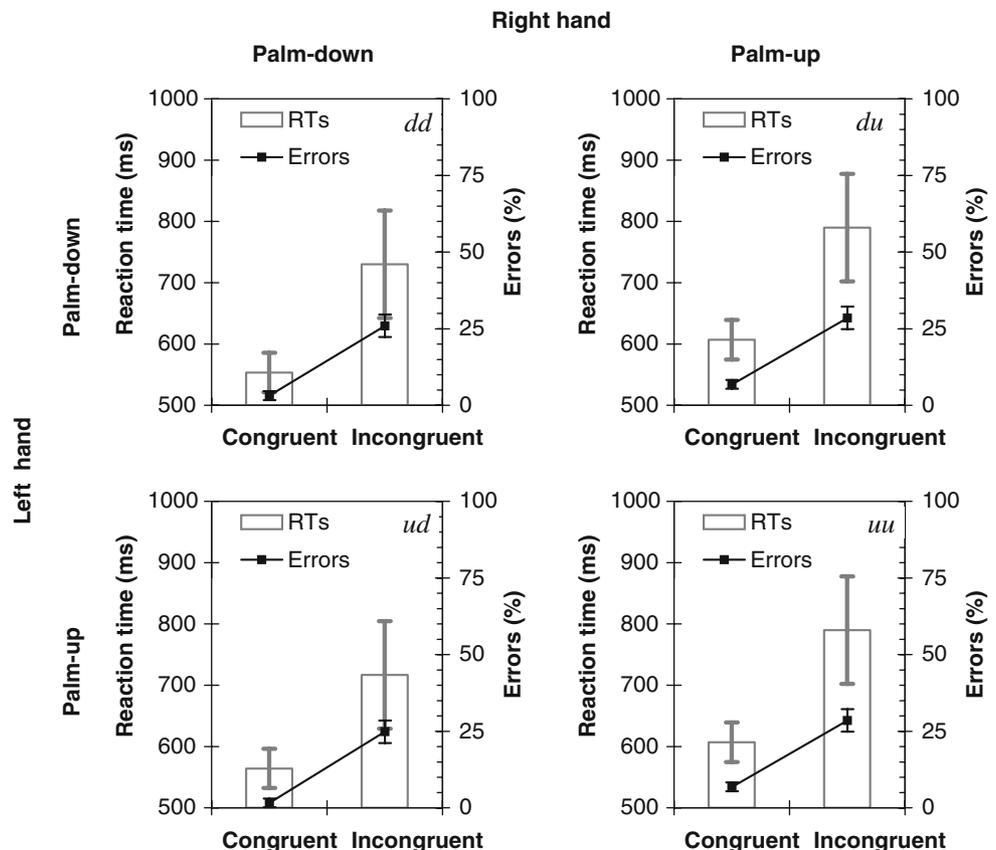
Fig. 3 Results of the *respond-to-digit* group of Experiment 1 (*bars* represent mean RTs and *lines* represent mean percentage of errors) averaged over participants (*error bars* represent the standard errors of the means). The results are shown separately for each posture adopted (see the *inset conditions labels* in each *graph*). Congruency is shown as a function of *anatomical* location (i.e., in terms of the task-relevant dimension)
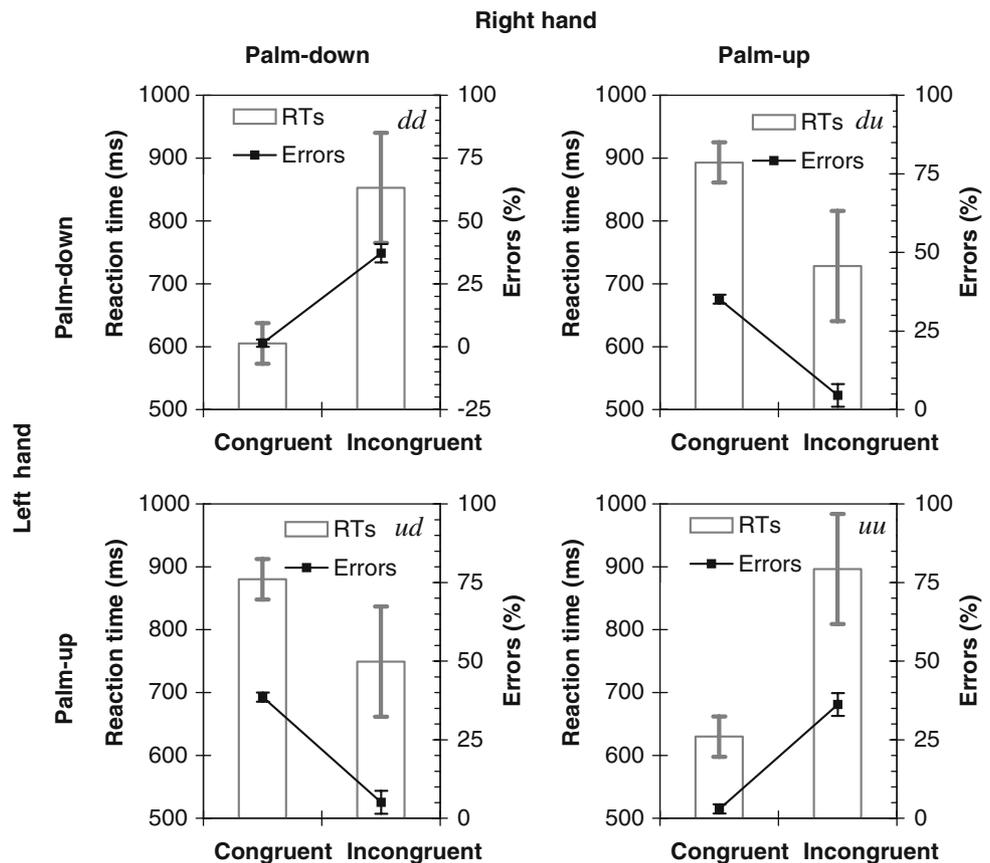
faster on congruent trials than on incongruent trials (mean congruency effect of 267 ms for *uu*, and 247 ms for *dd*, i.e., a typical congruency effect was observed). In contrast, this congruency effect reversed completely when the orientation of the participant's hands did not match (see Table 1).

In terms of the error data, neither of the two main effects in the analysis was statistically significant {congruency [$F(1,7) = 2.6$, $P = 0.149$], and posture [$F = 1.0$]}. The most relevant result, however, was the robust interaction between Posture and Congruency [$F(3,21) = 115.6$, $P < 0.001$]. Just as for the RT data, a significant positive congruency effect (reflecting the fact that participants' responses were more accurate on congruent trials than on incongruent trials) was observed when the participants' hands were placed in the same orientation (mean congruency effect of 35.8 and 33.2% for *dd* and *uu* trials, respectively), whereas a negative congruency effect was seen when the participants' hands were placed in different orientations (−30.6% for *du* and −33.5% for *ud*, see Table 1).

Discussion

By themselves, the results of Experiment 1 would appear to support the view that the spatial representation of tactile stimuli is primarily based upon an abstract coordinate sys-

tem, one that lies beyond a purely somatotopic representation. The results of the *respond-to-elevation* condition closely replicated those obtained previously by Soto-Faraco et al. (2004): that is, the spatial congruency effect between the target and distractor was determined by externally based coordinates, regardless of the specific posture adopted. This result is consistent with the view that when a participant's task is defined in terms of external locations, tactile events are coded in an externally- or body-part centered coordinate system. Perhaps more strikingly, the results of the *respond-to-digit* condition show that this externally based organization remains in place even when the participant's task explicitly requires them to make a response (i.e., finger vs. thumb) that is based on anatomically defined coordinates (i.e., the frame of reference that would correspond to the initial encoding of tactile space in primary somatosensory cortex). Participants tested in the *respond-to-digit* condition were specifically instructed to respond to the digit receiving the target vibration and yet, across all of the postures adopted, they invariably exhibited a robust interference (or congruency effect, slowing their reactions and making them more prone to error) from distractors presented at different elevations regardless of whether the actual digits receiving the target and the distractor were the same or not. The results of Experiment 1 would therefore appear to suggest

Table 1 Summary of results

			Task				
			Elevation (external)		Digit (anatomical)	
			Right hand		Right hand	
			d	u	d	U
E1: Foot response	Left hand	d	176 ms (23%)	183 ms (22%)	247 ms (36%)	-165 ms (-31%)
		u	152 ms (23%)	184 ms (24%)	-131 ms (-33%)	267 ms (33%)
E2: Verbal response	Left hand	d	131 ms (30%)	75 ms (28%)	129 ms (29%)	15 ms (22%)
		u	62 ms (27%)	97 ms (29%)	31 ms (20%)	88 ms (29%)

Note: mean congruency effects (congruent minus incongruent difference scores) for the RT and error data (in parenthesis) in Experiments 1 and 2. Task refers to the type of response required (top vs. bottom in the *respond-to-elevation* condition, or finger vs. thumb in the *respond-to-digit* condition), and response effector refers to the mode in which participants were to indicate their responses (toe vs. heel footpedal response in Experiment 1, and verbal response in Experiment 2). For each of the four inset tables the left hand orientation is depicted in the columns (*d* means palm-down and *u* means palm-up) while the right hand orientation differs between rows

that the spatial representation of tactile events relevant to participants' performance in the present task was based on an abstract frame of reference, one resulting from the multisensory binding of somatosensory and proprioceptive/visual information regarding limb position.

Nevertheless, an important question arising from the results of Experiment 1 is the role played by the particular stimulus-response mapping adopted by participants to perform the task. In particular, one could argue that the putatively automatic encoding of tactile location in terms of abstract (possibly external) coordinates observed in our first experiment could have been induced (or reinforced) by the type of response that our participants had to make. In particular, the fact that participants responded by lifting their foot off of one of two footpedals (one under the toes and the other under the heel of the dominant foot) could by itself be argued to have induced the adoption of an abstract spatial code mapping toe with front, or with top, and heel with back or bottom (see, for example, Austen et al. 2003). We therefore thought it important in our second experiment to address whether the externally based encoding of tactile stimulation found across the two different tasks performed by participants in Experiment 1 would still persist even when the participants had to respond in a manner that did not involve the execution of any such spatial responses as, for example, is the case when participants indicate their response verbally.

Experiment 2

Methods

Participants

Sixteen new participants (seven women; age range 19–26 years; $M = 21$ years) were recruited to take part in this experiment. They were all naïve as to the purpose of the study, and 14 were right-handed (two left-handed) by self-report. All reported normal tactile sensitivity and normal or corrected-to-normal vision. They were given a five pound (UK Sterling) gift-voucher in return for their participation.

*Apparatus, materials, design, and procedure*

These were identical to those used in Experiment 1 with the sole exception that the participants now responded verbally, with the responses 'up' vs. 'down' in the *respond-to-elevation* task condition, and the verbal responses 'finger' vs. 'thumb' in the *respond-to-digit* condition. Vocal response latencies were registered using a ProSound unidirectional microphone connected through a custom-made voice key to a computer running E-Prime (Psychology Software Tools, Inc., Pittsburgh, PA). To ensure an accurate classification of the responses given by the participants, the experimenter logged each response manually via the computer keyboard ('up,' 'down,' 'finger,' or 'thumb'). These data were used to determine the accuracy of participants' vocal response (and to provide appropriate feedback, as in Experiment 1).

Results

The RT and accuracy data were submitted to separate ANOVAs, with task (respond to digit vs. respond to elevation) as a between-participants factor and with congruency (congruent vs. incongruent) and posture (*dd*, *uu*, *du*, and *ud*) as the within-participants factors. The analysis of the RT data revealed significant main effects of congruency [$F(1,13) = 17.97$; $P < 0.001$] and a significant interaction between posture and congruency [$F(3,39) = 7.37$; $P < 0.001$]. None of the other main effects or interactions was significant (see Figs. 4, 5; note that, for consistency with Experiment 1, the *respond-to-elevation* and *respond-to-digit* groups are represented on separate graphs). A Scheffé post-hoc test on the interaction between posture and congruence showed that the congruency effect was significant for the *dd* posture ($P < 0.0001$) and for the *uu* posture ($P < 0.0001$), but not for any of the other postures (all Ps > 0.05).

The analysis of the error data revealed a very similar pattern of results (Fig. 6). That is, there was a significant main effect of Congruency [$F(1,13) = 118.29$, $P < 0.0001$], with

Fig. 4 Results of the *respond-to-elevation* group of Experiment 2 (*bars* represent mean RTs and *lines* represent mean percentage of errors) averaged over participants (*error bars* represent the standard errors of the means). Results are shown separately for each posture adopted (see the *inset conditions labels* in each *graph*). Congruency is shown as a function of the *external* location of the stimuli (i.e., in terms of the task-relevant dimension)
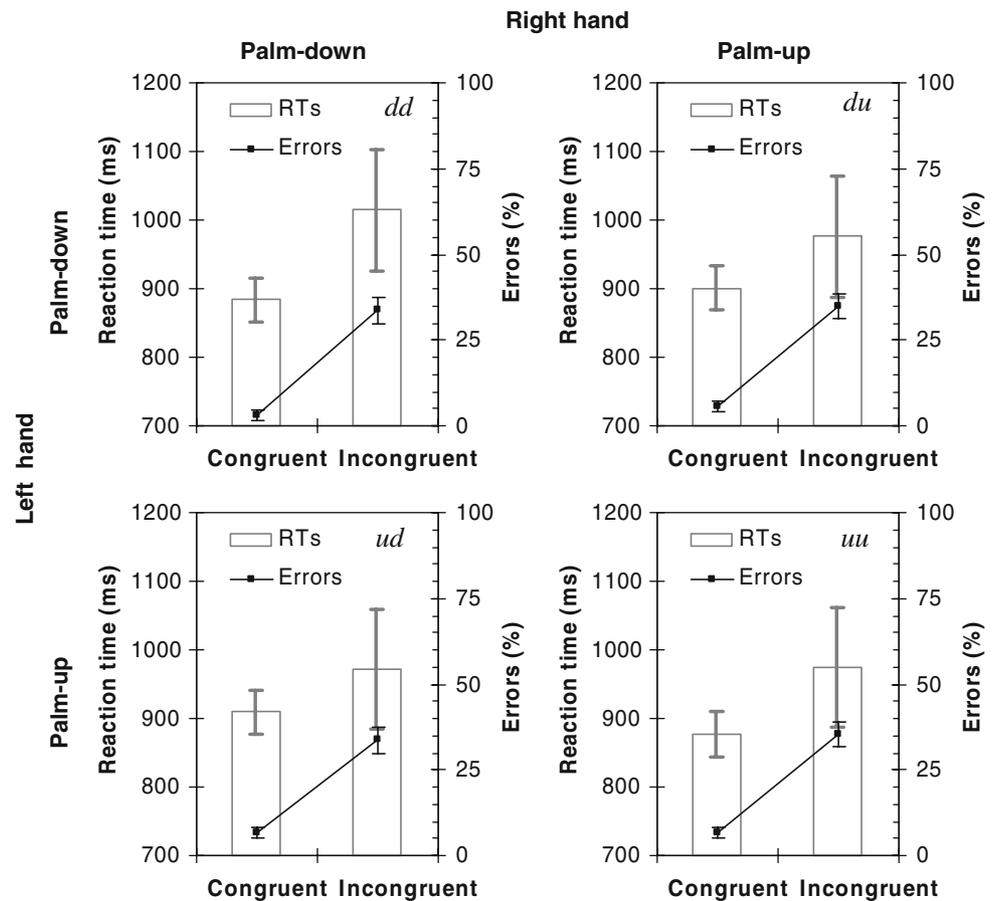
participants responding more accurately on the congruent trials than on the incongruent trials. The main effect of posture was also significant [$F(1,39) = 5.29$; $P < 0.01$]. The interaction between Posture and Congruency was borderline significant [$F(3,39) = 2.70$; $P = 0.058$]. A post-hoc Scheffe' test on this interaction revealed a significant effect of congruency for the all of the postures (all Ps < 0.0001).

Discussion

In Experiment 2, the participants made spatial judgments regarding the location (in either external or anatomical coordinates) of vibrotactile targets while attempting to ignore the position of irrelevant vibrotactile distractors. This task was the same as the one used in Experiment 1, with the sole exception that participants now indicated their responses verbally, rather than by using the (spatial) toe/heel footpedal response. Rather surprisingly, this simple change in the response effector resulted in a substantial alteration in the pattern of results that were observed. While the congruency relationships appeared to remain completely anchored to external locations in Experiment 1, regardless of whether the participants had to respond to the elevation of the target or to the identity of the digit stimu-

lated, this trend was almost completely eliminated in Experiment 2. Instead, the congruency effects exhibited more of a tendency to follow the frame of reference that was specifically relevant to the particular task that the participants had to perform (external in the elevation task, and both external and anatomical in the digit task).

The results of Experiment 2 therefore suggest that the use of a spatial toe vs. heel response in Experiment 1 may have resulted in participants adopting an abstract spatial code that influenced the way in which the tactile stimuli were coded in both tasks (report elevation and report digit). A similar modulation of performance by response set has also been observed in several previous studies that have investigated people's performance in tactile temporal order judgment (TOJ) tasks when two tactile stimuli are presented, one to either hand. These studies have typically highlighted a dramatic decrease in sensitivity (measured as an increase in the just noticeable difference or JND) when the hands are crossed over the body midline (e.g., Azañón and Soto-Faraco 2007; Kóbor et al. 2006; Röder et al. 2004; Shore et al. 2002; Yamamoto and Kitazawa 2002). Indeed, this crossed-hands deficit is most apparent when the participant's task implies some kind of left–right response mapping (responding

Fig. 5 Results of the *respond-to-digit* group of Experiment 2 (*bars* represent mean RTs and *lines* represent the mean percentage of errors) averaged over participants (*error bars* represent the standard errors of the means). The results are shown separately for each posture adopted (see the *inset conditions labels* in each *graph*). Congruency is shown as a function of the *anatomical* location of the stimuli (i.e., in terms of the task-relevant dimension)
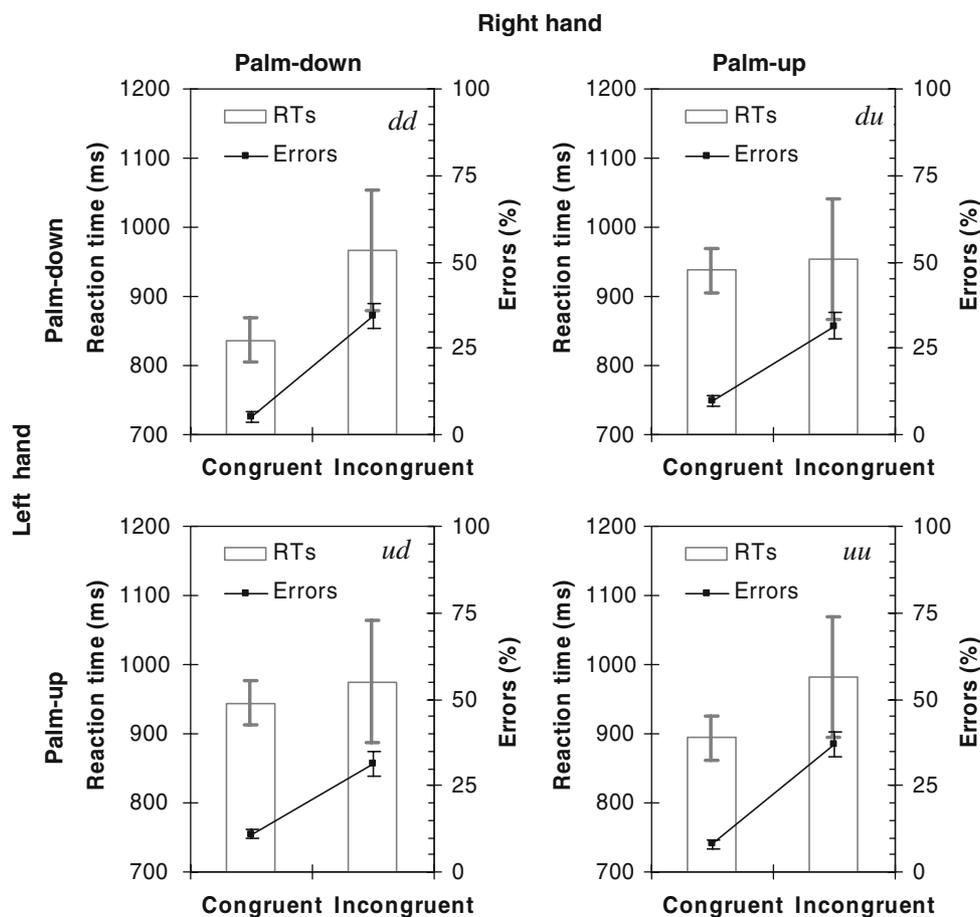
Fig. 6 Relative magnitude of the congruency effects reported in Experiment 2 in terms of (**a**) RTs and (**b**) error rates. The data are shown separately as a function of task (*gray bars* correspond to the *respond-to-elevation* group and *white bars* to the *respond-to-digit* group) and hand orientation (*different* includes the *du* and *ud* postures, while *same* includes the *dd* and *uu* postures)
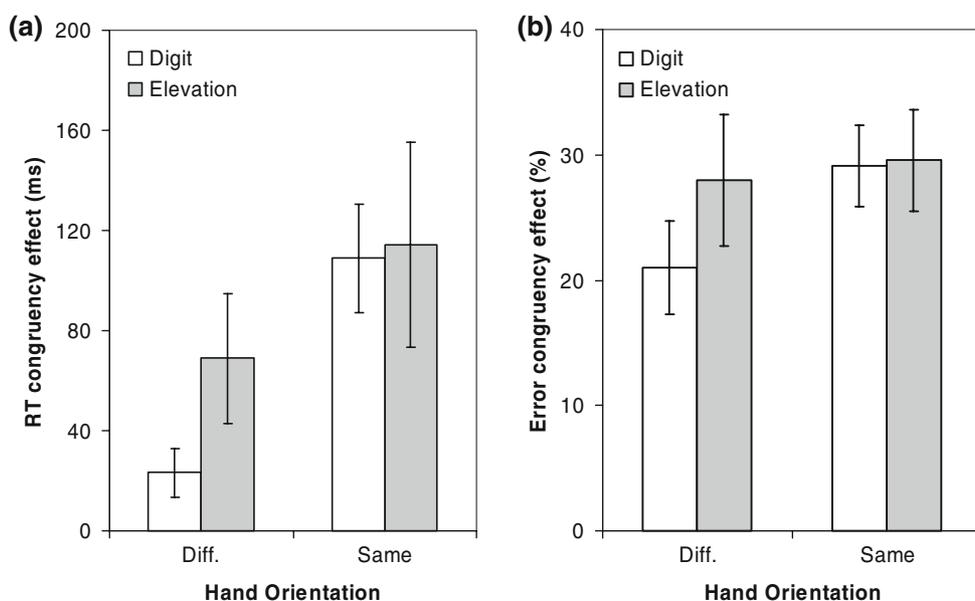
with the left and right fingers, feet, or using lateral eye-gaze; see also Groh and Sparks 1996). The effect is greatly reduced if the response code is orthogonal to the left–right dimension (i.e., top–bottom, i.e., Roberts and Humphreys 2006; Shore et al. 2006), and disappears

almost completely when participants are asked to indicate whether the two tactile events were presented simultaneously or successively (e.g., Axelrod et al. 1968; Geffen et al. 2000), rather than which side came first/second.

Experiment 3

In Experiment 2, we showed that an important part of the spatial congruency effect that was reported in Experiment 1 resided in the particular mapping of responses to effectors that participants had to adopt to perform the task. However, the net congruency effect itself was still significant in both experiments. Such congruency effects have often been interpreted as reflecting a failure to selectively attend to the information presented to one hand while ignoring the information presented to the other hand (e.g., Soto-Faraco et al. 2004; Spence and Walton 2005; Spence et al. 2000, 2004a, b). Nevertheless, it is important to note that this very effect might also be rooted, at least in part, in the fact that the spatial response evoked by the distractor is either congruent or incongruent, for there is actually no need for participants to determine which hand the target was presented to on the congruent trials, since both the target and distractor are associated with the same response. By contrast, on the incongruent trials, the participants had to determine which hand received the target to respond appropriately (given that the target and distractor are associated with opposing responses). It is perhaps worth noting here that Soto-Faraco et al. (2004; Experiment 2) obtained a significant congruency effect even when the target (and hence also the distractor) hand was fixed throughout each block of trials (so that participants knew in advance which hand would receive the target). Nevertheless, even though significant intramodal tactile congruency effects were still observed, they were somewhat reduced in magnitude as compared to those reported in those experiments where the target and distractor side varied unpredictably on a trial-by-trial basis (such as Experiments 1 and 2 in the present report).

In our third and final experiment, we addressed the potential source of the intramodal tactile congruency effect by using a 4-AFC task (in which the participants had to respond by pressing down with the finger that received the target vibration) where the responses evoked by target and distractors were always different. If significant congruency effects are still observed under such conditions, it would indicate a tendency to encode the elevation of the stimuli even when neither the task nor the responses necessarily evoke any reference to elevation.

Methods

Participants

Ten participants (six women and four men; age range 20–34 years; $M = 23.7$ years; nine right-handed) were recruited to take part in this experiment. None had taken part in either of the previous experiments and all were naïve as to the purpose of the study. All of the participants reported normal tactile sensitivity and normal or corrected-to-normal vision. They were given a five pound (UK Sterling) gift-voucher in return for their participation.

Apparatus, materials, design, and procedure

These were identical to Experiment 1 with the following exceptions: the four tactile stimulators were now mounted on a vertical wooden support rather than on two separate foam cubes. The vertical distance between the two tactors on each side of the setup was the same as in the previous experiments. The tactors on either side were separated by 40 cm. A response button was mounted beside each vibrotactile stimulator and adjacent to each of the four digits (index finger and thumb of both hands) that could potentially receive each target. The four vibrotactile stimulators were isolated from the rest of the setup by means of covering their entire surface with foam except for the one surface where the participant's fingers rested. This minimized the diffusion of any vibration across the setup. The participants had to localize each target vibration by pressing the spatially adjacent button, while ignoring the distractors presented to one of the two digits of the opposite hand (see Fig. 7).

The experimental session consisted of four blocks of 128 randomly presented trials, giving rise to a total of 512 trials. Prior to the start of each block, the participants were instructed to adopt one of the four postures (*dd*, *uu*, *ud*, or *du*; order randomized), just as in Experiments 1 and 2.

Results and discussion

The analysis of the RT data did not reveal any significant effects {Posture [$F(3,27) < 1$]; Congruency [$F(1,9) = 1.08$]; Posture by Congruency [$F(3,27) < 1$]}. The analysis of the error data did, however, reveal that the participants responded significantly more accurately on congruent trials ($M = 37.2\%$ errors) than on the incongruent trials ($M = 40.7\%$ errors) overall [$F(1,9) = 5.14$, $P < 0.05$] (see Fig. 8). However, neither the main factor of Posture [$F(3,27) < 1$] nor the interaction between Congruency and Posture [$F(3,27) < 1$] was significant.

The task manipulation utilized in Experiment 3 eliminated any explicit remapping of the stimuli in terms of the top/bottom dimension; therefore, the congruency effect found in the analysis of the data is somewhat surprising. Indeed, this finding suggests that the congruency effects obtained in Experiments 1 and 2 were, at least in part, related to the spatial representation used to encode the tactile events, and not solely attributable to effects present at the output stage. Note, however, that the congruency effect reported in Experiment 3 is far weaker than that reported in either Experiment 1 or 2. It is therefore likely that the

Fig. 7 The set-up used in Experiment 3, where participants had to respond by pressing a button with the finger that received the vibrotactile stimulation (4-AFC task). The participant's posture shown in the picture is both hands *palm down* (*dd*)

effects at the output stage had a significant influence on performance in addition to any failure at the stage of spatial selection. This result is relevant for understanding the nature of the effects observed in Experiments 1 and 2 and also to put into perspective the results of previous studies that have used similar bimanual congruency tasks (see Soto-Faraco et al. 2004). They may also be relevant to further understand similar congruency results reported in other crossmodal situations, although it should be noted that the magnitude of the effects reported in the crossmodal case are usually much larger and thus one should be careful not to overgeneralize (Spence and Walton 2005; Spence et al. 2000, 2004a, b). Nevertheless, the critical result is that although much smaller than observed previously, the spatial congruency effect observed in the intramodal tactile distractor interference task (taken to suggest the automatic involvement of a space-based neural representation in the processing of tactile stimuli) was once again observed in our final experiment.

It is worth noting that the error rates in Experiment 3 were higher than those reported in Experiments 1 and 2. One might wonder if this apparent increase in task difficulty in Experiment 3 should be attributed to the participants'

difficulty in localizing the tactile stimuli under the particular conditions of stimulus presentation utilized in our final experiment or to the specific response procedures used (four alternative choice response). Given that the major changes in Experiment 3 relate to the modality of response rather than to the conditions of stimulus presentation (note however that in Experiment 3 the vibrators were placed on a fixed frame rather than on hand-hold foam cubes), it would appear that the latter explanation is more likely. However, it would certainly be of interest in future research to further investigate the nature of the apparent difference in task difficulty (perhaps by using signal detection theory to discriminate more perceptual factors from response bias effects; cf. Gallace et al. 2006b).

General discussion

A growing body of empirical research now shows that tactile events are often remapped in terms of an abstract coordinate system (externally based, or body-part-based), and consequently somatic sensations are referred initially to spatial locations and not to the anatomical site of stimulation (e.g., Azañón and Soto-Faraco 2008; Gallace and Spence 2005, 2008; Kitazawa 2002). The main question addressed in the present study was whether this remapping of tactile information reflects a flexible adaptation to the particular demands of the behavioral situation (i.e., to the specific task being performed), or whether instead it reflects a mandatory, automatic, process. Our results indicate an important degree of flexibility, wherein the nature of the task affects the degree to which the abstract coding of stimulus location influences a participant's responses, yet they also indicate the presence of some component of automatic remapping, which produces a persisting (albeit reduced) spatial congruency effect even after removing any stimulus-response spatial compatibility relationships.

It is worth noting here that the role of spatial factors on the representation of tactile information has also been studied by researchers using raised line representations of tactile information. For example, in one study, Millar and Al Attar (2004) provided different kinds of spatial cues while their participants had to memorize haptically presented raised line maps. They reported that disrupting any body-centered reference to the locations on the map (i.e., by changing the orientation of the map with respect to the participant's body between the encoding and test phases of the experiment) increased the number of recall errors that they made. By contrast, adding external reference cues, by asking participants to use a surrounding frame of reference, when body-centered reference was disrupted (again by means of a change in the orientation of the map), resulted in performance returning to the same level of accuracy as that

Fig. 8 Results of Experiment 3 using the 4-AFC task (*bars* represent mean RTs and *lines* represent mean percentage of errors) averaged over participants (*error bars* represent the standard errors of the means). The results are shown separately for each posture adopted (see the *inset conditions labels* in each *graph*). Congruency is shown as a function of the external location of the stimuli
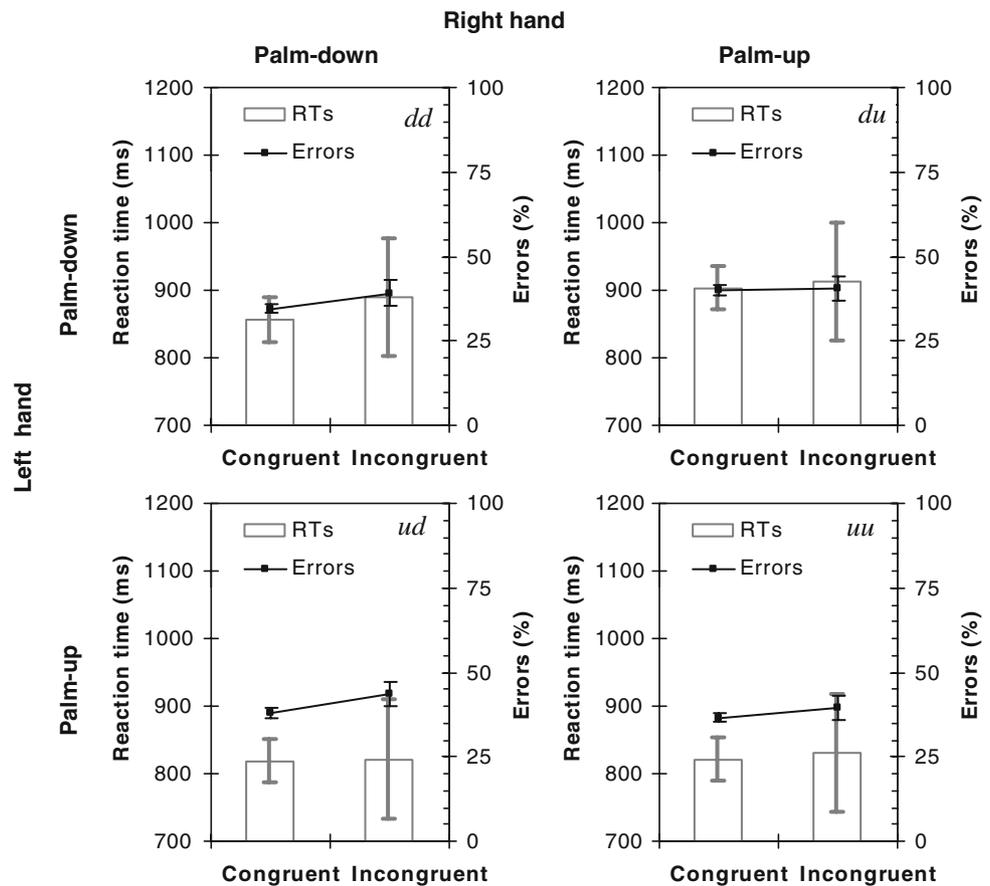
found in the 'no rotation' (baseline) condition. Millar and Al-Attar concluded that external and body-centered reference cues may have independent and additive effects on the representation of haptic information. That is, spatial factors (as mediated by different frames of reference) seem to play a very important role in the representation of tactile stimuli (see also Millar 1994; Millar and Al-Attar 2003). Our results would seem to confirm the plasticity of the code used to represent tactile stimuli as suggested previously by Millar and Al-Attar. By contrast, the present results appear to argue against the view that the way in which people represent tactile information is hard-wired in the brain and based on a single frame of reference (e.g., Natsoulas and Dubanoski 1964; Parsons and Shimojo 1987; see also Corcoran 1977; Oldfield and Phillips 1983, for discussion on this point).

The results of Experiment 1 were seemingly consistent with the claim that any tactile event that is presented on the skin will be transformed into an abstract frame of reference that is referred to a position in external space, even when the task requires a behavioral reaction based on the anatomically defined location (i.e., on somatotopic coding). However, as revealed by the results of Experiment 2, this type of encoding is actually dependent on the particular effectors used by participants to respond, as it was considerably attenuated when the motor response was not spatial (i.e., when participants responded verbally). Finally, the results of Experiment 3 led to a further qualification with regard to the nature of the intramodal tactile spatial congruency effect. In particular, the results showed that this effect arose from two different sources; the selection and representation of the stimuli on the basis of a specific spatial frame of reference, and a distractor-response compatibility effect (namely, the fact that the target and the distractor could also be mapped onto different response buttons when spatially congruent). The distractor-response compatibility effect can be characterized as an output effect, one that does not necessarily speak directly to the way in which stimuli are perceptually encoded (e.g., Kornblum et al. 1990). By contrast, the selection of an appropriate frame of reference for the representation of the tactile stimuli appears to be related to relatively earlier stages of information processing.

Localizing tactile events in space involves multisensory integration

Taken together, the results of the three experiments reported in the present study clearly place an important caveat on Kitazawa's previous claims that tactile stimuli/events presented to the skin are *always* referred to external

spatial locations (or that a representation of tactile stimuli that is always based on external frame of reference will necessarily be used for a participant's response; see especially Kitazawa 2002). As discussed in the Introduction, there are several previous findings that seemingly support a somatotopically based frame of reference for the encoding of tactile events under certain conditions of stimulus presentation (Evans and Craig 1991; Evans et al. 1992; Röder et al. 2002). Our results also support these claims by showing that the specific frames of reference used by participants for their responses may vary as a function of the demands of the task and that the spatial information regarding the stimuli presented might be simultaneously computed on the basis of different frame of references (see also Azañón and Soto-Faraco 2008).

The role of response mapping

Given that radical changes in the task-relevant feature (elevation in external space vs. anatomical location) seemed to exert little influence on the frame of reference adopted by the participants in Experiment 1, one might have thought that the actual effector used to respond might also play a minor role (cf. Spence and McDonald 2004). Yet comparison of the results of Experiments 1 and 2 suggests that one of the factors exerting a profound influence on the way in which our brain selects the appropriate frame of reference for responding to tactile stimulation depends on the nature of the actions used to respond to those events. Several cases have already been discussed in which dramatic and robust phenomena can vanish completely as a function of the task or response effector used (see the discussion of the results of Experiment 2; Graziano et al. 2004; cf. Andersen 1995; Cohen et al. 1994; Gottlieb et al. 1998; Pouget and Sejnowski 2001).

However, it is crucial to stress that some evidence for a role of an externally based frame of reference was still found under conditions where these potential correspondences in response-mapping were bypassed by the use of verbal responding (Experiment 2) or the 4-AFC task (Experiment 3). This suggests that the mapping of tactile events is not purely somatotopic, but that it is influenced to some degree by an abstract spatial code, albeit in an attenuated form. Similar cases in which the data is consistent with the remapping of the stimuli on different representations of space during cross-modal tasks have been reported previously in a number of studies ranging from human psychophysics (e.g., Azañón and Soto-Faraco 2008; Röder et al. 2002; Spence et al. 2003; Spence and Walton 2005), to animal electrophysiology (e.g., Cohen and Andersen 2000; Duhamel et al. 1997; Jay and Sparks 1987) and computational models (Pouget et al. 2002).

One should also consider the possibility that the results obtained in the experiments reported here are somehow specific to the particular part of the body where the stimuli were presented (i.e., the fingertips). Indeed, given that we often use our hands to perceive tactile information, the selection of the correct representation to be used to respond to the stimuli presented at that location might be more flexible than that of the stimuli presented on other regions of the body surface (or more spatial representation of the stimuli presented are available to be selected for a participant's response; see Schicke and Röder 2006). It would be interesting in future research to investigate the mapping of tactile stimuli when presented across different regions of the skin surface as a function of different response requirements (cf. Gallace et al. 2006a, 2007, 2008).

References

Andersen RA (1995) Encoding of intention and spatial location in the posterior parietal cortex. Cereb Cortex 5:457–469

Austen EL, Soto-Faraco S, Enns J, Kingstone A (2003) Visual influences on tactile localization depend on limb orientation and response mapping. Abstr Cogn Neurosci Soc Meet F316:225

Austen EL, Soto-Faraco S, Enns J, Kingstone A (2004) Mislocalizations of touch to a fake hand. Cogn Affect Behav Neurosci 4:170–181

Axelrod S, Thompson LW, Cohen LD (1968) Effects of senescence on the temporal resolution of somesthetic stimuli presented to one hand or both. J Gerontol 23:191–195

Azañón E, Soto-Faraco S (2007) Alleviating the 'crossed-hands' deficit by seeing uncrossed rubber hands. Exp Brain Res 182:537–548

Azañón E, Soto-Faraco S (2008) Changing frames of reference during the encoding of tactile events. Curr Biol 18(14):1044–1049

Baylis GC, Driver J, Rafal RD (1993) Visual extinction and stimulus repetition. J Cogn Neurosci 15:453–466

Botvinick M, Cohen J (1998) Rubber hands 'feel' touch that eyes see. Nature 391:756

Cohen YE, Andersen RA (2000) Reaches to sounds encoded in an eye-centered reference frame. Neuron 3:647–652

Cohen YE, Andersen RA (2004) Multimodal spatial representations in the primate parietal lobe. In: Spence C, Driver J (eds) Crossmodal space and crossmodal attention. Oxford University Press, Oxford, pp 99–121

Cohen JD, Romero RD, Servan-Schreiber D, Farah MJ (1994) Mechanisms of spatial attention: the relation of macrostructure to microstructure in parietal neglect. J Cogn Neurosci 6:377–387

Corcoran DWJ (1977) The phenomena of the disembodied eye or is it a matter of personal geography? Perception 6:247–253

Desimone R, Duncan J (1995) Neural mechanisms of selective attention. Annu Rev Neurosci 18:193–222

di Pellegrino G, Rafal R, Tipper SP (2005) Implicitly evoked actions modulate visual selection: Evidence from parietal extinction. Curr Biol 15:1469–1472

Driver J, Grossenbacher PG (1996) Multimodal spatial constraints on tactile selective attention. In: Inui T, McClelland JL (eds) Attention and performance XVI: information integration in perception and communication . MIT Press, Cambridge, pp 209–235

Duhamel JR, Bremmer F, BenHamed S, Graf W (1997) Spatial invariance of visual receptive fields in parietal cortex neurons. Nature 389:845–848

Eimer M, Driver J (2000) An event-related brain potential study of crossmodal links in spatial attention between vision and touch. Psychophysiology 37:697–705

Eimer M, Cockburn D, Smedley B, Driver J (2001) Cross-modal links in endogenous spatial attention are mediated by common external locations: evidence from event-related brain potentials. Exp Brain Res 139:398–411

Evans PM, Craig JC (1991) Tactile attention and the perception of moving tactile stimuli. Percept Psychophys 49:355–364

Evans PM, Craig JC, Rinker MA (1992) Perceptual processing of adjacent and nonadjacent tactile nontargets. Percept Psychophys 52:571–581

Gallace A, Spence C (2005) Visual capture of apparent limb position influences tactile temporal order judgments. Neurosci Lett 379:63–68

Gallace A, Spence C (2008) The cognitive and neural correlates of "tactile consciousness": a multisensory perspective. Conscious Cogn 17:370–407

Gallace A, Tan HZ, Spence C (2006a) Numerosity judgments in tactile perception. Perception 35:247–266

Gallace A, Tan HZ, Spence C (2006b) The failure to detect tactile change: a tactile analogue of visual change blindness. Psychon Bull Rev 13:300–303

Gallace A, Tan HZ, Spence C (2007) Multisensory numerosity judgments. Percept Psychophys 69:487–501

Gallace A, Tan HZ, Spence C (2008) The body surface as a communication system: the state of art after 50 years of research. Presence Teleoperators Virtual Environ 16:655–676

Geffen G, Rosa V, Luciano M (2000) Effect of preferred hand and sex on the perception of tactile simultaneity. J Clin Exp Neuropsychol 22:219–231

Gottlieb JP, Kusunoki M, Goldberg ME (1998) The representation of visual salience in monkey parietal cortex. Nature 391:481–484

Graziano MSA, Gross CG (1998) Spatial maps for the control of movement. Curr Opin Neurobiol 8:195–201

Graziano MSA, Gross CG, Taylor CSR, Moore T (2004) A system of multimodal areas in the primate brain. In: Spence C, Driver J (eds) Crossmodal space and crossmodal attention. Oxford University Press, Oxford, pp 51–67

Groh JM, Sparks DL (1996) Saccades to somatosensory targets: 1. Behavioral characteristics. J Neurophysiol 75:412–427

Holmes NP, Spence C (2005) Visual bias of unseen hand position with a mirror: spatial and temporal factors. Exp Brain Res 166:489–497

Holmes NP, Spence C (2006) Beyond the body schema: visual, prosthetic, and technological contributions to bodily perception and awareness. In: Knoblich G, Thornton IM, Grosjean M, Shiffrar M (eds) Human body perception from the inside out. Oxford University Press, Oxford, pp 15–64

Jay MF, Sparks DL (1987) Sensoriomotor integration in the primate superior colliulus. I. Motor convergence. J Neurophysiol 57:22–34

Kanwisher N, Driver J, Machado L (1995) Spatial repetition blindness is modulated by selective attention to color or shape. Cognit Psychol 29:303–337

Kennett S, Spence C, Driver J (2002) Visuo-tactile links in covert exogenous spatial attention remap across changes in unseen hand posture. Percept Psychophys 64:1083–1094

Kitazawa S (2002) Where conscious sensation takes place. Conscious Cogn 11:475–577

Kóbor I, Füredi L, Kovács G, Spence C, Vidnyánszky Z (2006) Back-to-front: Improved tactile discrimination performance in the space you can't see. Neurosci Lett 400:163–167

Kornblum S, Hasbroucq T, Osman A (1990) Dimensional overlap: cognitive basis for stimulus-response compatibility—a model and taxonomy. Psychol Rev 97:253–270

Làdavas E, Farnè A (2004) Neuropsychological evidence for multimodal representations of space near specific body parts. In: Spence C, Driver J (eds) Crossmodal space and crossmodal attention. Oxford University Press, Oxford, pp 69–98

Lakatos S, Shepard RN (1997) Time-distance relations in shifting attention between locations on one's body. Percept Psychophys 59:557–566

Lloyd DM, Shore DI, Spence C, Calvert GA (2003) Multisensory representations of arm position in human premotor cortex. Nat Neurosci 6:17–18

Maravita A, Spence C, Sergent C, Driver J (2002) Seeing your own touched hands in a mirror modulates cross-modal interactions. Psychol Sci 13:350–356

Millar S (1994) Understanding and representing space: theory and evidence from studies with blind and sighted children. Oxford University Press, Oxford

Millar S, Al-Attar Z (2003) Spatial reference and scanning with the left and right hand. Perception 32:1499–1511

Millar S, Al Attar Z (2004) External and body-centered frames of reference in spatial memory: evidence from touch. Percept Psychophys 66:51–59

Moscovitch M, Behrmann M (1994) Coding of spatial information in the somatosensory system: evidence from patients with neglect following parietal lobe damage. J Cogn Neurosci 6:151–155

Motter BC (1993) Focal attention produces spatially selective processing in visual cortical areas V1, V2 and V4 in the presence of competing stimuli. J Neurophysiol 70:909–919

Narici L, Modena I, Opsomer RJ, Pizzella V, Romani GL, Torrioli G et al (1991) Neuromagnetic somatosensory homunculus: a noninvasive approach in humans. Neurosci Lett 121:51–54

Natsoulas T, Dubanoski RA (1964) Inferring the locus and orientation of the perceiver from responses to stimulation of the skin. Am J Psychol 77:281–285

Oldfield SR, Phillips JR (1983) The spatial characteristics of tactile form perception. Perception 12:615–626

Paillard J (1999) Divided body schema and body image—a double dissociation in deafferented patient. In: Gantchev GN, Mori S, Massion J (eds) Motor control today and tomorrow. Academic Publishing House, Sofia, pp 197–214

Parsons LM, Shimojo S (1987) Perceived spatial organization of cutaneous patterns on surfaces of the human body in various positions. J Exp Psychol Hum Percept Perform 13:488–504

Pavani F, Spence C, Driver J (2000) Visual capture of touch: out-of-the-body experiences with rubber gloves. Psychol Sci 11:353–359

Penfield W, Rasmussen T (1950) The cerebral cortex of man. Macmillan, New York

Pick HL Jr (1974) Visual coding of nonvisual spatial information. In: MacLeod RB, Pick HL Jr (eds) Perception: essays in honor of James J. Gibson. Cornell University Press, Ithaca, pp 153–165

Polanyi ML (1962) Personal knowledge. Routledge & Kegan Paul, London

Pouget A, Sejnowski TJ (2001) Simulating a lesion in a basis function model of spatial representations: comparison with hemineglect. Psychol Rev 108:653–673

Pouget A, Deneve S, Duhamel J-R (2002) A computational perspective on the neural basis of multisensory spatial representations. Nat Rev Neurosci 3:741–747

Rapp B, Hendel SK (2003) Principles of cross-modal competition: evidence from deficits of attention. Psychon Bull Rev 10:210–219

Roberts RD, Humphreys GW (2006) Spatial and frequency judgments of tactile temporal order. Poster presented at the joint meeting of the Experimental Psychology Society and the Nederlandse Vereniging voor Psychonomie, Birmingham, UK, 10–12 April 2006

Röder B, Spence C, Rösler F (2000) Inhibition of return and oculomotor control in the blind. NeuroReport 11:3043–3045

Röder B, Spence C, Rösler F (2002) Assessing the effect of posture change on tactile inhibition-of-return. Exp Brain Res 143:453–462

Röder B, Rösler F, Spence C (2004) Early vision impairs tactile perception in the blind. Curr Biol 14:121–124

Schicke T, Röder B (2006) Spatial remapping of touch: confusion of perceived stimulus order across hand and foot. Proc Natl Acad Sci USA 103:11808–11813

Shore DI, Spry E, Spence C (2002) Confusing the mind by crossing the hands. Brain Res Cogn Brain Res 14:153–163

Shore DI, Gray K, Spry E, Spence C (2005) Spatial modulation of tactile temporal-order judgments. Perception 34:1251–1262

Shore DI, Gallace A, Mimnagh K, Spence C (2006). Assessing the frames of references involved in the crossed hands temporal order judgments deficit: the role of response demands. Paper presented at 7th Annual Meeting of the International Multisensory Research Forum, University of Dublin, Trinity College, Dublin, Ireland. Available at http://www.science.mcmaster.ca/~IMRF/2006/viewabstract.php?id=186

Soto-Faraco S, Ronald A, Spence C (2004) Tactile selective attention and body posture: assessing the contribution of vision and proprioception. Percept Psychophys 66:1077–1094

Spearman C (1907) An 'economic' theory of spatial perception. Mind 16:181–196

Spence C (2002) Multimodal attention and tactile information-processing. Behav Brain Res 135:57–64

Spence C, McDonald J (2004) The crossmodal consequences of the exogenous spatial orienting of attention. In: Calvert GA, Spence C, Stein BE (eds) The handbook of multisensory processing. MIT Press, Cambridge, pp 3–25

Spence C, Walton M (2005) On the inability to ignore touch when responding to vision in the crossmodal congruency task. Acta Psychol 118:47–70

Spence C, Pavani F, Driver J (2000) Crossmodal links between vision and touch in covert endogenous spatial attention. J Exp Psychol Hum Percept Perform 26:1298–1319

Spence C, Kingstone A, Shore DI, Gazzaniga MS (2001a) Representation of visuotactile space in the split brain. Psychol Sci 12:90–93

Spence C, Shore DI, Gazzaniga MS, Soto-Faraco S, Kingstone A (2001c) Failure to remap visuotactile space across the midline in the split-brain. Can J Exp Psychol 55:135–142

Spence C, Baddeley R, Zampini M, James R, Shore DI (2003) Crossmodal temporal order judgments: when two locations are better than one. Percept Psychophys 65:318–328

Spence C, Pavani F, Driver J (2004a) Spatial constraints on visual-tactile crossmodal distractor congruency effects. Cogn Affect Behav Neurosci 4:148–169

Spence C, Pavani F, Maravita A, Holmes N (2004b) Multisensory contributions to the 3-D representation of visuotactile peripersonal space in humans: evidence from the crossmodal congruency task. J Physiol (Paris) 98:171–189

Yamamoto S, Kitazawa S (2001) Reversal of subjective temporal order due to arm crossing. Nat Neurosci 4:759–765

Zampini M, Harris C, Spence C (2005) The effect of posture change on tactile perception: impaired direction discrimination performance with interleaved fingers. Exp Brain Res 166:498–508