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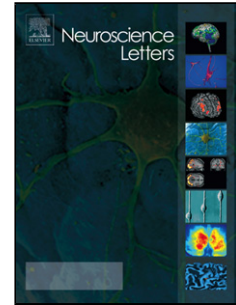
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DOUBLE SIMULTANEOUS TACTILE STIMULATION

Research highlights

- Interference effects from tactile double simultaneous stimulation (DSS) at the fingers emerge both within and between hands
- Between-hands DSS interference disappears when the hands adopt incongruent postures (one hand palm-up, the other hand palm-down)
- Somatotopic representations for touch code for finger identity more than finger side
- Tactile stimulation side becomes more prominent when postural update is required
- Multiple representation for touch likely coexist, possibly with different relative weightings as a function of tasks demands

Spatial coding of touch at the fingers:
Insights from double simultaneous stimulation within and between hands

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Running head: DOUBLE SIMULTANEOUS TACTILE STIMULATION

Abstract

We studied the effect of tactile double simultaneous stimulation (DSS) within and between hands to examine spatial coding of touch at the fingers. Participants performed a go/no-go task to detect a tactile stimulus delivered to one target finger (e.g., right index), stimulated alone or with a concurrent non-target finger, either on the same hand (e.g., right middle finger) or on the other hand (e.g., left index finger = homologous; left middle finger = non-homologous). Across blocks we also changed the unseen hands posture (both hands palm down, or one hand rotated palm-up). When both hands were palm-down DSS interference effects emerged both within and between hands, but only when the non-homologous finger served as non-target. This suggests a clear segregation between the fingers of each hand, regardless of finger side. By contrast, when one hand was palm-up interference effects emerged only within hand, whereas between hands DSS interference was considerably reduced or absent. Thus, between hands interference was clearly affected by changes in hands posture. Taken together, these findings provide behavioral evidence in humans for multiple spatial coding of touch during tactile DSS at the fingers. In particular, they confirm the existence of representational stages of touch that distinguish between body-regions more than body-sides. Moreover, they show that the availability of tactile stimulation side becomes prominent when postural update is required.

Introduction

During everyday life, we know where we have been touched on our body surface almost without effort. However, this seemingly simple ability hides the existence of multiple spatial representations of the tactile event in our brain [1,8,11]. A recently proposed flow-chart of somatosensory representations [19] suggests that touch is initially encoded into a sensory space within the primary somatosensory map [16], but the location of the tactile event is then coded also with respect to other representational levels in further processing stages. Specifically, tactile sensation can be mapped in a mental body representation, enabling us to localize tactile events with respect to body-parts and body-sides [8,18], or in egocentric/allocentric representations of external space, enabling the localization of tactile events in the outside world [1,2,5].

Double simultaneous stimulation (DSS), in which two concurrent tactile events compete with one another, has proven useful in the past to probe the sensory processing of touch. In unilateral brain-damaged patients this competition can lead to tactile extinction [3], whereby patients fail to report a contralesional touch when presented concurrently with an ipsilesional one. Extinction-like effects have recently been documented in neurologically healthy participants, when the conscious report of both stimuli is required [10]. Finally, a number of studies have reported modulations of tactile performance in neurologically-healthy individuals even when a single predefined target has to be consciously reported under DSS [9]. This interference typically occurs when the two tactile stimuli are presented in close temporal and spatial proximity [7], and its exact nature is still debated as it can reflect a competition occurring at the sensory level as well as a competition at the response level [15].

A consistent finding of this single-report approach is that DSS leads to decreased performance particularly when the stimulation occurs within the same hand, but to adjacent fingers, whereas the occurrence of between-hands interference remains more controversial [6,9]. However, interference effects occurring within the same hand are not discriminative of different body representational levels, because adjacent fingers on the same hand are near each other in somatotopic space, in

mental body space and in external space (unless finger posture is experimentally manipulated). By contrast, the presence (or absence) of interference effects between hands is more relevant for the understanding of the body representational level used when processing concurrent tactile targets. For instance, several findings converge to suggest that touch representations with a clear somatotopic organisation do not fully differentiate between body sides. Tactile localization errors at the hands are modulated as a function of somatotopic distance between the stimulated fingers [17], also when the stimulation is delivered to fingers of opposite hands [4]. Similarly, participants trained to discriminate punctuate pressure or roughness stimuli on one finger of the right hand (e.g., the index) can transfer this training to the first neighboring finger of the same hand (i.e., the right middle finger) as well as to the homologous finger of the opposite hand (i.e., the left index finger; [12]). In light of these results, DSS interference occurring both within and between hands would imply a dominant role of somatotopic representations in spatial coding of touch at the fingers. We should emphasise here that when referring to somatotopic representations of the body that distinguish between body-regions more than body-side, we anatomically imply a bilateral network of somatotopically organised regions, rather than just the primary somatosensory cortex (SI) contralateral to the stimulation. SI surely responds to touches from the contralateral body side at the early stages of tactile processing, particularly when distal regions such as the hands are involved. However, it also participates in somatotopic representation of touch that spans across the body midline in the time frame of behavioural experiments. This is due to the transcallosal connections between SI in the opposite hemispheres and to the reciprocal connections between SI and secondary somatosensory areas, which are characterized by bilateral receptive fields [14].

In the present study, by testing to what extent DSS interference occurs between as well as within hands we sought to establish the body representational level at which this interference occurs. Participants performed a go/no-go task to detect a tactile stimulus delivered to one target finger (e.g., right index), stimulated alone or with a concurrent non-target finger, either on the same hand (e.g., right

middle finger) or on the other hand (e.g., left index finger = homologous; left middle finger = non-homologous). Across blocks, the target finger was either the index or the middle finger of the right or left hand. In addition, we asked participants to perform the task in two different hands postures: both hands palm down or one hand palm down while the other is palm up.

Based on the previously reported studies on healthy and brain-damaged subjects [3,9], we expected worse performance in DSS trials compared to trials in which the target finger was stimulated alone (i.e., DSS interference). Second, based on previous studies documenting between hands interactions in touch perception [4,12], we expected DSS interference both within and between hands. In particular, we expected DSS interference when the non-target finger was adjacent to the target (e.g., middle left finger, when the target was the left index) and when the non-target finger was the non-homologous finger on the other hand (e.g., middle right finger). Finally, postural manipulations make spatial coding of touch in external space more prominent [1,2]. Accordingly, we expected less DSS interference between-hands when one hand was rotated into an unusual posture.

Materials and methods

Sixteen participants (mean age = 28 years, SD = 5; 8 females, 8 males; 13 right-handed) took part in the study, that was carried out according to the principles of the Declaration of Helsinki. All reported normal or corrected to normal vision and normal touch.

Tactile stimuli were delivered to the index and/or middle fingers of either hand by using four vibrators (Piezo System, Q220-A4-203YB model). Tactile stimulation was a square impulse, resulting from a fixed voltage of 40V fed into the vibrators for 8 ms. All participants clearly perceived this stimulation when delivered in isolation to each finger before the experiment. To maintain an homogeneous contact between the fingers and the vibrotactile stimulators across all posture changes, the distal and intermediate phalanges of each index and middle finger were inserted inside a plastic square parallelepiped (75x40x80 mm), padded inside with foamed-plastic. In addition,

stimulators were secured to the fingers using medical tape. Vibrators assigned to each finger were changed after every 4 participants, to control for possible intensity differences between the stimulation devices.

The stimulated fingers were arranged to form an imaginary square of 4 cm (at the fingertips; see Figure 1a). Vision of the hands was prevented throughout by means of a 17" flat computer screen, placed horizontally on a wooden structure fixed to the table, on top of the vibrators. The screen was used to present instructions prior to the experiment, and served for displaying the fixation cross during the experiment. Fixation was aligned with the midsagittal plane of the participant and fell at the centre of the imaginary 4 cm square created by the fingertips. Responses were collected using one foot-pedal positioned under the participant's right foot. Stimulus presentation and response collection were controlled by custom program written using MATLAB R2006b and Psychtoolbox. Throughout the experiment, white noise was presented over a closed-ear headphone to mask any sounds made by the operation of the tactile stimulators.

< Figure 1 >

At the beginning of each experimental block a drawing of the two hands with one single finger clearly marked (see Figure 1b) was displayed on the computer screen. This drawing designated the target finger for an entire block of trials. Participants also reported verbally to the experimenter which was the designated target finger for that experimental block. Participants were informed that they had to perform a speeded go-no-go task to indicate whether the target finger had been stimulated or not. Specifically, they were instructed to keep the right foot-pedal pressed, unless they wanted to indicate the presence of a tactile stimulus at the target finger.

Each experimental trial started with a black cross appearing on white background in the centre of the screen. Participants were instructed to fixate the cross throughout the duration of the experimental block. After a variable interval ranging between 200 and 400 ms from fixation onset, tactile stimulation was presented. The stimulation was

either: (1) a single touch delivered to the designated target finger (T-only trials); (2) two touches delivered simultaneously, one to the target finger and one to another finger (DSS trials); or (3) a single touch delivered to one of the non-target fingers (catch trials). The diagram in Figure 1 (b-d) illustrates all of the possible stimulation conditions for an example block in which the target-finger is the right index finger. Three DSS trials were possible (Figure 1c): target finger plus the neighboring finger of the same hand ('T+DFSH trials', for Target + Different Finger Same Hand); target finger plus the homologous finger of the other hand ('T+SFDH trials', for Target + Same Finger Different Hand); or target finger plus the non-homologous finger of the other hand ('T+DFDH trials', for Target + Different Finger Different Hand). Finally, catch trials were also presented as a function of the position of the non-target finger with respect to the target finger. Three types of catch trials were possible (Figure 1d): 'DFSH trials', for Different Finger Same Hand non-target; 'SFDH trials', for Same Finger Different Hand non-target; and 'DFDH trials', for Different Finger Different Hand non-target.

Fixation overstimulation for 100 ms then was replaced by a question-mark symbol that instructed participants to make their choice as to whether the target finger had been stimulated or not. Participants were instructed to react as fast and accurately as possible and were informed that they had a maximum of 2 seconds to respond before the beginning of the next trial.

The experiment comprised eight separate blocks. In four blocks, both hands were palm down (one block for each of the four possible target locations). In the remaining blocks, one hand was palm down while the other was palm up (i.e., one hand was rotated by 180 degrees around the major axis of the forearm). Half of participants rotated the left hand and the other half rotated the right hand. Note that with our setup, rotating one hand palm up changes the relative position of the fingers between the two hands (e.g., the right index finger faces the left middle finger after hand rotation). However, the coordinates of stimulation sites in external space remained unchanged.

Each block comprised 70 trials (i.e., 7 stimulation conditions repeated 10 times each), resulting in a total 560 trials. We pooled together the data when the target was

at the left and right hand, and also when the target finger was the index and the middle finger. This resulted in a 7 (stimulation) x 2 (posture) factorial design, with 40 trials for each cell of the design.

Results

We computed the percentage of errors in T-only and DSS trials based on the proportion of 'no-go' responses in the conditions where the target finger was stimulated. Note that 'no-go' responses could result from the perception that the target finger was not stimulated (i.e., detection errors), or from the perception that a different finger was stimulated (i.e., localisation error). The go-no-go paradigm adopted here does not distinguish between these two error-types. However, the analysis on catch trials is informative in this respect, because errors in catch trials could only reflect localisation errors.

Percentage of errors in T-only and DSS trials were entered into a repeated measure Analysis of Variance (ANOVA) with Stimulation Condition (T, T+DFSH, T+SFDH, T+DFDH) and Hands Posture (both palm-down, one palm-up) as within participant variables. The Newman-Keuls test was used for all post-hoc comparisons. This analysis revealed a significant interaction between Stimulation Condition and Hands Posture ($F_{(3,45)} = 2.850, p = 0.05$). As illustrated in Figure 2a, tactile DSS within hand resulted in worse performance with respect to target only trials (T-only: mean = 24%, SE = 0.07; T+DFSH, mean = 35%, SE = 0.06; $p < 0.03$). This DSS interference pattern was entirely unaffected by changes in hands posture (both hands palm down, mean = 35%, SE = 0.04; one hand palm up, mean = 35%, SE = 0.05). By contrast, between hands tactile DSS performance was present or absent as a function of the stimulated finger (homologous or non-homologous) and hands posture. When the finger non-homologous to the target (i.e. T+DFDH condition) was stimulated with both hands palm down, DSS interference emerged with respect to target only trials (mean = 33%, SE = 0.04; $p < 0.02$). Note that in this condition DSS interference was comparable to that obtained within hand ($p = 0.5$). However, DSS interference for the non-homologous finger disappeared when either hand was rotated palm up. Finally, when

the finger homologous to the target (i.e., T+SFDH condition) was stimulated no DSS interference emerged, irrespective of hands' posture (both hands palm down, mean = 21%, SE = 0.05; one hand palm up, mean = 25%, SE = 0.04; $p = 0.8$ with respect to T-only trials).

The main effect of Stimulation Condition was also significant ($F_{(3,45)} = 3.524$, $p < 0.02$), but was qualified by the higher-order interaction reported above. No other main effects were significant emerged ($F < 1.8$).

< Figure 2 >

Response time (RT) data for correct trials were entered into a similar analysis. This analysis only revealed a main effect of Stimulation Condition ($F_{(3,45)} = 17.910$, $p = 0.0001$), caused by faster responses in T-only trials (mean = 551 ms, SE = 40 ms) than in all DSS trials conditions (averaged DSS trials; mean = 610 ms, SE = 41 ms; $p < 0.004$ for all comparisons; see Figure 2b). Notably, participants were faster when between hands DSS occurred at the homologous (T+SFDH: mean = 590 ms, SE = 41 ms) compared to the non-homologous finger (T+DFDH: mean = 623 ms, SE = 42 ms; $p = 0.02$). This lower RT interference in T+SFDH than T+DFDH condition indicates relatively better performance precisely for the between-hands DSS pairing for which no accuracy cost was previously observed, thus excluding a speed-accuracy trade-off. No other main effect or interaction reached significance (all $F_s < 1.2$).

Finally, we examined the percentage of errors in the catch trials conditions (see Figure 2c) to examine localisation errors for our stimuli. The inter-participant percentage errors in catch trials were entered into a repeated measure ANOVA with Stimulation Condition (DFSH, SFDH and DFDH) and Hands Posture (both hands palm-down or one hand palm-up) as within-participants variables. This analysis revealed a main effect of Stimulation Condition ($F_{(2,30)} = 12.62$, $p = 0.0001$), caused by more errors for DFSH (mean = 6%, SE = 0.02) than SFDH (mean = 1%, SE = 0.004) or DFDH (mean = 1%, SE = 0.01; $p < 0.001$ for both comparisons). No other main effect or interaction was significant (all $F_s < 1$).

Discussion

In the present study we examined the modulations of DSS interference within and between hands as a function of hands posture, as a proxy for the study of spatial coding of touch at the fingers. Two main results emerged from the performance in DSS trials (as compared to target only trials). First, DSS interference emerged both within- and between-hands. Second, finger identity and hand posture selectively affected between-hands DSS interference. When both hands were palm down, between-hands DSS interference emerged reliably for the non-homologous finger in both response times and errors. When one hand was palm up, between hand DSS interference persisted only in terms of response times but disappeared in percent errors. This indicates that when there is no requirement for hand postural remapping a somatotopic processing dominates, resulting in DSS interference both within and between hands. However, when postural remapping is required the concurrent influence of non-somatotopic bodily representations emerges, reducing between-hands DSS interference. The two main findings will be discussed in turn, with emphasis on the presumed spatial coding of touch subserving each effect.

Finger-based DSS interference with both hands palm down

We observed DSS interference both in terms of percent errors and RTs. The occurrence of within-hand interference was predicted based on previous findings on competing touch at the fingers [6,9] and was largely confirmed with both measures. This strong and stable within-hand interference may reflect partial overlapping of tactile receptive fields for adjacent fingers in the somatosensory cortex [4,13]. This is also supported by the pattern of errors in catch trials, in which participants made significantly more errors when the non-target finger was stimulated alone on the same hand designated to contain the target, than on the other hand.

Additionally, we observed reliable between-hands DSS interference, when the stimulation was on the non-homologous finger of the opposite hand with respect to the target. Notably, the amount of DSS interference was generally comparable within-

and between-hands when non-homologous fingers were touched, indicating that non-target stimulation was not merely excluded on the basis of finger side. In contrast, when the homologous finger of the opposite hand was stimulated, interference was abolished (% errors) or considerably reduced (RTs). In sum, between-hands DSS interference was larger for the non-homologous than the homologous finger, indicating a prominent role of finger identity in this phenomenon.

These findings are in accord with the existence of somatotopic representations that distinguish more between body-regions than body-sides [4,12]. This pattern of interference is compatible with the idea that at some representational stage the differentiation between the two hands is less clearly defined as compared to the distinction between body-parts, and stimulation delivered to the non-homologous finger of the other hand can reach cortical territories ipsilateral to the target [4,14]. In other words, when both hands are tested palm down the pattern of DSS interference is compatible with a finger-based processing of touch that is largely insensitive to finger side.

Remapping hand posture changes DSS interference

The second main finding of the present work is that when the posture of either hand was changed, DSS interference remained unchanged within-hands, but became less consistent between-hands, persisting for RTs but not for percent errors. Indeed, when DSS performance was assessed while one of the subjects' hand was palm-up we documented a clear tactile interference for concurrent within-hand stimulation, which was independent of the hand's posture (see Figure 2a). In contrast, when concurrent stimulation was delivered between-hands no significant interference was observed in terms of change in accuracy for either homologous or non-homologous finger stimulation (Figure 2a). This posture-dependent modulation indicates a role for non-somatotopic spatial representations for touch, which takes into account the overall structure of the body as well as its layout in space. In other words, when hand postural incongruence alters fingers position in external space, the pattern of DSS interference within and between hands reveals that not only finger- but also body- or space-based

representations contribute to the processing of touch at the fingers, which helps distinguishing between the two body sides or hemispaces. The fact that DSS interference was present between-hands when considering subjects' RTs may precisely indicate that such a higher-level tactile representation does not completely override the lower-level one. However, it cannot be excluded that this RT result could also reflect some finger-based response competition.

These findings are in agreement with those recently reported by Haggard and colleagues [11], who showed that changes in hand posture affected the identification of which hand was stimulated, but not the simple detection of touches or identification of the stimulated finger. Within a hierarchical perspective, these authors suggested that tactile detection and finger identification occur at a somatotopic representational level, whereas hand identification occurs at a higher level which take postural information into account. Our results expand this finding by showing that postural remapping involving the hands can modify which spatial representation of touch tends to prevail, even when the participant's task always entails identification of the stimulated finger, rather than the stimulated hand.

What role for spatial attention?

Having asked participants to respond only when a specific finger was stimulated we surely induced an attention set. If participants oriented their tactile attention selectively to the target finger, distracting stimulation at non-target fingers should have been easily filtered out, resulting in little or no interference in DSS trials. More likely, however, participants attended the entire target hand (see [6]). The DSS interference observed within hand is compatible with this attention set: when selecting the target finger, participants also selected the distractor finger within the same hand, resulting in interference effects. However, this attentional account does not explain the presence of between-hand DSS interference in our study, because distracting stimuli at the non-target hand should have been filtered out. Thus, it appears that DSS competition can occur independently from the attentional selection of the target finger and target hand, at least to some extent. This could either occur

because DSS competition arise pre-attentively, or because the abrupt onset of the stimulation at the non-target finger captures attention exogenously, breaking the endogenous attentional set.

Conclusions

The current results show that tactile DSS can produce interference effects both within and between hands, that are more dependent upon the identity of the stimulated body-part (i.e., which finger is touched) than the body-side (i.e., which hemisoma is touched). This finding implies that at least some aspects of the processing of concurrent touches occur regardless of distinction based on stimulation laterality. In addition, we documented a posture-dependent modulation of the between-hands interference, in keeping with the notion of multiple spatial coding for touch. Altogether, these findings suggest that finger-based and space-based representation may coexist, possibly with different relative weightings as a function of tasks demands.

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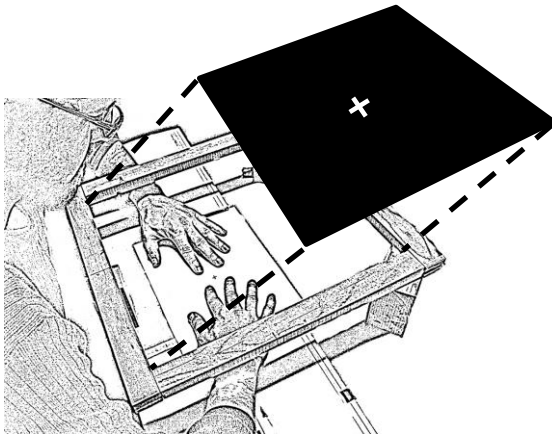
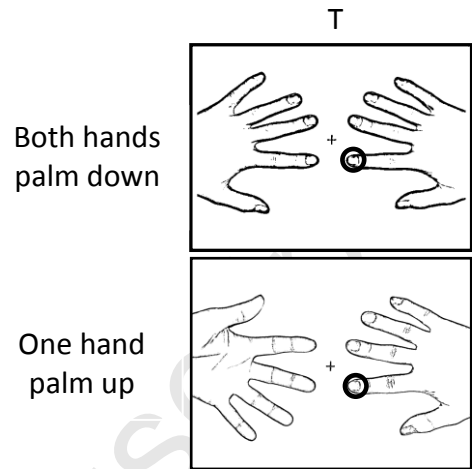
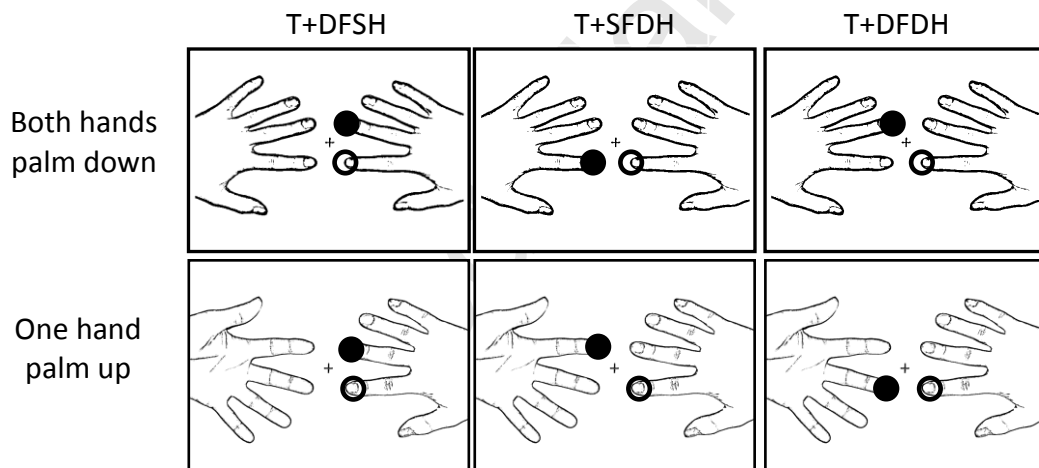
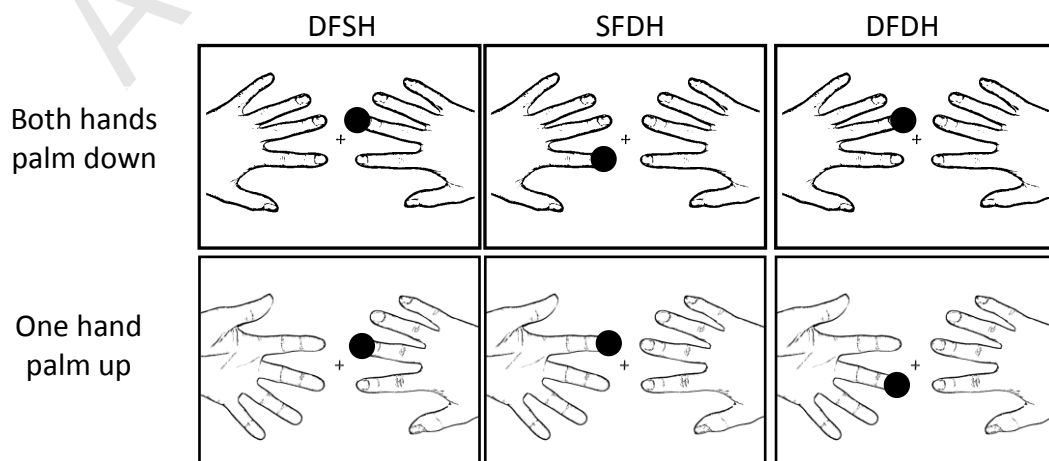
Figure captions

Figure 1. (a) Schematic drawing of the experimental setup; the computer screen is shown as lifted for illustrative purpose only. (b) T-only trials. (c) DSS trials: T+DFSH, T+SFDH, T+DFDH (see text). (d) Catch trials: DFSH, SFDH, DFDH. Unfilled circles: stimulation at the target finger; filled black circles: stimulation at the non-target finger.

Figure 2. Bar plots show (a) percent errors, (b) mean reaction times as a function of stimulation condition and hands' posture. (c) percent errors in catch trials. Error bars represent the Standard Error (SE).

DOUBLE SIMULTANEOUS TACTILE STIMULATION

Figure 1

(a) Stimulation setup**(b) Target only trials****(c) DSS trials****(d) Catch trials**

DOUBLE SIMULTANEOUS TACTILE STIMULATION

Figure 2

