Distinct neural processes of bodily awareness in crossed fingers illusion

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The tactile reassignment process supports the flexible and dynamic changes of body schema in various situations such as those involving tool use. Here, we show that there exist two distinct neural processes in the dynamical reassignment process. One process is involved in identifying the body part where the tactile stimuli are applied, whereas the other is involved in the assignment of the tactile stimuli in the external space including one's body. These processes, combined together, would facilitate the quick and appropriate acquisition of information from the environment, resulting in the speedy spatial perception and execution of motor activities. In addition, we show that the body posture affects the accuracy of tactile localization in the crossed fingers illusion. ***NeuroReport*** **20:467–472 © 2009 Wolters Kluwer Health | Lippincott Williams & Wilkins.**

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Introduction

Interaction through the tactile modality plays an essential role in the execution of many daily tasks. Tactile localization not only requires the information about tactile stimuli on the body surface but also the spatial information in the external spatial frame of reference including one's own body. The external frame of reference pertaining to the environment as well as the somatotopic frame of representation is involved in the tactile perception and localization. The interplay between these two elements, partially independent and partially interdependent, is of particular interest when one tries to understand how the body interacts with the environment.

Investigation of the nature of illusory perception facilitates the understanding of perception in general, as the neural mechanisms involved in normal and illusory perceptions are closely related and often share common processes. Dynamic reassignments of localization of tactile stimuli have been revealed for crossed fingers in the so-called Aristotle's illusion [1], where stimuli applied to the crossed portion of the fingers by rubbing a single finger against them is interpreted as consisting of separate stimuli on both sides of the finger. Studying the properties of tactile relocalization in such illusory perceptions provides unique opportunities for clarifying the nature of tactile perception in normal perceptual situations.

The tactile localization processes have been shown to extend to tools held in hands. Earlier studies have revealed the existence of reassignment processes of stimulus localization in the tactile perception for crossed tools held in uncrossed hands [2], and the reversal of temporal order judgment of two tactile stimuli applied in succession to crossed hands or to the tips of crossed tools held in uncrossed hands [2,3]. These studies focusing on the temporal properties of tactile perception [4] showed that the tactile localization process not only requires the representation of one's body surface in the primary somatosensory cortex (as was classically depicted in the so-called Penfield's homunculus [5]) but also spatial information about the body posture in the external space.

Perception based on the combination of heterogeneous cognitive processes has been reported, for example as shown in the dissociation between the 'where' and 'what' pathways [6–9] in the visual system. Compared with the relatively well-studied visual system, the nature of the functional segregation (if any) of cortical areas involved in the processing of body schema is yet to be clarified.

Here, we study differential cognitive processes underlying tactile localization in reference to the body surface and the external space by means of the illusory perception induced by crossed fingers. In the literature, it has been reported that the bodily posture affects tactile perception [3,10,11], active touch [12,13], tool use [2,14], and this aspects of bodily perception. In view of this evidence, we investigate the role of posture in the process of tactile perception.

Methods

Ten healthy adults (six male and four female, 21–55 years old, average=26.8 years old) participated in the

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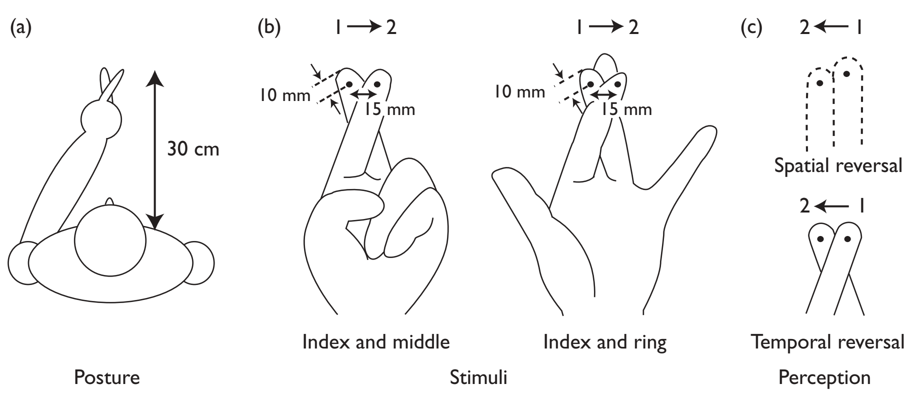
experiment. Six individuals participated in both the 'fingers crossed' and 'fingers uncrossed' conditions. Four individuals participated only in the 'fingers crossed' condition. All participants were right handed. The experiment was conducted in accordance with the Declaration of Helsinki. The participants were instructed about the general conditions of experiments and gave written informed consent. The experimental procedure was approved by the institutional ethics committee.

In experiment 1, we investigated the illusion caused by stimuli applied to the index and middle fingers when they were crossed. Preliminary experiments have found that the illusion of essentially the same nature occurrs for both the left and right hands. In this experiment, we report the results for left hands. The participant was seated in a chair and was instructed to keep his or her left hand either in the 'palm up' or 'palm down' posture, with their eyes closed. As our preliminary investigations have indicated that the hand posture ('palm up' or 'palm down') affects the accuracy of tactile localization [15], we compared the participant's performance between the two postures. The hand was held horizontally in front of the participant's midline, about 30 cm away from the chest, without an aid such as a desk to rest the arm on, while the elbow naturally touched the side belly (Fig. 1a). When crossed, the index finger was put on top of the middle finger when seen in the 'palm up' posture, that is, with the ventral side of the middle finger touching the dorsal side of the index finger (Fig. 1a). Stimulation points were marked with a pen as black spots on the middle line of fingers on the ventral side, at 10 mm from the fingertip on the finger pad. The configuration of the crossed fingers was adjusted so that the two marked stimulation points were placed at 15 mm apart in the external space, a distance at which the participants could keep the fingers crossed at ease. In the 'fingers uncrossed' posture, the fingers were adjusted so that the stimulation points were placed at 25 mm apart, a distance that could be maintained without difficulty. The sides of the index and middle fingers did not touch each other in the 'fingers uncrossed' posture. The stimuli were applied manually to stimulation points by the experimenter with a 500-ms interval by touching with a thin wooden stick of 2 mm diameter. The timing was cued to the experimenter by a digital metronome ('Auftakt' by K. Kimura, Shokei University, Japan) run on a notebook computer (IBM ThinkPad X23, New York, USA). Calibration experiments suggested that the temporal accuracy of the manual application of the stimuli by the experimenter was reasonably high, with a standard deviation of 31 ms. The participant's eyes remained closed during the whole procedure.

Before the test session, the participants practiced the judgment of which finger was to be touched second. This practice session was found to be necessary for the participant to be able to report in a manner faithful to what they were actually perceiving, which became possible after a transient period. Feedback (correct/wrong) was provided so that the participants could adjust their response. The participant was required to practice until they successfully made the correct 'finger judgment' for 10 consecutive times, to ensure that the transient period has passed. Then the test phase followed. For each of the four combinations of finger (crossed or uncrossed)

Fig. 1



Two possible mechanisms of illusion leading to a reversal in the direction judgment. (a) The posture of the participant. A schematic representation of the body posture is shown while the participant sits with the index and middle fingers of the left hand crossed either in the 'palm up' or 'palm down' posture. (b) Stimuli applied. The index and middle fingers (experiment 1), or the index and ring fingers (experiment 2) of the participant's left hand is crossed in the 'palm up' posture. The Arabic numerals represent the order of stimuli applied, whereas the arrow indicates the direction of motion. The distance between the two stimulation points is 15 mm in both experiments. (c) Perception. When the participants correctly recognize the temporal order of two stimuli while the finger crossing fails to be correctly represented in the somatosensory system, the direction judgment would again be reversed ('spatial reversal'). When the finger crossing is correctly represented in the somatosensory system while the temporal order of the two stimuli is reversed, the direction judgment would be reversed ('temporal reversal'). The two fingers represent the index and middle fingers (experiment 1) or the index and ring fingers (experiment 2).

and hand (palm up or palm down) postures, an experimental block consisted of 10 sets of stimuli being applied to the fingers followed by either the direction or finger judgment. Three experimental blocks were conducted for the direction and finger judgments each, resulting in 24 blocks for six participants ('fingers crossed' and 'fingers uncrossed' conditions), or 12 blocks for four participants ('fingers crossed' condition). Six experimental blocks were conducted in one sequence, lasting for about 2 min, followed by a break of 2 min. Given the short duration of the experiment, keeping the instructed arm and finger configurations was not strenuous for the participants.

In the direction judgment, the participant is essentially being asked to report the direction of the vector of motion [leftward (right-to-left) or rightward (left-to-right)], which entails both the spatial and temporal dimensions. There are therefore two possible reasons for which the participants make mistakes in the direction judgment. When the participant correctly judges the temporal order of the two applied stimuli while their respective spatial locations are interchanged, this would result in the misjudgment of the direction of motion ('spatial reversal'). Alternatively, if the participant correctly recognizes the locations of applied stimuli in space while the temporal order of two stimuli was misrepresented, this would again induce a reversal in the direction judgment ('temporal reversal') (Fig. 1c). These two reversals would be indistinguishable based on the rate of correct judgment alone.

To separate these two possibilities of cognitive failure, we made the interval between the two stimuli to be 500 ms, which was longer than the 30-ms interval, necessary for the correct judgment of temporal order of two stimuli applied on the body surface [16] and the 300-ms interval below which a reversal on temporal order judgment is incurred in the crossed hands condition [2]. Under this condition, a reversal on the temporal order judgment is excluded, so that a reversal in the direction judgment would be automatically translated into one in spatial judgment. If the participant correctly reports in the finger judgment while reversely reporting in the direction judgment, it would suggest that cognitive processes underlying the finger and location judgments are separate.

It is interesting to investigate the nature of interaction between the judgment in the external spatial frame of reference and one in the somatotopic frame of reference. For example, would the amount of interference increase as the distance between fingers increases in the external space, as measured with the fingers uncrossed? How would the performance be different when the index and ring fingers are crossed compared with the case where the index and middle fingers are crossed, while the distance between the tips of the crossed fingers is kept constant in the external space (Fig. 1b)? If the direction judgment depends on the distance between two fingers in the external frame of reference alone, there would be no difference between these cases.

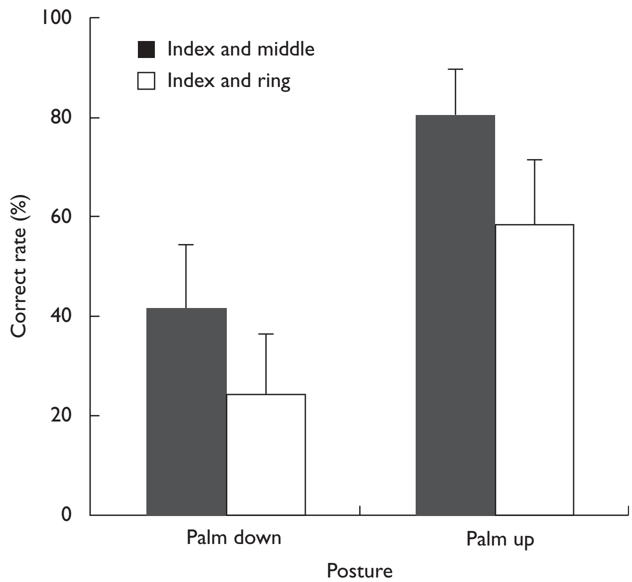
To investigate this point, we executed a further series of experiment (experiment 2) with the same participants. The stimulation points were marked in the same manner as in experiment 1. The index and ring fingers were crossed, with the ventral side of the ring finger touching the dorsal side of the index finger in the space ventral to the middle finger. The configuration of the hands was adjusted so that the distance between the two stimuli in the physical space was maintained at the same distance (15 mm) as that between the index and middle fingers in experiment 1. The participants held the hands either in the palm up or the palm down posture. When the fingers were uncrossed, the stimulation points were placed at 50 mm apart between the index and ring fingers to maintain a natural posture, with the sides of the index, middle, and ring fingers not touching each other. The procedures were otherwise the same as in experiment 1.

Results

In the test phase of experiment 1, the participants could make the finger judgment accurately, aided by the completion of the test phase. The correct rates (mean ± SEM) for the finger judgment were 96 ± 2.1 and 96.3 ± 1.6% for the palm down and palm up postures, respectively. There was no significant difference between these data by paired *t*-test (P=0.89, two tails, Fig. 2). Thus, the participants were able to accurately perceive which finger was being touched, after the passage of the transient period of confusion. The sufficiently large interval between the stimuli (500 ms) effectively ensured that a reversal in the temporal order judgment was absent. Thus, if the tactile localization of fingers supported by a knowledge of the crossed state of fingers automatically translates into the judgment of localization in external space, the direction judgment would exhibit a comparable level of accuracy.

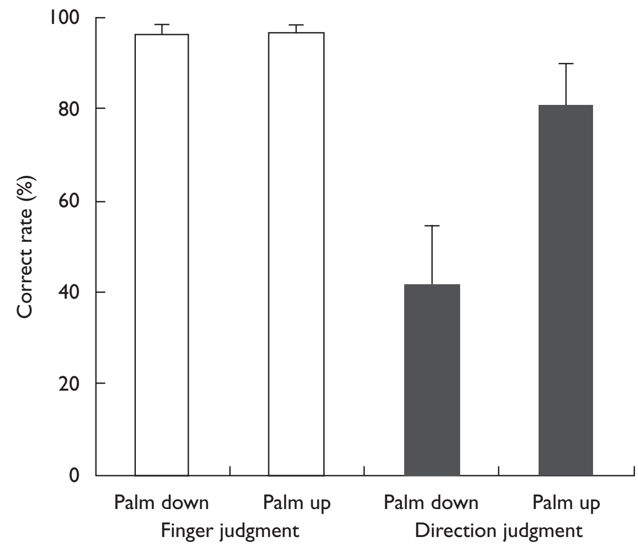
However, the correct rates (mean ± SEM) of direction judgment for stimuli applied to the crossed index and middle fingers were 41.3 ± 12.9 and 80.3 ± 9.4% for the palm down and palm up postures, respectively, exhibiting a significant difference from the finger judgment [$F(1,9)=9.939$, P=0.012]. In addition, the correct rate of judgments was significantly higher for the palm up compared with the palm down posture (paired *t*-test, P=0.010, two tails, Fig. 2), replicating the result of our previous research [15]. This 'posture effect' is an important element to be considered in clarifying the neural mechanisms involved.

Fig. 2



The effect of the distance between fingers in the direction judgment. Black and white bars indicate the correct rate of direction judgment for the crossing of index and middle fingers and index and ring fingers, respectively (% correct response ± SEM). There are significant differences between finger combinations (index and middle/index and ring) and between hand postures ('palm up' or 'palm down').

Fig. 3



Correct rates for finger and direction judgments when the index and middle fingers are crossed. White and black bars show the performances in the finger judgment and direction judgment, respectively (% correct response ± SEM). The correct rates for the direction judgment are significantly different between the two hand postures ('palm up' or 'palm down').

These results indicate the existence of two distinct neural processes. One process would be involved in identifying the body part where the tactile stimuli are applied, whereas the other process would be involved in the assignment of the tactile stimuli in the external space including one's body. Note that when the fingers were uncrossed these two processes could not be separated, as the correct rate for the direction judgment was 100%, without a single instance of error occurring during the experiment. Studying illusory direction judgment in crossed fingers thus enables us to separate these two processes.

In experiment 2, when the index and ring fingers were crossed, the correct rates (mean ± SEM) for finger judgment were 94 ± 4.7 and 95 ± 2.1% for the palm down and palm up postures, respectively, with no significant difference between the two postures (paired *t*-test, $P=0.79$, two tails). The correct rates (mean ± SEM) of direction judgment were 24.5 ± 11.9 and 58.3 ± 13.3% for the palm down and palm up postures, respectively, exhibiting a significant difference (paired *t*-test, $P=0.028$, two tails, Fig. 3). There was a significant difference between the correct rates for the direction judgment and finger judgment [$F(1,9)=19.614$, $P=0.002$], suggesting the existence of dissociable neural processes.

We conducted two-way analysis of variance for the performance on direction judgment, where the factors were the 'finger combination' (index and middle vs. index and ring) and the 'hand posture' (palm down vs. palm up). There was a significant effect of finger combination [$F(1,9)=10.576$, $P=0.010$] and hand posture [$F(1,9)=8.473$, $P=0.017$]. The interaction between finger combination and hand posture was not significant [$F(1,9)=0.652$, $P=0.218$] (Fig. 3). Thus, the pairing of fingers in the crossed posture affects the direction judgment, indicating an interference between the external frame of reference and the somatotopic frame of reference in the neural processes involved.

Discussion

In this study, we reported an illusion that occurs while the fingers of the participant was crossed. In order to separately evaluate the tactile localization in the external space and the judgment of which body part is being touched, the participants were asked to conduct two types of cognitive tasks for the same set of stimuli. In the Aristotle's illusion, the process of assignment of tactile stimuli on fingers is disrupted. In the illusion reported here, such a disruption is not observed. The accurate perception of which fingers are touched, combined with the absence of a reversal in temporal order judgment (ensured by a sufficiently long interval between the stimuli) would seem to result in a correct judgment in direction, provided that the knowledge that the fingers are crossed is properly used in the cognitive process. Our results suggest that this is not the case. The direction judgment remains disrupted while the finger judgment is correctly made. It is thus indicated that there are two distinct neural processes involved. One is concerned with the position judgment on the body surface, whereas the other is concerned with the direction judgment in the physical space. The cognitive processes in the brain concerned with these two processes are not necessarily consistent with each other, where one process successfully makes a use of the knowledge of the fact that the fingers are crossed, whereas the other fails to do so. These processes are likely to operate in parallel and enable the execution of automatic and reflective behaviors based on the body schema [17].

In the visual system, a segregation between the 'what' and 'where' pathways has been reported [6–9]. The coexistence of distinctive neural pathways that contribute differentially to cognition might thus be a property shared by different sensory modalities such as the visual and somatosensory processes.

There is a significant difference between the correct rates in the direction judgment between the 'palm up' and 'palm down' postures. The fact that the hand posture affects the verbally reported tactile perception is consistent with the observation that the neural activity leading to the conscious perception of body schema is in the parietal associated area including BA5 [18], whereas there is an evidence that suggests that the activity in the primary somatosensory area reflects the bodily awareness [19].

It is interesting to consider the underlying brain mechanisms as well as the functional implications of posture. It is known that the somatosensory activity is suppressed during motor activity [20], whereas a change in posture affects the motor area [21]. In the palm down posture, it is possible that the activity in the somatosensory cortex is suppressed because of the motor activity and the accuracy of tactile perception is therefore compromised. Some functional considerations might suggest the rationale for the prominence of the 'palm up' posture. In many situations of action execution in daily life, the palm down posture is the norm, where the elements involved in the sensorimotor coordination are processed unconsciously (e.g. writing with a pen, typing with the computer keyboard, etc.). In contrast, handling objects in the palm up posture is unstable in many processes of manual action (e.g. grabbing), where the brain may need to handle more details of tactile information to deal with the increased instability, resulting in an improvement of the accuracy of judgment [22].

Finally, the observation that the judgment of the direction is more accurate for the index and middle fingers than for the index and ring fingers would indicate that the distance on the body surface as measured in the 'default' hand posture with the fingers uncrossed affects the spatial judgment of the tactile stimuli. Such an interaction reveals the nature of the integrated processing of information on the bodily surface with one on the external space. Cortical areas responsible for the representation of fingers including the primary somatosensory cortex [23] are likely to be involved in such an integration process.

Conclusion

In this study, we have demonstrated the existence of distinct neural processes in bodily perception. One is associated with the judgment of which body part is being touched, whereas the other is concerned with the tactile localization in the physical space. These processes, combined together, are likely to support the flexible and dynamic changes of bodily awareness in response to the various modes of interaction with the environment, where the hand posture affects the accuracy of tactile localization.

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