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RESEARCH ARTICLE

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The brain's fingers and hands

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Abstract The brain keeps track of the changing positions of body parts in space using a spatial body schema. When subjects localise a tactile stimulus on the skin, they might either use a somatotopic body map, or use a body schema to identify the location of the stimulation in external space. Healthy subjects were touched on the fingertips, with the hands in one of two postures: either the right hand was vertically above the left, or the fingers of both hands were interwoven. Subjects made speeded verbal responses to identify either the finger or the hand that was touched. Interweaving the fingers significantly impaired hand identification across several experiments, but had no effect on finger identification. Our results suggest that identification of fingers occurs in a somatotopic representation or finger schema. Identification of hands uses a general body schema, and is influenced by external spatial location. This dissociation implies that touches on the finger can only be identified with a particular hand after a process of assigning fingers to hands. This assignment is based on external spatial location. Our results suggest a role of the body schema in the identification of structural body parts from touch.

Keywords Touch · Somatosensory · Finger · Hand · Body schema · Human

Introduction

The human cerebral cortex contains several neural representations of the body. Primary somatosensory cortex (SI) is the best understood of these. It contains a somatotopic map of the contralateral body surface (Weber 1834; Penfield and Rasmussen 1950). Intra-cranial stimulation here evokes localised tactile sensations (Penfield and Rasmussen 1950) while TMS suppresses tactile sensation (Oliveri et al. 2000). SI therefore provides a map for identifying and localising tactile inputs.

A second more abstract and poorly understood body representation is the so-called "body schema" (Head and Holmes 1911). This refers to an abstract representation of the location of the body parts in external space, which is dynamically updated during movement, and used to estimate body configurations. Although the explanatory value of the body schema is not clear, spatial patterns of interaction between viewing and reproducing body configurations (Reed and Farah 1995) suggest that such a representation does exist. On theoretical grounds, an abstract body representation is also needed to relate the body surface defined in SI to external egocentric space (Graziano and Gross 1993), to allow aimed movements to egocentric locations (Wolpert et al. 1998) and to represent geometric properties of tactile objects (Taylor-Clarke et al. 2004).

Tactile identification tasks offer an interesting test of body representation. In such tasks, subjects receive an unseen tactile stimulus and report where on their body they perceived the stimulus, by naming the appropriate body part. In principle, such tasks can be solved either in a somatotopic or an egocentric external frame of reference. In somatotopic identification, subjects identify the stimulated region of skin using a mapped representation like that in SI. In egocentric external identification, subjects might use a body schema to identify both the location of the tactile stimulus in external space, and the body part currently occupying that space.

Several experimental studies have investigated the relation between primary body surface representations and external spatial representations by comparing the processing of identical tactile stimuli delivered in different body postures. These studies show a clear difference between effects of hand posture and effects of finger posture. When the hands are crossed over into the contralateral hemifield, the brain successfully and automatically updates the position of each hand within

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the body schema to its new location. Thus, a visual stimulus in the right hemifield can interfere with processing of a tactile stimulus on either the right hand when hand posture is normal or the left hand when the hands are crossed (Spence et al. 2000). The proximity of stimuli in external space seems to be more important than the anatomical location to which the stimuli are delivered. Yamamoto and Kitazawa (2001a, b) asked subjects to perform a temporal order judgement between vibrotactile stimuli delivered either to the fingertips or to the endpoints of sticks held in the hands. They found that the normally monotonic temporal order judgement curve was flattened or inverted at short SOAs when the stimulators were crossed into the opposite hemifield, regardless of whether the stimulators were held in the hands, or on sticks. This suggests that the brain must first represent the spatial location of the limb endpoint before temporal order can be retrieved.

In contrast, crossing the *fingers* over one another reveals a clear difficulty in updating finger locations in external space. This results in Aristotle's Illusion, in which a single object held between two crossed fingers is felt to be two objects. According to the most accepted explanation of the illusion, the positions of fingers are not updated when they are crossed. Thus, stimuli to the lateral surface of the fingers are felt in the positions that they would occupy in the uncrossed posture, rather than their actual positions (Benedetti 1985).

Neuropsychological evidence supports the dissociation between neural representations of fingers and other body parts. The parietal cortex may remap the body surface into external space. Parietal patients may be unable to maintain an internal estimate of the current position of their limbs (Wolpert et al. 1998). In contrast, microstimulation methods have linked the disorders of *finger* representation to the angular and supramarginal gyri (Roux et al. 2003). In finger agnosia, patients make errors in the finger identification tasks (Kinsbourne and Warrington 1962). Finger agnosia dissociates from other disorders of body representation. The primary deficit appears to be in individuating fingers, rather than tracking their location in external space. Kinsbourne and Warrington (1962) postulated a specific process of individuating the fingers, and maintaining their separate neural representations. Their patients' performance suggested that finger representations had become collectively fused and undifferentiated. A developmental literature has focussed on finger gnosis tasks, in which the subject must identify to which finger an unseen tactile stimulus is applied (Benton 1959).

Both behavioural and neuropsychological evidence suggests, then, that finger and hand schemata are distinct. However, the relation between finger and hand representation in the brain has rarely been studied. Identification of the body part on which a tactile stimulus is located offers an interesting approach to this problem. When we are touched on one of our fingers, we are able to localise the stimulus either according to which finger was touched (finger identification) or according to which hand was touched (hand identification). The same stimulus might be localised using a specialised finger schema in the former case and a general body schema in the latter case. We performed several experiments in which normal subjects identified suprathreshold tactile stimuli delivered to the fingertips in a variety of hand postures. Subjects made speeded responses to identify either the finger that had been touched, or the hand that had been touched. Our working hypothesis was that finger identification would use a somatotopic frame of reference, while hand identification would use an egocentric external frame of reference. The effects of hand posture in egocentric external space should therefore be found for hand identification, but not finger identification.

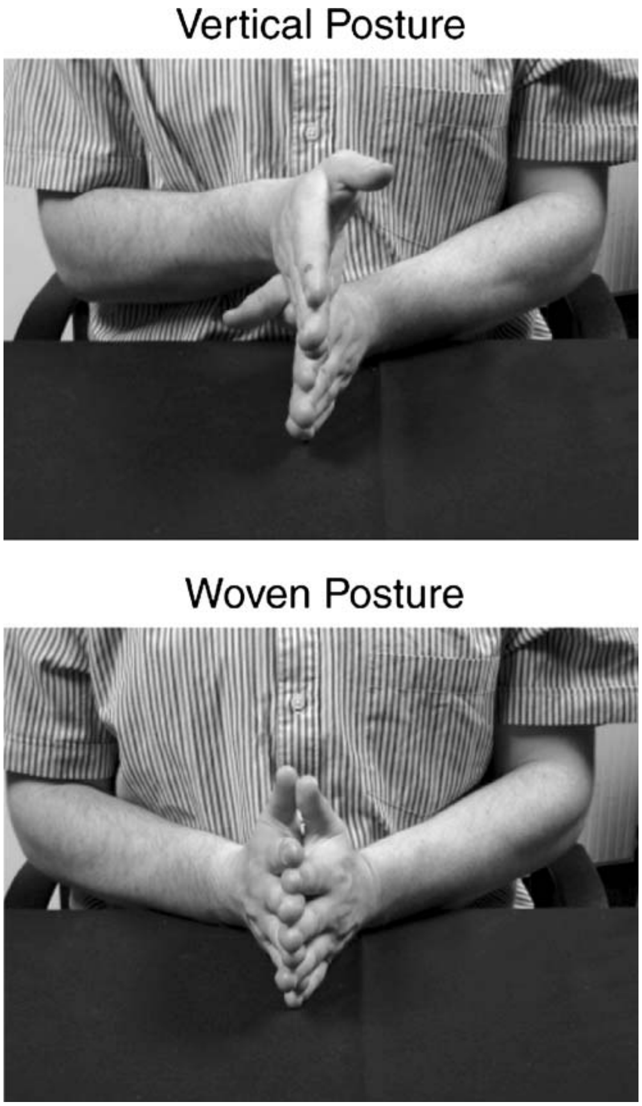
Experiment 1

Methods

Twelve healthy subjects (ages 21–45) participated in simple detection, finger identification and hand identification tests. The study was carried out according to the principles of the Declaration of Helsinki, on the basis of informed consent, and was approved by the local ethical committee. Each subject performed the tasks in a different random order. Subjects sat at a table with hands placed in the midline, palms in the vertical plane, wearing headphones and listening to white noise. The hands were covered by a box so that an experimenter sitting across the table from the subject could clearly see them, but the subject could not. Subjects fixated the top of the box, just above their hands, throughout. Small metal discs were taped to the tips of the fingers, excluding the thumbs. Tactile stimuli were delivered by tapping one of these discs at random with a short steel rod. The discs were clearly labelled to ensure the experimenter hit the correct one on each trial. The experimenter tapped each of the 4 fingers of each hand twice, producing 16 trials in each task. The order of trials was always randomised within each task. Subjects responded to each tactile stimulus with a speeded verbal response, but the tasks differed in the way the subject had to process the tactile stimuli. In detection, subjects simply detected the occurrence of the tactile stimulus, and made a single arbitrary vocal response ("Aah!") irrespective of stimulus location. They were given 1 s to respond. In finger identification subjects had to respond with the name of the finger that was touched. Subjects were clearly told that it did not matter which hand was touched for this task. They had 5 s in which to respond. In hand identification, subjects reported which hand was touched ("left" or "right"), and were told that it did not matter which finger had been touched. They had 5 s in which to respond.

Within each task, we used a 2×2 factorial design. First, to investigate the effects of external spatial location, subjects performed each task in two different postures. In the *vertical* posture, the hands were held in the midline, with the right hand above the left. In the *interwoven* posture, the hands were held with the palms touching and the fingers interwoven, and aligned in the midline (see Fig. 1).

Importantly, the fingers and hands never crossed the midline, or crossed over each other. Second, subjects performed each task in two lateral contact conditions. In the *contact* condition, the fingers naturally touched each other on their lateral surface. In the *separated* condition, the fingers were separated by 1 mm sheets of rigid plastic inserted between each pair of fingers, and running from fingertip to base. This reduced any possible mechanical transmission of the tactile stimulus delivered by the steel rod to the fingers adjacent to the touched finger. The separation condition also controlled for possible tactile contribution to postural effects. Removing the lateral contact between fingers should leave only proprioceptive cues regarding each finger's location in external space.


Vertical Posture

Woven Posture

Fig. 1 Vertical and woven hand postures used (Experiments 1, 2)

Reaction time measurement

The auditory click of the rod tapping the metal disc and the subject's verbal response were recorded with a microphone and stored. The auditory click associated with the tap was verified in pilot testing to be inaudible to the subject, due to the white masking noise. In later analysis, responses were scored for accuracy, and the reaction time for each trial was calculated by measuring the interval between the onset of the click/tap and the onset of the verbal response in the acoustic waveform. Median reaction times for correct trials and error rates were calculated and used for statistical analysis. Sixty-six trials (2.8%) were lost due to experimenter error (tapping the wrong finger, delivering a tap which hit two fingers, or which did not produce a clear audible click) or subject error (failure to respond, unclear response).

Results

The mean and standard error across subjects of median reaction times and error rates is shown in Table 1. The three tasks differed in overall reaction time, with simple detection being faster than hand identification, which was faster than finger identification. This may reflect the different number of alternative responses in the three tasks, and is not of interest here. Instead, we focus on how the posture of the hands modulated reaction time and accuracy data (see Fig. 2).

The data from each task were analysed separately using ANOVA. Hand posture did not influence performance in either detection or finger identification (both $P > 0.288$). However, the interwoven posture produced significant increases in RT ($F_{1,11} = 42.47$, $P < .001$) and a trend towards reduced accuracy of hand identification ($F_{1,11} = 4.32$, $P = 0.062$) compared to vertical posture.

The interwoven posture gives lateral contact between the fingers of the two hands. This could affect hand identification performance for two artefactual reasons quite unconnected with spatial body representation. First, there could be mechanical transmission of the tactile stimulus between the hands. Second, the lateral contact between hands could lead subjects to confuse the hand response categories. Indeed, we found an interaction between effects of posture and contact ($F_{1,11} = 10.334$, $P = 0.008$). We therefore used simple effects analysis (Howell 1997) to compare normal and inverted postures both with and without lateral contact. The difference between vertical and woven postures was greater when lateral contact was available than when it was not (means 213 vs 101 ms). However, this posture effect was highly significant in both conditions (with contact: $F_{1,11} = 44.828$, $P < .001$; separated: $F_{1,11} = 12.825$, $P = .004$). This last result suggests that hand identification involves an external spatial representation, since the performance decrement associated with woven posture persists when the fingers are interleaved but do not touch.

Table 1 Mean and SE across subjects of median reaction time and errors for Experiment 1

Task	Posture	Lateral contact	Reaction time errors	
			(ms)	(%)
Detection	Vertical	Touching	295 (9)	
Detection	Vertical	Not touching	311 (15)	
Detection	Woven	Touching	308 (13)	
Detection	Woven	Not touching	321 (17)	
Hand-identification	Vertical	Touching	464 (26)	1.60 (0.83)
Hand-identification	Vertical	Not touching	511 (20)	1.56 (1.12)
Hand-identification	Woven	Touching	677 (35)	6.32 (2.04)
Hand -identification	Woven	Not touching	610 (32)	2.64 (1.22)
Finger-identification	Vertical	Touching	782 (36)	5.45 (2.52)
Finger-identification	Vertical	Not touching	824 (38)	6.98 (2.34)
Finger-identification	Woven	Touching	829 (44)	6.44 (1.91)
Finger-identification	Woven	Not touching	811 (36)	4.97 (2.19)

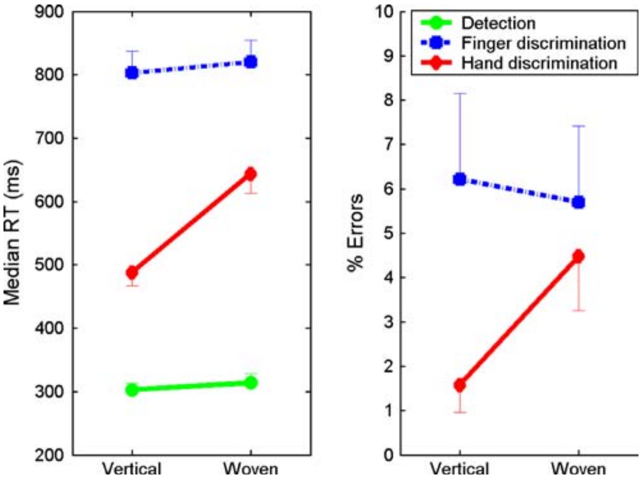


Fig. 2 Results for simple detection, finger identification and hand identification in vertical and woven postures (Experiment 1). *Error bars* show standard error across subjects. Errors did not occur in simple detection

Discussion

Our interest focuses on the different effects of posture across the three tasks. We found a significant deterioration in hand identification performance when the fingers of the two hands were interwoven, compared to a condition where the hands were vertically aligned. There were no such effects on stimulus detection, or on identifying the *finger* on which the stimulus occurred. Recall that an effect of hand posture indicates that the identification of the stimulated body part involves an egocentric external frame of reference, while absence of such effects is consistent with a somatotopic frame of reference. Our results suggest that finger identification may occur in a somatotopic frame of reference, but hand identification involves an external frame of reference. In particular, identifying which hand has been touched is harder when the fingers of the two hands are interwoven then when they are arranged one above the other. The presence of digits of the untouched hand in close spatial proximity to the touched finger seems to cause an interference effect. This interference seems to be mediated by proprioceptive signals about hand posture, since it was observed in the absence of vision, and also in the absence of lateral tactile contact between the fingers.

It may seem paradoxical that hand posture can influence hand identification but not finger identification. This pattern of results suggests that identifying the finger does not imply identifying the hand. Once a touched finger has been identified, for example the index finger, some additional neural process seems to be required to specify whether it was the index finger on the left or right hand. This additional process seems to involve assigning finger representations to hands, and clearly depends on egocentric spatial information, perhaps linked to a proprioceptive body schema. The assignment process would be harder in the interwoven posture, because the hands cannot be discriminated on the basis of spatial location.

Experiment 2

Method

Experiment 2 was based on the hand identification task of Experiment 1, but avoided “left” and “right” verbal responses. The experimenter tapped two fingertips simultaneously on each trial, and subjects responded “same” or “different” according to whether the taps were delivered to the same hand or different hands. The taps were always delivered to different, non-homologous but adjacent fingers (e.g. index and middle, middle and ring, ring and little). Twelve possible combinations of taps were tested, and 4 of these were performed twice, giving 16 trials. Of these, eight involved stimulation of both hands (response “different”), four involved stimulation of the left hand only (response “same”) and four involved stimulation of the right hand only (response “same”). For example, tapping the ring finger of the right hand and the ring finger of the left hand requires the response “different”. Subjects performed the task in the vertical and interwoven postures (cf. Experiment 1 and Fig. 1) in counterbalanced order. Eight healthy subjects participated (ages 21–60, two previously participated in Experiment 1). Other methods were as Experiment 1. One trial was lost due to experimenter error. Analysis of 19 randomly selected acoustic recordings showed that the average time between taps was 62 ms.

Results and discussion

Hand identification performance was much slower than in Experiment 1, perhaps because the present experiment involved processing two simultaneous stimuli on each trial. A strong posture effect was predicted on the basis of Experiment 1, and was again found. Reaction times and error rates were significantly higher in the woven condition (1,350 ms (SE 118 ms), 34% (SE 4%)) than in the vertical condition (1,015 ms (SE 79 ms), 13% (SE 3%) ($F_{1,7}=14.549$, $P=0.004$ for RT, $F_{1,7}=18.904$, $P=0.002$ for errors). One-tailed probabilities are reported, as the direction of these effects was predicted from Experiment 1. This result suggests that the effects of interwoven posture on hand identification are not linked to the use of the verbal response labels "left" and "right". By using same/different responses, it was necessary only to individuate the hands, in the sense of representing each one separately. No explicit label for either hand was required. A highly significant effect of posture was nevertheless found.

Experiment 3

Introduction

Experiment 1 suggested that spatial proximity between the hands leads to interference in hand identification. In Experiment 3, we used further variations of hand posture to identify whether this interference occurs for spatial proximity of *any* fingers of the untouched hand, or whether proximity of homologous fingers is important. The latter result would suggest that, following a touch on the index finger (say), the spatial locations of the left and right index fingertips are an important source of information regarding which one of these was touched.

Experiment 3 varied the spatial adjacency of homologous fingers independently from hand posture. Subjects performed hand identification or finger identification, as in Experiment 1. Now, however, the right hand was pronated 180° (see Fig. 3), giving two postures: an inverted vertical posture and an inverted woven posture. Only the index and middle fingers were stimulated. Note that in the inverted vertical posture, index fingers are adjacent and middle fingers are separated, while in the inverted woven posture, middle fingers are now adjacent and index fingers are separated. Other methods were as Experiment 1. Subjects performed eight trials per condition. The experiment was run in a single session with Experiment 2 using the same subjects. 12 trials (4.69%) were lost due to experimenter error or no response before cutoff time.

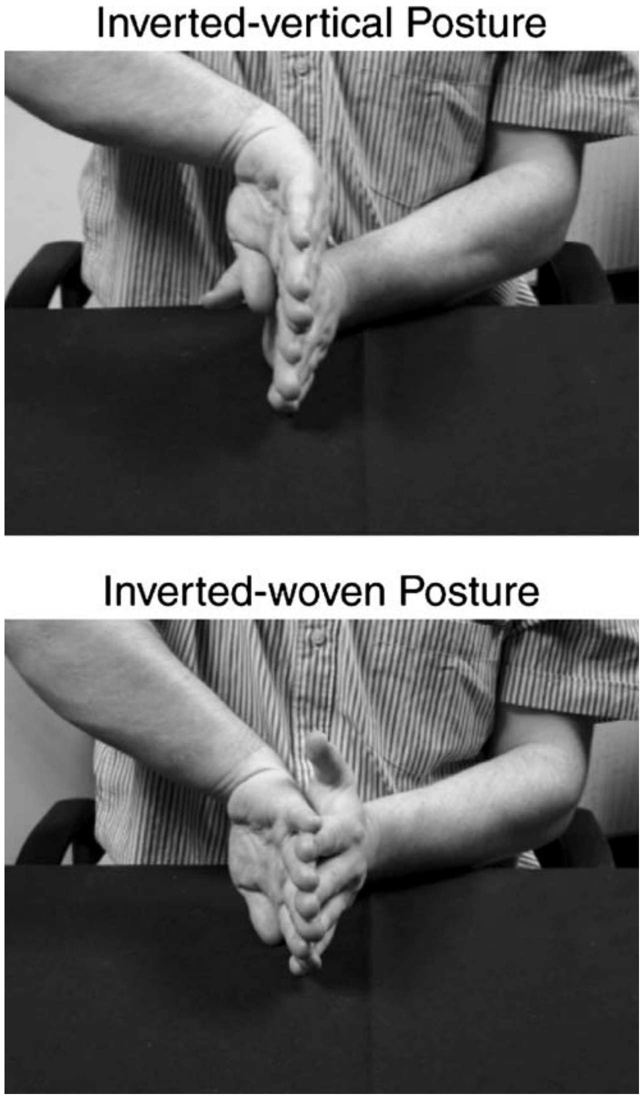


Fig. 3 Inverted-vertical and inverted-woven hand postures used in Experiments 3 and 4. Note the 180° pronation of the right hand in both postures. In the inverted woven posture, the middle fingers of the two hands are spatially adjacent, but the index fingers are not

Results and discussion

The reaction time and accuracy data are shown in Fig. 4. We analysed the data using factorial ANOVA with factors of task, posture and finger touched. The main effects of task are not of interest here, since the tasks may differ for reasons irrelevant to identification, such as differences in speech output latencies for finger names and hand names. Instead, our main interest again

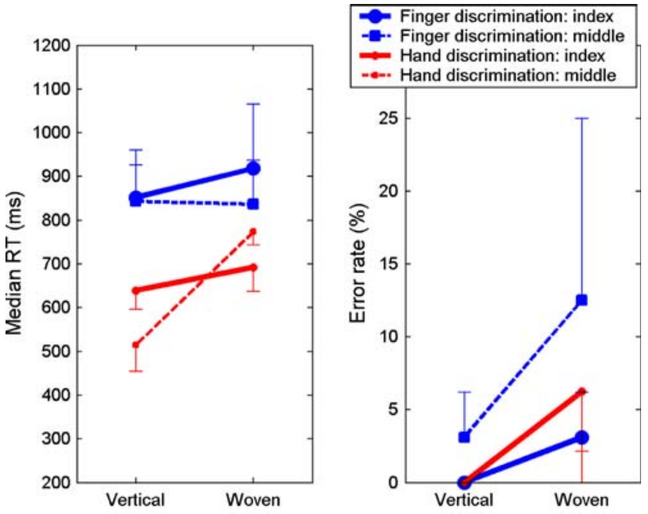


Fig. 4 Finger and hand identification performance with the right hand inverted (Experiment 3). Vertical and interwoven arrangements of the hands were compared. Results are shown separately for index and middle fingers. Note poorer hand identification performance for middle finger than for index finger in inverted-woven posture. The error rates for index and middle fingers in hand identification were identical, and the two traces superimpose. *Error bars* show standard error across subjects. Note that all subjects performed with total accuracy in some conditions, hence no error bars

lies in the interactions involving the effect of hand posture. Hand identification was slowed by the woven posture, to a greater extent than finger identification (task by posture interaction $F_{1,7}=11.21$, $P=0.006$—because the direction of this effect was predicted from Experiment 1, a one-tailed probability is reported). We then observed that this interaction further depended on the finger stimulated ($F_{1,7}=7.10$, $P=0.037$—a two-tailed probability is reported as the direction of this effect was not predicted). In inverted vertical posture, hand identification was faster following stimulation of the middle finger (mean 514 ms) than following stimulation of the index finger (639 ms). This pattern was reversed in the inverted woven posture: now hand identification performance was faster following index finger stimulation (mean 692 ms) than following middle finger stimulation (mean 773 ms). Figure 4 shows a clear crossover interaction between finger and posture within the hand identification reaction times, which is not seen in finger identification. This did not merely reflect speed–accuracy tradeoff: similar ANOVA of error rates showed no significant interactions involving the finger factor (all $F\text{s} < 1$).

Inverting the right hand makes the middle but not the index fingers adjacent, in the woven posture. As a result, hand identification was harder for middle finger stimulation than index finger stimulation. Since this effect is absent in finger identification, it presumably arises in a process occurring after finger identification, but relevant to hand identification. These data are again compatible with interference in a process by which fingers are assigned to hands on the basis of their spatial location.

Experiment 4

Method

Experiment 4 sought to replicate and extend Experiment 3's finding of a specific interference in hand identification due to the proximity of the homologous finger of the untouched hand. This finding in Experiment 3 was based on a small number of trials for each stimulated finger, was restricted to an inverted posture of the right hand, and was not compared directly to finger-specific effects in finger identification. Experiment 4 therefore used an increased number of trials per subject, contrasted normal and inverted posture of the right hand and contrasted hand and finger identification tasks. It also used more precisely delivered tactile stimuli. To reduce mechanical transmission of stimulation to adjacent fingers, we attached miniature solenoids (rswww.com model 330-5213) to the tip of the index and middle fingers of each hand. The solenoids were held in place by thin rubber strips running from the nail over the fingertip to the fingerpad. The typical peak force exerted by the solenoids on the fingertip was 1 gf. A control test confirmed that this was too low to allow mechanical transmission: when the subject interwove their hand with the experimenter's, and the experimenter's hand was stimulated, the subject could not detect the stimulation at all.

In a further improvement, subjects now made motor responses rather than verbal responses, by extending the thumb to close a microswitch. In hand identification, subjects responded with the thumb of the stimulated hand. This arrangement was chosen to provide as direct and automatic a mapping as possible between stimulus and response, without need for verbal labels, interhemispheric transfer and perhaps bypassing traditional response selection stages altogether (Frith and Done 1986). If posture effects are found even with directly mapped responses, they are likely to arise at the level of body perception rather than at the response stage. In finger identification, subjects responded with the left thumb if the index finger was stimulated and with the right thumb if the middle finger was stimulated. Subjects had 2,000 ms to respond.

Subjects performed finger and hand identification tasks in counterbalanced order. Subjects performed each task in four postures, generated by the factorial arrangement of the factor vertical versus woven (as in Experiment 1) and the factor of right-hand orientation (normal or inverted-pronated posture, as in Experiment 3). Each finger was touched 16 times in each of the 4 postural conditions in each task. Eight new subjects, aged 20–35, participated. Twenty-eight trials (0.5%)

were lost due to double responses, or no response within the cutoff period.

Results

We first aimed to replicate the task by posture interaction in hand identification from Experiment 1. This data is shown in Fig. 5. The data showed the task by posture interaction previously seen in Experiment 1 ($F_{1,7} = 4.081$, $P = 0.042$—a one-tailed probability is reported based on the predictions from Experiments 1 and 3), in the direction predicted from Experiment 3, while error rates showed a trend in the same direction ($F_{1,7} = 2.932$, $P = 0.066$). Thus, the data are consistent with the hand identification task in previous experiments.

We next focussed on the specific role of the homologous finger suggested by Experiment 3, using higher-order ANOVA interactions. The four-way interaction of task, posture, right hand orientation and finger stimulated was significant ($F_{1,7} = 5.727$, $P = 0.024$). As the direction of this effect was predicted on the basis of Experiment 3, a one-tailed probability is reported. Follow-up tests (simple effects; Howell 1997) were used to identify the source of this interaction. This arose because the hand identification data in the inverted right-hand condition showed a significantly greater effect of woven posture for the middle finger (mean difference 253 ms) than for the index finger (mean difference 130 ms). A follow-up t test confirmed that this difference was significant: $t_7 = 3.152$, $P = 0.016$, one-tailed). Error rates showed a similar effect ($t_7 = 2.119$, $P = 0.036$, one-tailed). We conducted identical follow-up tests of finger specificity in finger discrimination, and also in hand discrimination for the non-inverted normal posture of the right hand. None of these approached significance (all $P > 0.175$). Thus, finger-specific effects on performance were found only for the inverted posture and not the normal posture of the right hand, and only in hand identification, not finger identification. Again, hand identification was difficult when spatial proximity produced interference between homologous fingers of each hand, replicating and extending the effects seen in Experiment 3.

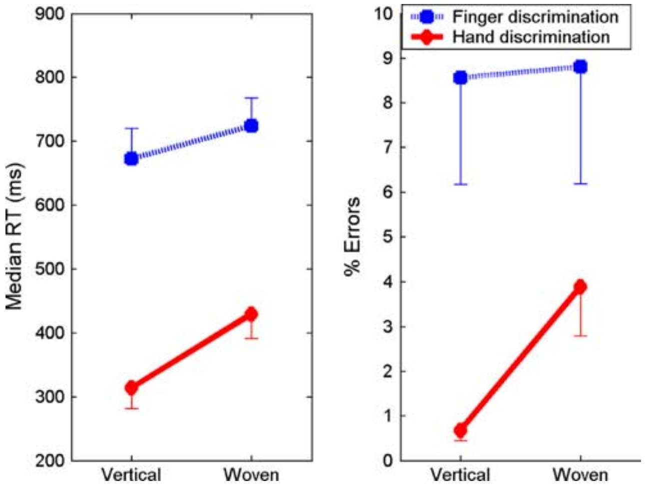


Fig. 5 Finger and hand identification performance in Experiment 4, using direct motor responses and low-intensity, electronically controlled stimulation. *Error bars* show standard error across subjects

Discussion

First, Experiment 4 found postural effects on hand identification using a direct motor response, much less intense mechanical stimuli that did not spread to adjacent fingers, and stimuli that were mechanically identical in every trial and electronically controlled. These results confirm that the spatial arrangement of the fingers is not relevant to finger identification, but is highly relevant to hand identification. They also rule out artefactual explanations based on mechanical transmission and experimenter bias in stimulus delivery.

Second, although we made no predictions about main effects of task, we comment briefly on the relative speed of finger and hand identification. In Experiment 4, unlike Experiments 1–3, both tasks used a common response method. We still found slower finger identification than hand identification. This may seem surprising. We speculate that this may reflect unusually fast post-perceptual processing in hand identification in Experiment 4, rather than slow finger identification. Subjects responded by moving the thumb of the stimulated hand. These responses benefit from a spatial compatibility effect that is not present in the finger identification task. In finger identification, the mapping from finger stimulated to response hand was arbitrary. This compatibility effect could have favoured post-perceptual processes in hand identification relative to those in finger identification. This is supported by comparison of Experiments 3 and 4. The two experiments have comparable reaction times for finger identification, but Experiment 4 has faster hand identification. Importantly, note that the main effect of task is not relevant to our argument that fingers must be attributed to hands before hand identification takes place. Reaction times for finger identification might yet be faster than for hand identification, because the reaction time measure includes several post-identification processes as well.

Finally, Experiment 4 replicates, with several methodological improvements, the finding in Experiment 3 of a specific difficulty in hand identification when homologous fingers of the two hands are in close spatial proximity. Our finding of poor identification in conditions of spatial proximity recalls the result of Spence et al. (2003). They found that multi-sensory temporal order judgements between tactile stimuli delivered to the two hands were poorer when the stimuli came from similar locations than when they came from different locations. They suggested that spatial separation between two sources provides a spatial identification which is redundant with temporal discrepancy, and therefore improves temporal order judgement. Our results in hand identification suggest that spatial redundancy may have a role in the organisation of the body representation itself.

General discussion

In several experiments, we delivered tactile stimuli to the fingertips and asked subjects to identify which finger had been touched, or which hand had been touched. The position of the fingers and hands in space influenced hand identification, but not finger identification. The hand identification effect arose because of interference when the fingers of the untouched hand were in close spatial proximity to the site of stimulation. The interference between homologous fingers was particularly marked.

Our findings suggest a surprising difference between the neural representation of fingers and of hands. Both finger and hand identification could, prima facie, be performed in one of two ways. Either the identification could occur in a somatotopic frame of reference, for example within the neural map of the body surface in SI. This map contains the body surface information required for all the tasks studied here. Alternatively, the stimulus could be transformed into an egocentric external frame of reference. A body schema, perhaps based on proprioceptive information, could update and store the current posture of body parts, and transform tactile stimuli into egocentric coordinates using this information. Studies of tactile temporal order judgements (Roder et al. 2004) confirm that both frames of reference exist in the brain, but that the egocentric external one tends to dominate. Those authors found that crossing the hands impaired judgements of temporal order for tactile stimuli delivered to the two hands in sighted subjects, but not in congenitally blind subjects. Those authors suggested that the congenitally blind used a somatotopic frame of reference which was immune to such postural effects. Blind subjects who had benefited from some early vision performed like sighted subjects. This last finding suggests that vision may be required to enable the body schema's computation of the position of body parts in external space. Once this computation is possible, however, they found that it dominates the somatotopic frame.

We assume that finger identification is achieved using somatotopic information directly, since it was insensitive to spatial and postural factors. This result contrasts with previous claims (Yamamoto and Kitazawa 2001a, b; Roder et al. 2004) that egocentric spatial frames are automatically engaged and dominate somatotopic frames. Finger identification appears to be immune from egocentric dominance.

At first sight, hand identification appears highly redundant with finger identification. If a stimulus is represented in the contralateral somatosensory cortex in a way that supports identification of which finger was touched, it should logically follow that the contralateral hand was touched. However, our data strongly suggests that the two tasks involve quite different processes in the brain. In particular, hand identification is strongly dependent on body posture or location in egocentric external space, while finger identification is not. We suggest that when discriminating *hands*, the brain automatically engages a distinct computational process, which assigns the stimulated fingers to a hand. This assignment depends on location of the touched body part in external space. Hand identification was particularly impaired when homologous fingers were spatially adjacent (Experiments 3, 4). Possible artefacts based on verbal confusion, response biases, mechanical transmission of stimuli, or somesthetic information provided by lateral touch cannot explain this result. At the same time, our results do not support the view that hand and finger identification involve completely independent, parallel pathways. The pattern of errors observed showed that hand identification difficulty depended on the configuration of the fingers, being particularly poor when homologous fingers were adjacent to each other. Complete independence of the two systems would produce random errors. At least some processes must be shared between hand and finger identifications.

We suggest that recoding into external space occurs for hand identification, but *not* for finger identification. Other processes may be common to both tasks. Our data therefore support a dissociation between two separate representations of the body, a somatotopic finger schema and an egocentric, spatial body schema. The importance of external space for tactile representation is well known (Yamamoto and Kitazawa 2001a, b; Spence 2002). However, two perceptual illusions demonstrate the unusual relation between body-surface and external space for fingers. In Aristotle's Illusion (Benedetti 1985) an object held between crossed fingers is felt to be two objects. The sensations at the sides of the fingers are referred to their uncrossed spatial locations, because the relation between body-surface and external spaces is not updated to reflect crossed fingers. Our study shows that this independence of posture applies to finger identification, as well as to object gnosis. In the "Japanese illusion" (Henri 1898; Van-Riper 1935; Schilder and Klein 1935), the hands are crossed, and the fingers recrossed so that the left index finger is seen in the normal right index position. If the subject is asked to lift a finger touched by the experimenter, a common error involves lifting the homologous finger, on the other hand, or a finger adjacent to the homologous one. This class of error is normally interpreted as visual dominance of other senses. The touched finger *looks like* the left index finger, and this overrides tactile input coming from the right index finger. Moreover, the finger lifted is usually spatially close to the finger touched. We suggest this reflects a visual and spatial contribution in the process of assigning fingers to hands. However, we show that neither visual input nor crossing the midline is necessary to induce such assignment errors. In our design, subjects never saw their hands, and the hands never crossed the midline.

We conclude with some discussion of the postulated process for assigning fingers to hands. This process is not based on inter-hemispheric comparison, but instead combines tactile input and external space representations to determine which fingers "belong" to which hand. That is, a body schema is used to localise tactile inputs in space, and then to identify which body parts are positioned there. This suggests a hitherto unrecognised role for the body schema in organising stimuli on the continuous tactile field of the skin into a structured body representation.

The body schema thus translates skin space into body space. In our case, it must assign a tactile stimulus on the finger to the appropriate hand, using external spatial information. The neural substrate of assignment is not completely clear. However, the non-primary somatosensory areas include both the tactile and proprioceptive representations that would be required to assign touch to body parts on the basis of location. Area 5 neurons may code the position of the hand in external space, and also contains many cells with tactile responses (Kalaska et al. 1990; Nixon et al. 1992). It thus contains the information required to match body surface with external locations, translating skin space to body space. However, many of these neurons have bilateral tactile-receptive fields (Iwamura 2000). The information coded by these neurons alone would not therefore be sufficient for hand identification. Hand identification might require a combination of lateralised tactile information from primary areas, and integrated multi-sensory information from secondary areas.

The brain then maintains a variety of body maps. In particular, it contains a somatotopic finger schema and an egocentric body schema used for hands, and presumably for other body parts. These schemata can be dissociated. The body schema is based on external spatial locations, which are updated with posture changes, while the finger schema is not. Identifying a finger does not immediately imply which hand it belongs to: an additional, intermediate process appears to be involved, in which primary stimuli on the fingers are assigned to hands. This assignment process depends on external spatial location. We therefore suggest that identification of hands (and presumably of other body parts) may be a new role for the body schema. The brain's fingers and hands also reveal two separate organising principles for mental body representation. Fingers are represented in a somatotopic skin space, while hands (and presumably other body parts) are represented in egocentric external space. In general, external spatial location seems to be an important organising principle for the structural descriptions of the body on which body part identification is based.

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