



# Reversal of subjective temporal order due to arm crossing

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**How does the brain order successive events? Here we studied whether temporal order of two stimuli delivered in rapid succession, one to each hand, is determined before or after the stimuli are localized in space. When their arms were crossed, subjects could accurately report the temporal order, even when the interval between stimuli was as short as 70 ms. In most trials, subjects could also judge temporal order when their arms were crossed, but only if given adequate time (>1 s). At moderately short intervals (<300 ms), crossing the arms caused misreporting (that is, inverting) of the temporal order. Thus, at these intervals, the determining factor of temporal order was the spatial location of the hands. We suggest that it is not until the spatial locations of the hands are taken into account that the cutaneous signals from the respective hands are ordered in time.**

When a stimulus is delivered to the skin of the hand, the evoked cutaneous activity conveys the location of the stimulus on the body surface. However, the hands are mobile sensory organs, and in order to determine the location of the stimulus in space, the brain must factor in the spatial locations of the hands. There is considerable evidence that human subjects can identify the spatial location of a stimulus to the hand even when vision is blocked<sup>1-4</sup>, suggesting that the subjects can attend to the spatial location of the stimulus in addition to the location on the body surface.

It is known that the brain can resolve the order of two stimuli that are separated in time by as little as 30 ms<sup>5,6</sup>. However, there is little consensus on how and where such discriminations are made<sup>5-13</sup>. To test whether the temporal order is determined before or after the stimuli are localized in space, we examined the ability of human subjects to sense the temporal order of two stimuli delivered one to each hand. We found that subjects could correctly report the order of two closely spaced taps when the hands were uncrossed, but often misreported their order when the two hands were crossed.

## RESULTS

Seated subjects ( $n = 20$ ) were asked to close their eyes and to judge the temporal order of two successive mechanical stimuli, one delivered to the right hand and the other to the left hand, and to respond by extending the index finger of the hand that received the first (or, in half of the experiments, the second) stimulus.

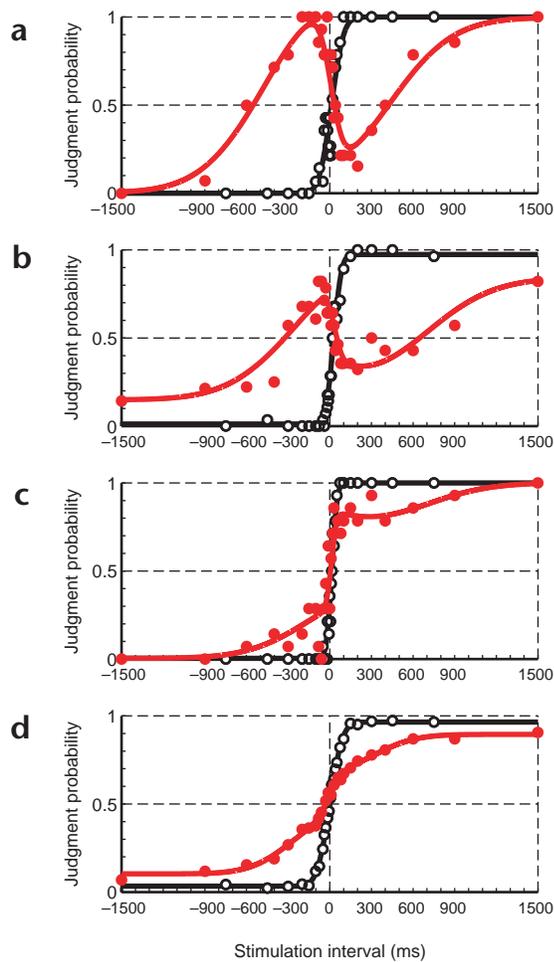
When the arms were uncrossed, the subjects could accurately report the temporal order of two stimuli in more than 80% of trials, even when the interval was as short as 70 ms (Fig. 1a-d, open circles). The order-judgment probability ( $p_u$ ) that the right hand was stimulated first was well approximated by a monotonic sigmoid function (Eq. 1, see Methods), not only when the data were pooled for all subjects (Fig. 1d, black curve,  $r^2 = 0.998$ ), but also when the data were analyzed subject by subject ( $r^2 > 0.88$ ; for example, black curves in Fig. 1a-c). The time constant  $\sigma_u$  in

Eq. 1, corresponding to the stimulation interval that yielded 84% correct responses (relative to the asymptote), was 74 ms for the pooled data (Fig. 1d), and ranged from 30 to 131 ms (mean  $\pm$  s.d.,  $71 \pm 25$  ms) for individual subjects (for example, Fig. 1a-c).

Surprisingly, when the arms were crossed, many subjects reported inverted judgment at intervals of around 100–200 ms (for example, red dots in Fig. 1a and b). In the most apparent case (Fig. 1a), the subject's report was completely inverted when the stimulation interval was 100–200 ms. The correct judgment was restored as the interval approached 1,500 ms (Fig. 1a, red dots), clearly indicating that the inverted judgment was not caused by a trivial confusion in distinguishing between the two hands.

This was further confirmed in a reaction time task in which a single stimulus was delivered randomly to one of the two hands. The subjects ( $n = 20$ ) could correctly respond in most trials, whether the arms were crossed (97.5%;  $n = 2,400$ ) or uncrossed (99.5%;  $n = 2,400$ ), indicating that the simple error in identifying which hand was stimulated was negligibly small, even when the arms were crossed.

In 5 of 20 subjects (for example, Fig. 1a and b), the tendency for reversal in the crossed condition was so strong that the response curve became N-shaped with a decreasing portion at short intervals within  $\sim 300$  ms. The N-shaped order-judgment probability curves cannot be explained by simple monotonic functions (such as Eq. 1). To develop a new function, we evaluated the probability of judgment reversal by subtracting the order-judgment probability in the uncrossed condition ( $p_u$ , black curves in Fig. 1) from that in the crossed condition ( $p_c$ , red dots in Fig. 1). Because the order-judgment probability in the uncrossed condition ( $p_u$ , black curves in Fig. 1) approached zero or one at intervals longer than 100 ms, the difference ( $p_c - p_u$ ) at these longer intervals (less than  $-100$  ms and greater than 100 ms) reflects the probability of judgment reversal. The difference ( $p_c - p_u$ , red dots) decayed with the stimulation interval and in a Gaussian manner (blue curves) (Fig. 2a and b). Therefore, we



**Fig. 1.** Temporal order judgment in the crossed (filled red circles) and the uncrossed (open black circles) conditions. Data from three individual subjects (**a**, subject K.K.; **b**, T.K.; **c**, Y.S.) and from all subjects (**d**,  $n = 20$ ) are shown. The order-judgment probability (ordinate) that the right hand was stimulated earlier than the left is plotted against the stimulation interval (abscissa). A positive interval indicates that the right hand was stimulated first. Each circle represents the order-judgment probability calculated from 14 responses in (**a–c**), and from 280 responses in (**d**). Black and red curves show the results of model fitting in the uncrossed condition (**Eq. 1**) and in the crossed condition (**Eqs. 2–4**), respectively.

range ( $362 \pm 177$  ms) for individual subjects (for example, 459 ms for subject K.K. in **Fig. 2b**). The height ( $A_l$ ) and depth ( $A_r$ ) of the Gaussian curves (**Fig. 2a**) reflect the probability that the subject's judgment would show inversion from 'left first' to 'right first,' and from 'right first' to 'left first,' respectively. These values were 0.32 ( $A_l$ ) and 0.20 ( $A_r$ ) for the pooled data (**Fig. 2a**), and were as large as 1 ( $A_l$ ) and 0.81 ( $A_r$ ) in subject K.K. (**Fig. 2b**), but varied widely among the 20 subjects (**Fig. 2c**). Nonetheless, the flip model succeeded in reproducing the wide variety of response curves, from N-shaped (**Fig. 1a** and **b**) to monotonic (**Fig. 1c**).

In **Fig. 2c**,  $A_l$  was larger than  $A_r$  in most (15 of the 20) subjects. The number of subjects with larger  $A_l$  (15) and the number of subjects with smaller  $A_l$  (5) were significantly deviated (goodness-of-fit test;  $\chi^2 = 5.0$ ,  $df = 1$ ,  $p = 0.025$ ) from the evenly split number (10 and 10), suggesting that the left-hand-first stimulation was generally more subject to the judgment reversal than the right-hand-first stimulation. This asymmetry might have some relevance to the lateralization in the judgment of temporal order<sup>9</sup>, though it remains an open question requiring further studies.

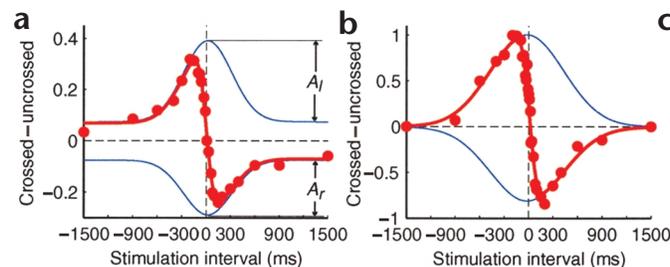
The mean reaction time in the crossed condition (red dots) was longer than 600 ms over the entire stimulation interval, and was longer by 100–200 ms than in the uncrossed condition (**Fig. 3**, open circles). To see if there was any improvement in the responses when more time was given for reaction, three subjects were asked to respond after a beep sound delivered with a delay of 1–1.5 s after the second stimulus. The tendency of reversal errors in the crossed condition obtained from these subjects ( $A_l = 0.39$ ,  $A_r = 0.21$ ) were as strong as in the self-initiated response condition. This might suggest that the proportion of errors due to premature responses was already small, if any, with the mean reaction time of 600 ms in the self-initiated response condition.

The mean reaction time was longer by 80–90 ms in the crossed condition even when a single stimulation was delivered in control experiments (right single and left single). The effect of

hypothesized that the order-judgment probability in the crossed condition ( $p_c$ ) is reversed from that in the uncrossed condition ( $p_u$ ) by a flip probability ( $f_l$  or  $f_r$ ) that decays in a Gaussian manner as the interval ( $t$ ) increases (**Eqs. 2, 3 and 4**, see Methods). The flip model successfully explained the N-shaped changes (**Fig. 1a** and **b**, red curves). In addition, the model successfully explained data from all the other individual subjects, who showed smaller differences between the crossed and the uncrossed conditions (for example, **Fig. 1c**), as well as the pooled data from all subjects (**Fig. 1d**). Determination coefficients ( $r^2$ ) were larger than 0.8 in 17 of 20 subjects, and 0.995 for the pooled data (**Fig. 1d**).

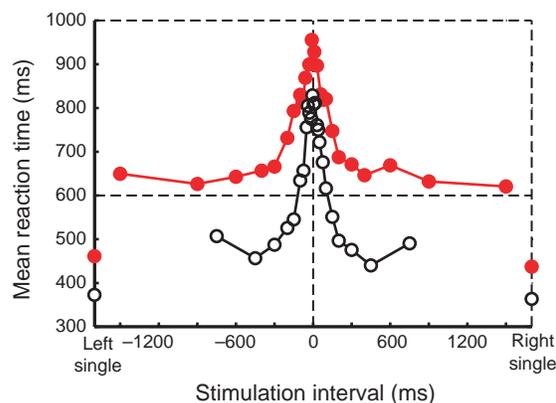
The standard deviation of the Gaussian function (**Fig. 2a** and **b**,  $\sigma_f$  in **Eqs. 3 and 4**) can be considered as the time window of the judgment reversal. The width of this time window was 293 ms for the pooled data (**Fig. 2a**) and distributed in a similar

**Fig. 2.** The Gaussian flip model. (**a**, **b**) The difference between the order-judgment probability in the crossed condition and uncrossed condition (ordinate) is plotted against the stimulation interval (abscissa). (**a**) Pooled data from 20 subjects. (**b**) Subject K.K. The difference (red dots) shown in (**a**) and (**b**) was calculated from the pooled data from all subjects (**Fig. 1d**) and the data from subject K.K. (**Fig. 1a**), respectively. The upward and downward Gaussian curves (blue) correspond to the flip functions,  $f_l$  and  $f_r$ , of the judgment probabilities as defined in **Eqs. 3 and 4** in the Methods. Peak amplitudes of the Gaussian flips ( $A_l$  and  $A_r$  in **Eqs. 3 and 4**) are indicated in (**a**). (**c**) Peak amplitudes of the Gaussian flip functions ( $A_l$  against  $A_r$ ) in 20 subjects. Note that most plots (15 of 20) are above the line  $y = x$  (solid line).





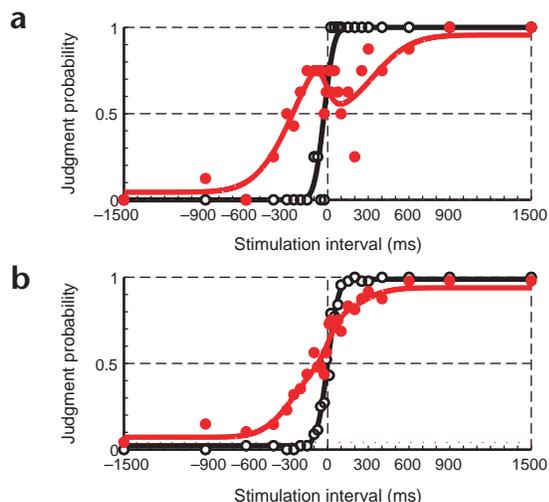
**Fig. 3.** Reaction time in the temporal order judgment. The mean reaction time measured from the second stimulus (ordinate) is plotted against the stimulation interval (abscissa). Filled red and open black circles show data in the crossed and the uncrossed conditions, respectively. Right single and left single, mean reaction time in the simple reaction time task with a single stimulation. Each dot represents mean reaction time calculated from 280 trials in the temporal order judgment task (14 trials  $\times$  20 subjects), and from 1200 trials in the simple reaction time task (60 trials  $\times$  20 subjects).



hand crossing on the reaction time to a single stimulation was in basic agreement with results reported in previous studies<sup>14,15</sup>. The effect shows that the information-processing sequence between a stimulus and a response is crucially dependent on correspondence between the spatial position of the stimulus and the anatomical laterality of the effector, constituting a kind of stimulus-response compatibility<sup>14-16</sup>.

To test whether the reversal errors critically depend on the response method, we required six subjects to respond by making saccadic eye movements to the right or left, rather than by extending the corresponding index fingers. The results in the eye-response condition (Fig. 4) were basically similar to those in the hand-response condition (Fig. 1). The subject with an N-shaped response curve in the hand-response condition (Fig. 1a) again yielded an N-shaped response curve in the eye-response condition (Fig. 4a). The flip parameters ( $A_l = 0.41$ ,  $A_r = 0.18$ ,  $\sigma_f = 220$  ms) calculated from the pooled data (Fig. 4b,  $n = 6$ ) were comparable to those ( $A_l = 0.32$ ,  $A_r = 0.20$ ,  $\sigma_f = 293$  ms) in the hand-response condition (Fig. 1d). The results suggest that the reversal error occurs centrally before the specific motor response is generated.

We further evaluated responses in 6 arm positions in 16 subjects (Fig. 5). In 4 conditions (Fig. 5a-d), the positions of the hands were systematically changed in steps of 45 degrees without crossing the arms, until each hand was placed in the contralateral hemifield (Fig. 5d). In the fifth condition (Fig. 5e), the hands were placed in the same contralateral positions as in the fourth (Fig. 5d) but the arms were now crossed. The last condition (Fig. 5f) was the same as the crossed condition used in the experiments reported above. When the two successive stimuli (with an interval of 200 ms) were delivered to only one of the hands (horizontal red lines), subjects responded correctly more than 80% of the time even when the arms were crossed (Fig. 5e and f, horizontal lines), though the correct response rate was smaller than in the uncrossed condition (>95%).



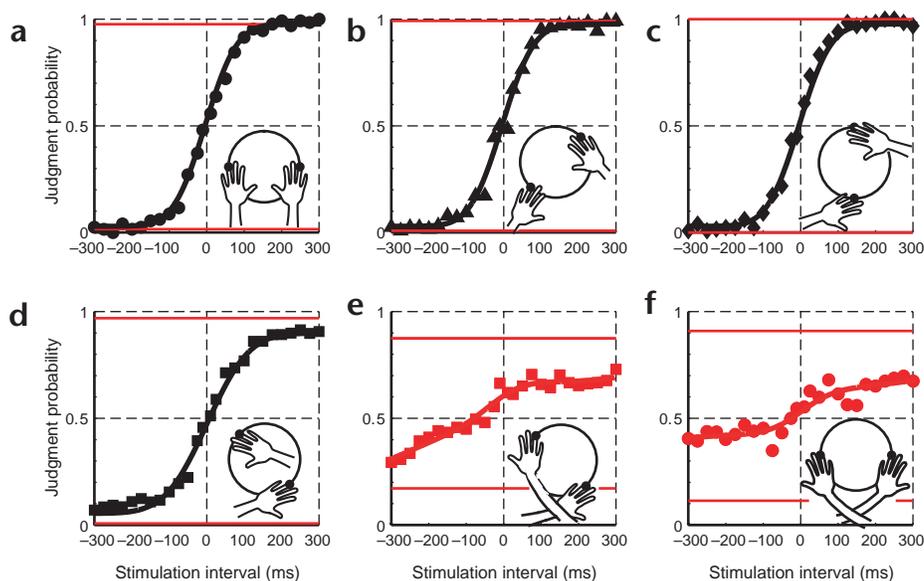
The judgment was basically unchanged as long as the hands were placed in the ipsilateral hemifield (Fig. 5a and b) or aligned sagittally (Fig. 5c). The same sigmoid function (Fig. 5a-c, black curves;  $\sigma_u = 67$  ms,  $p_{max} = 0.977$ ,  $p_{min} = 0.029$ ,  $d = -4$  ms) could fit the data in all three conditions (goodness-of-fit test;  $\chi^2 < 31.8$ ,  $df = 21$ ,  $p > 0.06$ ,  $r^2 > 0.994$ ). When the hands were placed in the contralateral hemifield when arms were not crossed (Fig. 5d), the time constant ( $\sigma_u$  in Eq. 1) became slightly longer (88.3 ms, solid curve,  $r^2 = 0.995$ ). However, the data could still be well fitted using the smaller time constant of 67 ms ( $\chi^2 = 21.9$ ,  $df = 21$ ,  $p = 0.46$ ,  $r^2 = 0.994$ ).

The largest changes occurred in the fifth condition (Fig. 5e), in which the hands were in the same (contralateral) positions as in the fourth condition (Fig. 5d) but the arms were crossed. When the sigmoid function (Eq. 1) was fitted to the data, the time constant was 271 ms ( $r^2 = 0.92$ ), which was significantly greater than the 67 ms ( $\chi^2 = 127$ ,  $df = 21$ ,  $p < 10^{-14}$ ). The fitting by the Gaussian flip model (Fig. 5e, red curve,  $r^2 = 0.96$ ) yielded flip parameters of 0.54 ( $A_l$ ) and 0.32 ( $A_r$ ). These flip parameters were as large as those estimated for the crossed condition shown in Fig. 5f (0.42 and 0.37). These results suggest that crossing of the forearms was critically important for the inverted judgment.

It can still be argued, however, that it is not the arm position in space, but the mutual contact of the arms in the crossed condition that was responsible for the reversal. Therefore, we compared the judgment probability in the crossed condition with mutual contact of the arms with that in another condition where the arms were crossed but mutual contact was avoided by using a bridge over the lower arm. The judgment in the crossed conditions with (filled red circles) and without (open red squares) mutual contact overlapped (Fig. 6a). The data in the two conditions were explained by a common response curve (Fig. 6a, red curve) derived from the same set of parameters (Fig. 5b;  $A_l = 0.37$ ,  $A_r = 0.28$ ,  $\sigma_f = 281$  ms;  $\chi^2 < 20.2$ ,  $df = 18$ ,  $p > 0.33$ ,  $r^2 > 0.98$ ). We conclude that the reversal of judgment was not caused by mutual contact of the skin, but by the crossed arrangement of the arms in space.

We finally tested whether visual stimuli from hands in the crossed condition could cause the reversal of subjective temporal order. The subjects were thus required to order two successive visual stimuli delivered from two light-emitting diodes attached

**Fig. 4.** Temporal order judgment in eye-movement response tasks. Data from one individual subject (a, subject K.K.) and from six subjects (b) are shown for the crossed (filled red circles) and the uncrossed (open black circles) conditions. Other conventions are as in Fig. 1.



**Fig. 5.** Temporal order judgment in six arm arrangements. The order-judgment probability (ordinate) is plotted against the stimulation interval (abscissa), as in Fig. 1. Responses differ according to whether the arms were uncrossed (**a–d**; inset) or crossed (**e, f**). Each symbol represents the order-judgment probability calculated from 128 responses (8 trials  $\times$  16 subjects). Black (**a–d**) and red (**e, f**) curves show the results of model fitting using the sigmoid model (Eq. 1; **a–d**) and the Gaussian flip model (Eqs. 2–4; **e, f**), respectively. Red horizontal lines show the correct response rates in catch trials ( $n = 128$ ) in which successive stimuli (200-ms intervals) were delivered to a unilateral hand.

to the distal surface of the fourth digits. With the visual stimuli, the judgment in the crossed condition (Fig. 7, filled red circles) was as precise as in the uncrossed condition (open black circles). The data in the two conditions were well fitted by a common response curve (Fig. 7, black curve) derived from a same time constant of 54 ms ( $\chi^2 < 35.8$ ,  $df = 25$ ,  $p > 0.07$ ,  $r^2 > 0.96$ ). The results suggest that pathways for the transduction of somatosensory signals are critically involved in producing the reversal errors.

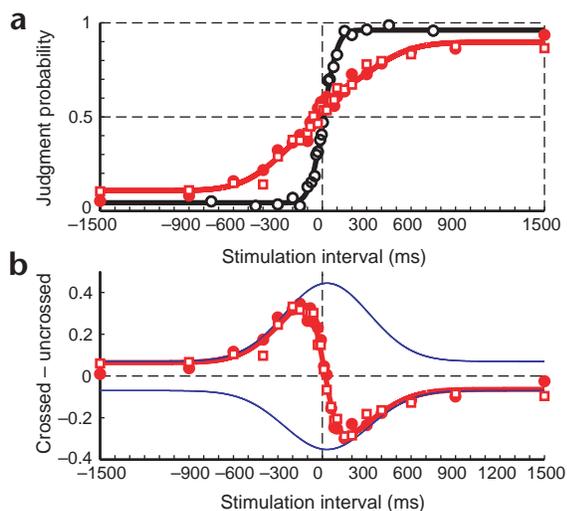
## DISCUSSION

Here we demonstrated that the subjective temporal order of two stimuli delivered to the two hands can depend critically on whether the two arms are crossed or uncrossed. In a quarter of the subjects, the effect was so strong as to yield N-shaped response curves, indicating clear reversal errors at mod-

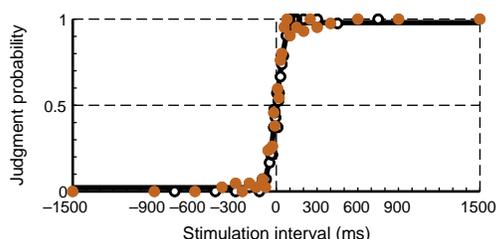
erately short intervals ( $< 300$  ms). The reversal errors in the crossed condition were not due to simple confusion between the two hands, as the subjects could respond correctly in most trials when a single stimulus was delivered, when the stimulation interval exceeded 1 s (1.5 s), and when successive stimuli separated by 200 ms were delivered to the same hand. The probability of reversal was dependent on the stimulation interval, the reversal errors gradually subsiding in a Gaussian manner as the interval exceeded 300 ms (Eqs. 2–4, Fig. 2).

It is reported, in contrast, that crossing the hands has no effect on the judgment of whether the two stimuli, one to each hand, are simultaneous or not<sup>17</sup>. The results do not necessarily contradict with ours, but rather suggest that the judgment of simultaneity and the judgment of temporal order are two distinctive processes; indeed, these processes have been modeled as such<sup>13</sup>.

Because crossing the arms causes subjects to sometimes misreport the order of two stimuli applied one to each hand in rapid succession, subjects cannot be basing their judgments simply on the locations of the stimuli on the body surface; these locations are unaffected by the crossing of the arms. We suggest that subjects ordinarily base such judgments on a reconstruction of the spatial locations of the stimuli in the external world, a process that takes time and requires information about the locations of the two hands from efference copy and/or proprioception.



**Fig. 6.** Temporal order judgment in the crossed conditions with (filled red circles) and without (open black circles) mutual contact of the arms. Ten subjects participated in the experiments. (**a**) The order-judgment probability (ordinate) is plotted against the stimulation interval (abscissa). Each circle represents 140 responses from 10 subjects. (**b**) The difference between the order-judgment probability in the crossed conditions and the uncrossed condition calculated from the data shown in (**a**). Gaussian flip functions (blue curves) common to both conditions (with and without mutual contact) are superimposed.



**Fig. 7.** Temporal order judgment of successive visual stimuli from hands. The order-judgment probability (ordinate) in the crossed (filled red circles) and the uncrossed (open black circles) conditions is plotted against the stimulation interval (abscissa). Each dot represents the order-judgment probability calculated from 42 responses of 6 subjects. A sigmoid curve (black) common to both conditions (crossed and uncrossed) is superimposed.

We suggest that, with moderately short intervals in our study (<300 ms), the second stimulus is given before the first stimulus is adjusted for the crossed position of the hands; hence, the subject makes errors. We suggest that the system has a default condition that assumes that the hands are not crossed; the right hand occupies the right side of space and the left hand occupies the left side of space, and a process of remapping<sup>18</sup> is subsequently done to correct the position. Observations in saccadic eye movements to somatosensory targets<sup>19</sup> might support this idea; when human subjects performed the task with crossed hands, the incidence of curved saccades increased, initially toward the unstimulated hand and then to the correct hand. One possibility is that remapping is an active process triggered on demand only when the need for it arises; in our situation this occurred in some subjects only when the stimulus was delivered to the hand. We suggest that it might take around 300 ms for the completion of this remapping, based on the occurrence of reversal errors at smaller intervals. Inter-subject variability may be due to varying degrees of active preparation for the remapping.

In our suggested scheme, neurons have cutaneous receptive fields located on the hands but organized in spatial coordinates. This spatial representation requires the dynamic remapping of these cutaneous inputs as the hands move within this space, perhaps through adjustments of their synaptic weights by efference copy and/or proprioceptive inputs signaling the spatial locations of the arms. This is analogous to the transient shifts in the receptive fields of some visual neurons in the lateral intraparietal area<sup>20,21</sup>, and the eye-position-dependent somatosensory activity found in the superior colliculus<sup>22</sup>. Putative sites for such remapping include the superior parietal lobe, where invisible hand positions are represented in the human<sup>23</sup>, as well as the hand region of area 5 (refs. 24, 25), which in the monkey has neurons receiving bilateral cutaneous inputs<sup>26,27</sup>. Other candidates are the premotor cortex<sup>28–30</sup> and the putamen<sup>30,31</sup>, which contain neurons that have response properties that show dependence on arm position<sup>28–31</sup>.

Signals from both hands converge not only in the association cortices but also in the first and the second somatosensory cortices<sup>26,27</sup> that are coactivated in the early processing of somatosensory input<sup>32</sup>. A possible advantage of making discriminations at such early stages of cortical processing might be that it allows the temporal information to be packaged and forwarded to other areas in the brain free of contamination by subsequent events<sup>8</sup>. We show that this is not the case; rather, the brain orders events

in time after the cutaneous signals have been localized in spatial coordinates by factoring in the positions of hands. Thus, the present behavioral protocol, involving the influence of hand position on the discrimination of temporal order, might prove useful for investigating how a unified body image is formed through the dynamic binding of cutaneous and proprioceptive signals in a spatial coordinate framework.

## METHODS

**Subjects.** Thirty-nine healthy volunteers (21 men and 18 women) participated; they were naive to the purpose of the experiments. All the subjects but one were strongly right-handed according to the Edinburgh Inventory<sup>33</sup>. The studies received approval from the institutional human review committee, and all subjects gave written informed consent according to institutional guidelines.

**Standard temporal order judgment tasks.** Twenty subjects (11 men, 9 women) participated. Subjects were asked to sit with their hands palm down on a desk with their arms crossed in one condition (crossed condition), and uncrossed in the other (uncrossed condition). In the crossed condition, the left arm was placed over the right arm in half of the experiments, and vice versa in the other half. One of the two conditions (left over right, and right over left) was assigned randomly to each subject and the two conditions were counterbalanced among the subjects. Piezoelectric skin contactors<sup>34</sup> (custom-made, TIK, Tokyo, Japan) were used to deliver mechanical stimulation to the dorsal surface of the fourth digit of each hand, between the distal interphalangeal joint and the nail. A rectangular voltage pulse (50 V, 7 ms) was applied to the piezoelectric device to produce a small movement of the contact along the skin surface. The applied voltage was at least 4 times as large as the threshold voltage (mean, 7 V) measured before each experiment. The distance between the contacts, that is, the distance between the fourth digits, was 20 cm in both conditions. A photosensor was placed at the tip of the subjects' index fingers to detect reaction (extension of the index finger) in each trial. All data were recorded and stored on a PC for later analyses. During all experiments, the subjects were asked to close their eyes, and white noise (80 dB) was played through headphones over their plugged ears. Thus, subjects could not see or hear, and could only feel the mechanical stimulation delivered to the skin.

Two successive stimuli were delivered, one to each hand, with an interval randomly assigned from 24 intervals from -750 to 750 ms (-750, -450, -300, -200, -150, -100, -75, -50, -40, -30, -15, -5, 5, 15, . . . 750 ms) in the uncrossed condition, and from -1500 to 1500 ms (-1500, -900, -600, -400, -300, -200, -150, -100, -80, -60, -30, -10, 10, 30, . . . 1500 ms) in the crossed condition. Positive intervals indicate that the right hand was stimulated earlier than the left and vice versa. Subjects were asked to judge the order of stimulation, and to respond in a forced choice manner by extending the index finger of the hand that was judged as stimulated earlier than the other, or (in half the experiments) later than the other. These two response strategies (earlier and later) were chosen to counterbalance the tendency to react with a preferred hand when the subjects were not confident of the judgment (compare with ref. 35). Subjects were encouraged to respond as soon as possible after the second stimulus. When the reaction time was larger than 3,000 ms in a certain trial, a trial with the same interval was added at the end of each experiment. No feedback was given to the subjects as to the reaction time, or as to whether their responses were correct.

All 20 subjects participated in 4 experiments designed in a factorial manner: two arm postures (crossed and uncrossed), and two response strategies (earlier and later). The arms touched each other at the distal end of the forearm in the crossed condition. The order of the four experiments was counterbalanced across subjects. Each experiment consisted of 7 epochs, in each of which the 24 intervals were permuted in a random order. Thus, one experiment consisted of 168 trials. Intertrial intervals were randomly chosen from two to four seconds.

**Eye-movement response tasks.** Six subjects (one of the 20 subjects and 5 newly recruited subjects) participated. Eye movement instead of finger extension was used for the response. Each subject was seated with his or



her head restrained by a chin rest and a head band, facing a tangent board 80 cm apart. Subjects were asked to fixate a central target on the board at the beginning of each trial, and to respond by looking at one of the two targets located 20 cm to the right or left of the central target. Subjects were asked to make a saccade to the left target when the hand in the left hemisphere was the result of his or her judgment, and vice versa. The eye movements were monitored by a house-made system with a CCD camera (30-Hz sampling, Sony, Tokyo, Japan) and fed to a PC for the detection of response. Each subject participated in three experiments: one for the uncrossed condition, and two for the crossed conditions (random order). Two response strategies (earlier and later) were counterbalanced among the subjects. One experiment consisted of 4 epochs, in each of which 24 intervals (−1,500 to 1,500 ms) were permuted in a random order.

**Temporal order judgment tasks with visual stimuli.** Six other subjects participated. Two light-emitting diodes were attached, one to each hand on the distal and dorsal surface of the fourth digit, with plastic bands. Subjects were asked to fixate the middle point of the two light-emitting diodes and to judge the temporal order of two visual stimuli with their eyes open. Two response strategies (earlier and later) were counterbalanced among the subjects. They responded by extending the index finger. Each subject participated in two experiments, one for the crossed and one for the uncrossed condition. One experiment consisted of 7 epochs, in each of which 30 intervals (−750 to 750 ms in the uncrossed, and −1,500 to 1,500 ms in the crossed condition) were permuted in a random order.

**Reaction time tasks.** Before each test experiment, a reaction time task was used as a control. A single stimulus was delivered to only one of the two hands in a random order for 60 trials, and subjects were asked to react by extending the index finger of the stimulated hand, or by looking at the side of stimulation.

**Temporal order judgment in additional arm arrangements.** We further examined responses in other arm positions in 16 subjects, 8 of whom were newly recruited. In half the subjects ( $n = 8$ ), six hand positions were chosen as illustrated in Fig. 5 (insets); hand positions were altered in a counterclockwise direction, with a step of 45 degrees from the original uncrossed condition (Fig. 5a) to the crossed condition (Fig. 5f). In the other subjects ( $n = 8$ ), hand positions were altered in a clockwise direction. Data from both groups were combined, because there were no apparent differences in the data from the two groups. All 16 subjects participated in twelve experiments designed in a factorial manner: six arm postures, and two response strategies (earlier and later). The 12 experiments were permuted in a random order for each subject. Each experiment consisted of 4 epochs, in each of which 26 intervals (−300, −275, −250, −225, −200, −175, −150, −125, −100, −75, −50, −25, −10, 10, 25, . . . 300 ms) and 2 catch trials were permuted in a random order. In the catch trials, successive stimuli with an interval of 200 ms were delivered to one hand (right or left), with which the subjects were asked to respond. Thus, one experiment consisted of 112 trials including 8 catch trials.

**Analysis.** The response data from the earlier and later response strategies were combined and sorted by stimulation interval to calculate order-judgment probabilities that the right hand was stimulated earlier (or the left hand was stimulated later) in the uncrossed ( $p_u$ ) and crossed ( $p_c$ ) conditions. Data with a reaction time larger than 3,000 ms were excluded from the analysis. The order-judgment probability in the uncrossed condition ( $p_u$ ) was fitted by a cumulative density function of a Gaussian distribution.

$$p_u(t) = (p_{\max} - p_{\min}) \int_{-\infty}^t \frac{1}{\sqrt{2\pi}\sigma_u} e^{-\frac{(\tau-d_u)^2}{2\sigma_u^2}} d\tau + p_{\min} \quad (1)$$

Here  $t$ ,  $d_u$ ,  $\sigma_u$ ,  $p_{\max}$  and  $p_{\min}$  denote the stimulation interval, the size of the horizontal transition, the time constant, and the upper and lower asymptotes of the judgment probability, respectively. Matlab (optimization toolbox) was used for the fitting to minimize Pearson's chi-square statistic<sup>36</sup> ( $df = 19$ ), which reflects the discrepancy between the sampled

order-judgment probability (24 data points) and the prediction using the four-parameter model. In the optimization, the upper and lower asymptotes ( $p_{\max}$  and  $p_{\min}$ ) were constrained within the 99% areas of the judgment probability at 750-ms and −750-ms intervals, respectively. The time constant ( $\sigma_u$ ) is a good measure of temporal order resolution, because the value is independent of the general error in response that is reflected in the upper and the lower asymptotes.

**The Gaussian flip model.** The order-judgment probability (right first) in the crossed condition ( $p_c$ ) was assumed to be flipped from the order-judgment probability in the uncrossed condition ( $p_u$ ) in a manner formulated as follows.

$$p_c(t) = f_l(t)\{1 - p_u(t)\} + \{1 - f_r(t)\} p_u(t) \quad (2)$$

$$f_l(t) = A_l \cdot e^{-\frac{(t-d)^2}{2\sigma_f^2}} + c \quad (3)$$

$$f_r(t) = A_r \cdot e^{-\frac{(t-d)^2}{2\sigma_f^2}} + c \quad (4)$$

Here,  $f_l$  denotes the flip probability of judgment from 'left first' to 'right first' and  $f_r$  from 'right first' to 'left first.' We estimated five parameters in the flip probabilities that follow the Gaussian functions shown in Eqs. 3 and 4: the peak flip amplitudes of the Gaussian functions ( $A_l$  and  $A_r$ ), the size of the horizontal transition ( $d$ ), the time window of the flip ( $\sigma_f$ ) and a constant ( $c$ ). The degree of general error in response is reflected by the constant ( $c$ ). Matlab (optimization toolbox) was used for the estimation to minimize the Pearson's chi statistics<sup>36</sup> ( $df = 18$ ). The model was not rejected in any subject by the goodness of fit test using the Pearson's chi-square statistic ( $\chi^2 < 26$ ,  $df = 18$ ,  $p > 0.1$ ) or in all subjects as a whole ( $\chi^2 = 15.9$ ,  $df = 18$ ,  $p = 0.60$ ; Fig. 1d).

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- Dassonville, P. Haptic localization and the internal representation of the hand in space. *Exp. Brain Res.* **106**, 434–448 (1995)
- Cordo, P. J., Gurfinkel, V. S. & Levik, Y. Position sense during imperceptibly slow movements. *Exp. Brain Res.* **132**, 1–9 (2000)
- Hocherman, S., Aharonson, D., Medalion, B. & Hocherman, I. Perception of the immediate extrapersonal space through proprioceptive inputs. *Exp. Brain Res.* **73**, 256–262 (1988).
- Haggard, P., Newman, C., Blundell, J. & Andrew, H. The perceived position of the hand in space. *Percept. Psychophys.* **68**, 363–377 (2000).
- Hirsh, I. J. & Sherrick, C. E. Perceived order in different sense modalities. *J. Exp. Psychol.* **62**, 423–432 (1961).
- Pöppel, E. A hierarchical model of temporal perception. *Trend Cogn. Sci.* **1**, 56–61 (1997).
- Sternberg, S. & Knoll, R. L. in *Attention and Performance* (ed. Kornblum, S.) 629–685 (Academic, New York, 1973).
- Dennett, D. C. & Kinsbourne, M. Time and the observer: the where and when of consciousness in the brain. *Behav. Brain Sci.* **15**, 183–247 (1992).
- Efron, R. The effect of handedness on the perception of simultaneity and temporal order. *Brain* **186**, 261–284 (1963).
- Gibbon, J. & Rutschmann, R. Temporal order judgment and reaction time. *Science* **47**, 413–415 (1969).
- Allan, L. G. The relationship between judgment of successiveness and judgment order. *Percept. Psychophys.* **18**, 29–36 (1975).
- Ulrich, R. Threshold models of temporal order judgments evaluated by a ternary response task. *Percept. Psychophys.* **42**, 224–239 (1987).
- Jaśkowski, P. Two-stage model for order discrimination. *Percept. Psychophys.* **50**, 76–82 (1991).
- Simon, J. R., Hinrichs, J. V. & Craft, J. L. Auditory S-R compatibility: reaction



- time as a function of ear-hand correspondence and ear-response-location correspondence. *J. Exp. Psychol.* **86**, 97–102 (1970).
15. Kornblum, S., Hasbroucq, T. & Osman, A. Dimensional overlap: cognitive basis for stimulus-response compatibility—a model and taxonomy. *Psychol. Rev.* **97**, 253–270 (1990).
  16. Simon, J. R. in *Stimulus-Response Compatibility* (eds. Proctor, R. W. & Reeve, T. G.) 31–86 (Elsevier, Amsterdam, 1990).
  17. Axelrod, S., Thompson, L. W. & Cohen, L. D. Effects of senescence on the temporal resolution of somesthetic stimuli presented to one hand or both. *J. Gerontol.*, **23**, 191–195 (1968).
  18. Driver, J. & Spence, C. Cross-modal links in spatial attention. *Phil. Trans. R. Soc. Lond. B Biol. Sci.* **353**, 1319–1331 (1998).
  19. Groh, J. M. & Sparks, D. L. Saccades to somatosensory targets. I. Behavioral characteristics. *J. Neurophysiol.* **75**, 412–427 (1996).
  20. Duhamel, J. R., Colby, C. L. & Goldberg, M. E. The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* **255**, 90–92 (1992).
  21. Colby, C. L. & Goldberg, M. E. Space and attention in parietal cortex. *Annu. Rev. Neurosci.* **22**, 319–349 (1999).
  22. Groh, J. M. & Sparks, D. L. Saccades to somatosensory targets. III. Eye-position-dependent somatosensory activity in primate superior colliculus. *J. Neurophysiol.* **75**, 439–453 (1996).
  23. Wolpert, D. M., Goodbody, S. J. & Husain, M. Maintaining internal representations: the role of the human superior parietal lobe. *Nat. Neurosci.* **1**, 529–533 (1998).
  24. Obayashi, S., Tanaka, M. & Iriki, A. Subjective image of invisible hand coded by monkey intraparietal neurons. *Neuroreport* **11**, 3499–3505 (2000).
  25. Graziano, M. S. A., Cooke, D. F. & Taylor, C. S. R. Coding the location of the arm by sight. *Science* **290**, 1782–1786 (2000).
  26. Iwamura, Y., Iriki, A. & Tanaka, M. Bilateral hand representation in the postcentral somatosensory cortex. *Nature* **369**, 554–556 (1994).
  27. Iwamura, Y. Hierarchical somatosensory processing. *Curr. Opin. Neurobiol.* **8**, 522–528 (1998).
  28. Graziano, S. M. A., Xin, T. H. & Gross, C. G. Visuospatial properties of ventral premotor cortex. *J. Neurophysiol.* **77**, 2268–2292 (1997).
  29. Graziano, S. M. A. Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. *Proc. Nat. Acad. Sci. USA* **96**, 10418–10421 (1999).
  30. Graziano, S. M. A. & Gross, C. G. Spatial maps for the control of movement. *Curr. Opin. Neurobiol.* **8**, 195–201 (1998).
  31. Graziano, S. M. A. & Gross, C. G. A bimodal map of space: somatosensory receptive fields in the macaque putamen with corresponding visual receptive fields. *Exp. Brain Res.* **97**, 96–109 (1993).
  32. Karhu, J. & Tesche, C. D. Simultaneous early processing of sensory input in human primary (SI) and secondary (SII) somatosensory cortices. *J. Neurophysiol.* **81**, 2017–2025 (1999).
  33. Oldfield, R. C. The assessment and analysis of handedness: the Edinburgh Inventory. *Neuropsychologia* **9**, 97–113 (1971).
  34. Geldard, F. A. & Sherrick, C. E. Space, time and touch. *Sci. Am.* **254**, 84–89 (1986).
  35. Shore, D. L., Spence, C. & Klein, R. M. Visual prior entry. *Psychol. Sci.* (in press).
  36. Linhart, H. & Zucchini, W. *Model Selection* (Wiley, New York, 1986).