Referral of Tactile Sensation to the Tips of L-Shaped Sticks

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Yamamoto, Shinya, Shunjiro Moizumi, and Shigeru Kitazawa. Referral of tactile sensation to the tips of L-shaped sticks. J Neurophysiol 93: 2856–2863, 2005; doi:10.1152/jn.01015.2004. When we touch something with a tool, we feel the touch at the tip of the tool rather than at the hand that holds the tool. We reported previously that judging the temporal order of two successive stimuli delivered to the tips of straight sticks held in each hand was dramatically altered by crossing the sticks without changing hand position. The results suggested that tactile signals are referred to the tip of a tool held in the hand. Here we examined temporal order judgement using L-shaped sticks instead of straight ones to determine whether the shape of a tool affects the way tactile signals are referred. Subjects reported the order of stimuli correctly in most trials when the tip of each L-shaped stick occupied the hemispace ipsilateral to the anatomical laterality of the hand holding the L-shaped stick. The subjects, however, misreported the order of stimuli presented at moderately short intervals (<300 ms) when the tip of the stick occupied the hemispace contralateral to the anatomical laterality of the hand holding it. The judgment reversal occurred irrespective of the number of physical crossings between the sticks and the arms (0, 1, and 3), as long as the tips of L-shaped tools were placed in the contralateral hemispace. Our results suggest that our brain refers tactile signals from the hand directly to the tip of the tool, rather than at the hand, so we could assume that they were unfamiliar. To test whether sensory signals are referred to the tips of unfamiliar L-shaped sticks, we examined temporal order judgments of stimuli delivered to the tips of the L-shaped sticks, in conditions that varied the spatial configurations of the arms and the sticks. The number of physical crossings among the two tools and arms was systematically altered from zero to three. In addition, the tips of L-shaped tools can be placed in the contralateral hemisphere while maintaining relatively similar positions of the two hands without physically crossing the tools (Fig. 1D), allowing us to test whether it is necessary to physically cross the tools to alter a temporal order judgement.

METHODS

Subjects

Seventeen healthy, paid volunteers (12 men and 5 women; age, 18–29 yr) participated in this study. They were all naive as to the purpose of the study. All subjects were native Born. All subjects were trained in the tasks and conditions before the study began. The study was approved by the ethics committee of Juntendo University School of Medicine.

INTRODUCTION

When we touch something with a tool, we subjectively feel the touch at the tip of the tool, rather than at the hand that holds it (Gibson 1966; Head and Holmes 1911; Paillard 1993; Polanyi 1983; Vaugh et al. 1968). By using a temporal order judgement task, we provided objective evidence for the referral of tactile signals to the tip of a tool in the hand (Yamamoto and Kitazawa 2001b). In our study, subjects were required to judge the order of successive stimuli that were directly delivered to each hand, we found that temporal order judgement was often reversed when the two hands were crossed (Fig. 1A). However, the judgement was altered only slightly when the hands were placed in the contralateral hemispace without crossing the hands (Fig. 1B). It seems that it is critically important for judgement reversal that arms be crossed, but not important whether the hand occupies the hemispace ipsilateral or contralateral to its anatomical laterality. We wanted to study whether physically crossing tools held in the hands led to a judgement reversal of stimuli delivered to the tips of those tools, as we had found previously in the arms-crossed condition.

To answer those questions, we used L-shaped sticks (Fig. 1D) instead of straight ones (Fig. 1C). Most of us have had little, if any, experience using an L-shaped stick in our daily lives, so we could assume that they were unfamiliar. To test whether sensory signals are referred to the tips of the unfamiliar L-shaped sticks, we examined temporal order judgments of stimuli delivered to the tips of the L-shaped sticks, in conditions that varied the spatial configurations of the arms and the sticks. The number of physical crossings among the two tools and arms was systematically altered from zero to three. In addition, the tips of L-shaped tools can be placed in the contralateral hemisphere while maintaining relatively similar positions of the two hands without physically crossing the tools (Fig. 1D), allowing us to test whether it is necessary to physically cross the tools to alter a temporal order judgement.

It has also been reported that actively using a straight stick extends cross-modal interactions between visual stimuli at the tip of the tool and tactile stimuli on the hand wielding the tool (Berti and Frassinetti 2000; Farnè and Làdavas 2000; Holmes et al. 2004; Maravita and Iriki 2004; Maravita et al. 2001, 2002). These studies support referral of tactile signals evoked at the hand to the tip of the tool. However, since studies to date have used ordinary straight sticks (Fig. 1A), we wanted to find out whether tactile signals are referred to the tips of tools that have different, unfamiliar shapes.

In another study (Yamamoto and Kitazawa 2001a) in which successive stimuli were directly delivered to each hand, we found that temporal order judgement was often reversed when arms were crossed (Fig. 1A) (see also Shore et al. 2002). However, the judgement was altered only slightly when the hands were placed in the contralateral hemispace without crossing the arms (Fig. 1B). It seems that it is critically important for judgement reversal that arms be crossed, but not important whether the hand occupies the hemispace ipsilateral or contralateral to its anatomical laterality. We wanted to study whether physically crossing tools held in the hands led to a judgement reversal of stimuli delivered to the tips of those tools, as we had found previously in the arms-crossed condition.
purpose of the experiments. All subjects were strongly right-handed according to the Edinburgh Inventory (Oldfield 1971). Approval of the study was granted by the institutional human review committee, and all subjects gave written informed consent in accordance with institutional guidelines.

**Standard procedure**

The subjects sat in chairs with sticks in both hands (Fig. 2). Their arms and sticks were in one of several configurations (Figs. 3–7, insets). Subjects placed the tips of the sticks on the piezoelectric contactors; they positioned the sticks by themselves, but were given no practice in handling the sticks. During the experiments, the subjects were required to visually fixate on a central target placed at the midpoint between the two stick tips. Two foot pedals were placed on the floor for the subjects to make their responses (Fig. 2). The right and the left feet were placed on the right and the left pedals, respectively.

Piezoelectric contactors were used to deliver mechanical stimulations to the tips of the sticks. The distance between the contactors, i.e., the distance between the tips of sticks, was 10–20 cm. A rectangular voltage pulse (50 V, 7 ms) was applied to the piezoelectric device to produce a small movement of the contactor. The applied voltage was ≈3.5 times as large as the threshold voltage (mean, 6.4 V) measured before each experiment. The mechanical stimulations delivered to the tips were so small (about 0.5 mm) that the subjects were never able to judge the order of the two stimuli from the visual input alone. We confirmed this by requiring five subjects to detect the delivery of a single stimulus without holding the sticks while they focused on the same target and the foot responding instead of responding with the stick in hand.

Ten subjects participated in experiments with L-shaped sticks. Six participated in the first series of experiments under two conditions: arms were uncrossed (Fig. 4A) or crossed (Fig. 4B), and the L-shaped sticks were crossed twice. Four subjects participated in the second series, in which the crossings between the L-shaped sticks were altered between one (Fig. 5A) and two (Fig. 5B), and the arms were always crossed. These four subjects also participated in the experiments with straight sticks (Fig. 3). In the third series of experiments, in which the same six subjects as in the

**Arrangements of sticks and arms**

Five subjects using straight sticks participated in four $2 \times 2$ factorial experiments: arms uncrossed or crossed (first/second columns in Fig. 3) by sticks uncrossed or crossed (first/second rows). In the arms-crosse conditions, the two arms were in contact. In the sticks-crosse conditions, the two crossed sticks were 2–3 cm apart so that mechanical stimulation did not transfer from one stick to the other. This was the same method that was used in our previous study (Yamamoto and Kitazawa 2001b), except for visual fixation on a central target and the foot responding instead of responding with the stick in hand.

Two successive stimuli were delivered, one to each tip, at 28 random intervals ranging from −1,500 to 1,500 ms (−1500, −900, −600, −400, −300, −200, −150, −100, −80, −60, −40, −30, −20, −10, 10, 20, . . . , 1,500 ms). Positive intervals indicate that the tip of the stick in the right hand was stimulated earlier than that in the left hand (right-hand-first stimuli) and vice versa (left-hand-first stimuli). The subject was required to judge the order of stimulus presentation, and to respond in a forced choice manner by pressing the foot pedal below the tip that was judged to be stimulated last (Fig. 2). The positions of the contactors and the foot pedals were roughly aligned with the direction of the gaze (Fig. 2). Subjects were encouraged to respond as quickly as possible after delivery of the second stimulus. If their reaction time was >3,000 ms or <100 ms, another trial with the same stimulation interval was repeated at the end of each experiment. No feedback was given to the subject either about their reaction time or whether their responses were correct. Intertrial intervals were spaced randomly from 2 to 4 s.

Each experiment consisted of five or six epochs, within which the 28 intervals were permuted randomly. One experiment consisted of 140 or 168 trials, and each subject participated in two to four experiments per day. The subjects took a rest of 5–20 min between the experiments.

**FIG. 2.** Experimental procedure. Seated subjects were required to put the tip of each stick on one of two piezoelectric contactors (10–20 cm apart) in a specified arrangement of their arms and sticks. An arrangement in the control condition is shown. Subjects were required to judge the order of two mechanical stimuli, delivered one to each stick tip, while they visually fixated on a target at the midpoint of the two contactors. They responded by pressing down the foot pedal that was located on the side of the stick tip that was judged as being stimulated after the other. Eyes, stick tips, and foot pedals were roughly aligned with one another.
first series participated, the tip of each L-shaped stick was placed in the hemispace contralateral to the hand that held it, and the sticks were not crossed (Fig. 6). In the L-shaped sticks condition, temporal order judgments were compared in the arms-uncrossed (Fig. 6A) and arms-crossed conditions (Fig. 6B).

All subjects participated at least once in the experiment with straight sticks in the arms-uncrossed condition (Fig. 3A), which served as the control condition.

**Eye movement response tasks**

Six subjects were additionally recruited in a series of experiments in which orthogonal eye movements instead of left/right foot movements were used for response. Each subject was seated with his or her head rested on a chin rest. Subjects were asked to fixate a central target between the tips of sticks at the beginning of each trial and to respond by looking at one of the two targets located ~20 cm to the far or near of the central target along the intersection of the midsagittal and horizontal planes. Three subjects were asked to look at the nearer target when the tip in the right hemispace was the result of his or her judgment, and vice versa. The other three were asked to look at the nearer target when the tip in the left hemispace was the result of judgement, and vice versa. The eye movements were monitored by a house-made system with a CCD camera (30-Hz sampling) and fed to a PC for the detection of response. Each subject participated in two experiments: one for the uncorrected condition with straight sticks and the other for the crossed condition in which L-shaped sticks were crossed twice in addition to crossing the arms (Fig. 7).

**Reaction time tasks**

Before each experiment, subjects performed a reaction time task to establish baselines. A single stimulus was delivered randomly to one of the two stick tips for 40 trials, and the subjects were required to press the foot pedal located below the stimulated tip.

**Data analysis**

Data of two subjects were excluded from the analysis because they errred in more than one-half of trials in at least one condition, even at the longest stimulation interval of ~1,500 or 1,500 ms. One was excluded from five subjects who participated in the experiments with straight sticks, and the other was excluded from the six subjects who participated in the first and third series of experiments with L-shaped sticks. Of the data from 15 remaining subjects \((n = 13,048)\), we additionally excluded 96 trials with reaction times between 100 and 200 ms. The response data that remained \((n = 12,952)\) were combined and sorted by stimulation interval for each condition to calculate order-judgement probabilities that the tip of the stick in the left hand was stimulated later than the stick in the right hand.

The order-judgement probability \((p_{ij})\) when the arms and the straight sticks were crossed (uncorrected condition; Fig. 3A) was fitted by a cumulative density function of a Gaussian distribution as

\[
p_{ij}(t) = \frac{1}{\sqrt{2\pi\sigma}} \int_{-\infty}^{t} e^{-\frac{(u-u_{ij})^2}{2\sigma^2}} du + p_{max}
\]

where \(t, \sigma, u, p_{max}\), and \(p_{max}\) denote the stimulation interval, the size of the horizontal transition, the time constant, and the upper and lower asymptotes of the judgement probability, respectively. Matlab (optimization toolbox) was used for the fitting to minimize Pearson’s \(\chi^2\) statistic (Linhart and Zucchini 1986), which reflects the discrepancy between the sampled order-judgement probability (28 data points) and the prediction using a four-parameter model.

The order-judgement probability of the other conditions \((p_{ij})\) was assumed to be flipped from the order-judgement probability in the uncorrected condition \((p_{ij})\), in a manner formulated as follows (flip-model)

\[
p_{ij}(t) = f(t)(1 - p_{ij}(t)) + (1 - f(t))p_{ij}(t)
\]

where \(f(t) = A_1 \cdot e^{-\frac{(t-d)^2}{2\sigma^2}} + c\) (3)

and \(f(t) = A_2 \cdot e^{-\frac{(t-d)^2}{2\sigma^2}} + c\) (4)

where \(f(t)\) denotes the flip probability of judgement from “left first” to “right first” and \(f(t)\) 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 \((A_1, A_2)\), the size of the horizontal transition \((d)\), the time window of the flip \((\sigma)\) and a constant \((c)\). General response error is reflected by the constant \((c)\). Matlab (optimization toolbox) was used to minimize Pearson’s \(\chi^2\) statistic (Linhart and Zucchini 1986). The model was not rejected in any test conditions by the goodness-of-fit test using the Pearson’s \(\chi^2\) statistic \((\chi^2 < 28, df = 22, P > 0.16)\). The flip model also yielded determination coefficients larger than 0.86 (mean, 0.95) in all test conditions.

To evaluate whether the judgement in the test condition was reversed from the uncrossed condition, we tested the null hypothesis that the peak flip amplitudes in the flip model \((A_1, A_2)\) were zero and that the remaining parameter is only \(c\) in the flip model. If the goodness-of-fit test using the Pearson’s \(\chi^2\) statistic produced \(P > 0.05\), we judged that there was no reversal, because the null hypothesis was not rejected. On the other hand, if \(P < 0.05\), we judged that the reversal was significant, in that either peak flip amplitude would be significantly greater than zero. When the reversal was significant, we used the peak flip amplitudes \((A_1, A_2)\) as the quantitative measures of the reversal.

The mean reaction time in each condition was compared with that in the uncrossed control condition in a two-way ANOVA. The two-way ANOVA evaluated two factors: the stimulation interval (28 intervals, \(df = 27\)) and the condition (test vs. control, \(df = 1\)) and their interaction. The hypothesized linear model in the ANOVA is expressed as

\[
t_i = \mu + s_i + (sc)_j + e_{ij} (i = 1, 2, \ldots 28; j = 1, 2)
\]

In this notation, \(t_i\) represents reaction time, \(\mu\) represents a constant, \(s_i\) (stimulation interval) and \(c_j\) (condition) represent the main effects, \((sc)_{ij}\) represents the interaction of the two factors, and the last term is error. When the main effect of condition was significant \((P < 0.01)\), the difference of the estimated parameters, \(c_j - c_i\), was used to estimate reaction time differences between the test and the control conditions. Reaction time increased or decreased according to whether the value \((c_j - c_i)\) was positive or negative, respectively.

**RESULTS**

**Temporal order judgement with straight sticks**

When neither straight sticks nor arms were crossed (Fig. 3A), subjects responded correctly in most trials, even at intervals as short as 100 ms. The probability that the stick in the right hand was stimulated first (Fig. 3A, ○) was well-approximated by a sigmoid function (Fig. 3A; \(r^2 = 0.98\)). The sigmoid function served as a control to evaluate judgement reversal.

When the arms were crossed without crossing the sticks (Fig. 3B), many subjects misreported the temporal order, especially at intervals <300 ms (red filled triangles). Peak flip amplitudes (Eqs. 3 and 4) were 0.55 (\(A_1\)) and 0.34 (\(A_2\)). When the sticks were crossed with the arms uncrossed (Fig. 3C), many subjects again misjudged the order at intervals <300 ms (\(A_1 = 0.40, A_2 = 0.40\)). However, when both sticks and arms were crossed (Fig. 3D), judgments approached the control sigmoid response, as indicated by much smaller peak flip.
amplitudes ($A_1 = 0.17, A_2 = 0.07$) compared with when either sticks or arms were crossed but not both (0.34 ~ 0.55). These results were comparable with those in our previous study (Yamamoto and Kitazawa 2001b) and suggest that somatosensory signals evoked at the hands are referred to the tips of the straight sticks.

**Temporal order judgement with L-shaped sticks**

When the L-shaped sticks were crossed twice without crossing the arms (Fig. 4A), there was no judgement reversal (green open diamonds). On the other hand, when the L-shaped sticks were crossed twice after crossing the arms (Fig. 4B), judgments showed a tendency to reverse (red filled squares; $A_1 = 0.57, A_2 = 0.27$). This might imply that somatosensory signals were referred to the tips of the L-shaped sticks; however, it could be argued that tactile signals were simply referred to the hands that were uncrossed in Fig. 4A or crossed, as in Fig. 4B.

We further recruited four subjects to see if their judgments depended on the number of crossings between the L-shaped sticks in the arms-crossed condition. There was a significant difference between the conditions in which the L-shaped sticks

![Fig. 3. Temporal order judgement with straight sticks. A–D: order-judgement probability (ordinate) that the stick in the left hand was stimulated later than the stick in the right hand is plotted against the stimulation interval (abscissa). Positive intervals show that the stick in the right hand was stimulated first. Insets: arm and stick arrangements: arms uncrossed (A and B) and sticks uncrossed (C and D) and sticks uncrossed (A and C) crossed (B and D). Each symbol represents 24 judgments from 4 subjects. Curves show fitting by models as defined in Eq. 1 (A) and Eqs. 2–4 (B–D). Data in A (control condition, open circles and black curves) are superimposed on the other panels (B–D). Horizontal lines show the judgement in the control trials with single stimuli delivered to the tip of the stick in the right (red) and the left (blue) hand. Fitting parameters are as follows: \(A\): \(d_u = 6.5\) ms, \(d_l = 63\) ms, \(d_{min} = 0.5, d_{max} = 1.0, r^2 = 0.98\); \(B\): \(A_1 = 0.55, A_2 = 0.34, d = -44\) ms, \(A_1 = 255\) ms, \(c = 0.06, r^2 = 0.87\); \(C\): \(A_1 = 0.40, A_2 = 0.40, d = -15\) ms, \(A_1 = 220\) ms, \(c = 0.11, r^2 = 0.88\); \(D\): \(A_1 = 0.17, A_2 = 0.07, d = 29\) ms, \(A_1 = 443\) ms, \(c = 0, r^2 = 0.97\). E–H: mean reaction time measured from the 2nd stimulus (ordinate) is plotted against the stimulation interval (abscissa) for each of the 4 conditions shown in A–D. Symbols and conditions in E–H correspond to those in A–D. Rightmost and leftmost plots in each panel show mean reaction time in the simple reaction task with a single stimulation to the tip of the stick in the right hand and in the left hand, respectively. Number of physical crossings (0, 1, or 2) is shown in each panel.](http://jn.physiology.org/)

![Fig. 4. Temporal order judgement with L-shaped sticks crossed twice. Arms were uncrossed (A and C) crossed (B and D). Top: order-judgement probability. Bottom: mean reaction time. Each symbol represents 50 judgments from 5 subjects. Open circles and black curves show data in the control condition. Fitting parameters are as follows: \(A\): \(A_1 = 0, A_2 = 0, c = 0.02, r^2 = 0.99\); \(B\): \(A_1 = 0.57, A_2 = 0.27, d = 152\) ms, \(A_1 = 345\) ms, \(c = 0.10, r^2 = 0.93\). Other conventions are as in Fig. 3.](http://jn.physiology.org/)
were crossed once (Fig. 5A) or twice (Fig. 5B). No judgement reversal occurred when L-shaped sticks were crossed once (Fig. 5A, green open triangles), but judgments were clearly reversed when the L-shaped sticks were crossed twice (Fig. 5B, red filled squares; \( A_l = 0.53, A_r = 0.30 \)). These results indicate that tactile signals were not referred to the hands but to the tips of the L-shaped sticks, even though those tools must have been unfamiliar to the subjects.

To test whether judgement reversal requires physically crossing the tools, the L-shaped sticks were positioned so that, while the straight lines connecting the bases and the corresponding tips were crossed, the segments of the L-shaped sticks did not physically cross each other (Fig. 6, insets). Judgments were reversed (Fig. 6A, red filled triangles; \( A_l = 0.08, A_r = 0.33 \)) when the arms were uncrossed and the tip of each stick occupied the hemispace contralateral to the anatomical laterality of the hand that held it. The results show that judgments were reversed when the tips of tools were located in the hemispaces contralateral to the anatomical laterality of the hands holding them, and it did not matter whether the tools were physically crossed.

When the arms were crossed, but the tip of each stick occupied the hemispace ipsilateral to the anatomical laterality of the hand (Fig. 6B), judgments generally approached the control sigmoid response, but it was still significantly reversed (green inverted open triangles; \( A_l = 0.20, A_r = 0.15 \)).

**Reaction time in different conditions**

We analyzed the mean reaction time from the onset of the second stimulus to see if reaction time increased as the number of physical crossings increased. In experiments with the straight sticks (Fig. 3, E–H), the mean reaction time was generally greater when either the arms (Fig. 3F; 68 ms longer; \( F = 14.9, df = 1, P = 0.00012 \)) or the sticks (Fig. 3G; 188 ms longer; \( F = 96.2, P < 0.0001 \)) were crossed, i.e., there was one physical crossing (red filled symbols) compared with when neither straight sticks nor arms were crossed (Fig. 3E, 0 crossings). When both the arms and the sticks were crossed (Fig. 3H, 2 crossings), the mean reaction time (green open squares) was similar to that of the control condition (\( F = 1.5, P = 0.21 \)).

When there were two crossings with L-shaped sticks (Fig. 4C, green open diamonds), the mean reaction time was slightly (24 ms) but significantly (\( F = 5.4, P = 0.021 \)) longer than that of the control condition. In contrast, when the number of crossings was increased to three by crossing the arms (Figs. 4D and 5D, red filled squares), the mean reaction time generally increased by 100–200 ms compared with the control. The estimated elongation was 162 ms when the data in Figs. 4D and 5D were combined (\( F = 251, df = 1, P < 0.0001 \)). It is also worth noting that the elongation of the mean reaction time was asymmetric (Figs. 4D and 5D); the elongation was more apparent in response to the left-hand-first stimulus (negative
stimulation intervals) than in response to the right-hand-first stimulus (positive stimulation intervals). When the number of crossings was decreased to two, by separating the L-shaped sticks (Fig. 5C, green open triangles), the mean reaction time was significantly less, by 90 ms, than the control condition ($F_{1,11005} = 33.1, P < 0.0001$).

When the tip of each stick was located in the contralateral positions (Fig. 6C), but there was no physical crossing, the mean reaction time was greater by 226 ms than in the control condition ($F_{1,11005} = 315, P < 0.0001$), as in previous cases when there were odd numbers (1 and 3) of crossings. When the arms were additionally crossed (Fig. 6D), the mean reaction time was still greater by 202 ms than the control condition ($F_{2,11005} = 230, df = 1, P < 0.0001$). In this case, the mean reaction time did not fully recover to the control level, even though the tips were located in the ipsilateral positions.

Experiments with eye response

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 far or near targets rather than by pressing down the foot pedals that were spatially congruent to the locations of the tips. It is worth noting that the eye movements were made in the midsagittal plane and thus the movements were neutral to the laterality of stimuli. Results did not depend on the response methods. When neither straight sticks nor arms were uncrossed, subjects responded correctly in most trials even at intervals as short as 100 ms (Fig. 7A, ○). When the L-shaped sticks were crossed twice after crossing the arms, judgments showed a tendency to reverse (Fig. 7A, red filled square; $A_s = 0.33, A_r = 0.34$) as when the foot was used for response (Fig. 4B; $A_s = 0.57, A_r = 0.27$). The mean reaction time was significantly greater by 242 ms than the control condition ($F_{1,11005} = 180, df = 1, P < 0.0001$) when the L-shaped sticks were crossed twice with arms crossed (Fig. 7B).

**Response methods**

The foot was used to make a response in this study, rather than the stick in the hand (Yamamoto and Kitazawa 2001b), for two reasons. First, responding with the L-shaped stick was difficult for subjects, especially when there were three physical crossings. Second, we wanted reaction time differences to reflect differences in the time it took to judge the temporal order of two stimuli rather than a difference in the time it took to make a physical response. Since time for a hand (stick)
response to a stimulus inevitably depends on the configuration of the arms, we chose a foot response to ensure that the interval between making a judgement and producing a response could be evaluated independently.

Although subjects did not respond with the stick in this study, results with the straight sticks (Fig. 3) were comparable with those in our previous study (Yamamoto and Kitazawa 2001b) in which the stick in hand was used to make a response with their eyes closed. In addition, judgment reversal occurred even when the subjects were required to respond by moving the eyes. These results suggest that a spatial interaction between the tip of a tool and tactile stimuli occurs without actively using the tool. In this study, however, the subjects themselves positioned the tips on the piezoelectric contacters and were required to keep the tips on the contactors during the experiments while they visually fixated on a central target. Their efforts to keep the tip in place with peripheral vision would have contributed to establishing a spatial interaction between the tip of the tool and tactile stimuli received on the hand, although subjects did not actively wield the tools during the present experiments (cf. Holmes and Spence 2004; Iriki et al. 1996; Maravita et al. 2001, 2002; Riggio et al. 1986). If vision and active tool use both strengthen the referral of tactile signals to the tip, combination of foot response and no vision might reduce the degree of judgment reversal in the crossed condition.

Effects of the number of physical crossings

Analyzing judgement response curves revealed, in principle, that the curve was determined according to whether the tips of the L-shaped or straight sticks were positioned in the ipsilateral hemispace (ipsilateral conditions) or in the contralateral hemispace (contralateral conditions), irrespective of the number of physical crossings. This could imply that our brain refers tactile signals from the hand directly to the location of the tip without accounting for the route that connects hand and tip. However, it may be that the time required for the referral of sensation increases as the complexity of the physical connection increases. To clarify this issue, we examined reaction times. The reaction times were generally greater by 100–200 ms in the contralateral conditions compared with the ipsilateral conditions, but reaction time did not directly correlate with the number of physical crossings in both ipsilateral (0, 1, and 2 crossings) and contralateral (0, 1, and 3 crossings) conditions. These results supported the direct referral explanation with a few caveats.

First, slight but significant judgment reversal remained in two ipsilateral conditions with one (Fig. 6B, L-shaped sticks) and two (Fig. 3D, straight sticks) physical crossings. On the other hand, there was no judgment reversal in the other two ipsilateral conditions with two physical crossings (Figs. 4A and 5A, L-shaped sticks). We do not know the reason for this variation of results in the ipsilateral conditions. However, it might be worth noting that, in one ipsilateral condition with two physical crossings (Fig. 5A), reaction times were not greater but significantly less, by 90 ms, than that in the control ipsilateral condition (0 crossing with straight sticks). On the other hand, reaction times in the ipsilateral condition with one physical crossing (Fig. 6D) were greater by 187 ms than in the control condition. We may hypothesize that our brain might refer tactile signals more directly and more quickly to the action point of the tool, when information about the pathway from the hand to the tip becomes too complicated as in Fig. 5A (2 crossings). On the other hand, the brain might use information about the pathway from the hand to the tip when the pathway is not too complicated as when there was only one physical crossing (Fig. 6B).

Second, judgement reversal in the contralateral condition did not require physically crossing the tools, as shown in Fig. 6A (contralateral condition with 0 crossings). This contrasts with the data in our previous study (Yamamoto and Kitazawa 2001a), in which stimuli were delivered directly to the hands. In that study, we found that subjective temporal order was inverted when the arms were actually crossed (Fig. 1A), but little affected when the hands were placed in the contralateral hemifield without crossing the arms (Fig. 1B). Anteroposterior spatial difference in Fig. 1B cannot explain the lack of judgment reversal, because the judgment was inverted when the hands were in the same positions as in Fig. 1B but the arms were crossed (Fig. 5E of Yamamoto and Kitazawa 2001a). These differences in results suggest that the bodily image of each forearm is represented over its entire length in the brain, but only the tip, not the whole distal segment, of the L-shaped stick is represented. Because subjects were not given any time to become familiar with the L-shape sticks, the differences in results may be a consequence of more familiarity in using their arms. More extensive training might support the acquisition of a stronger internal representation of each segment of the L-shaped stick, and judgments would not be inverted in the contralateral condition that lacks any physical crossing of the L-shaped sticks (Fig. 6A).

Third, judgments of the left-hand-first stimuli tended to be inverted more often than the right-hand-first stimuli in the contralateral conditions in which the arms were crossed (Figs. 3B, 4B, and 5B). As reflected not only in the flip parameters (Fig. 5B; A₀ = 0.27, Fig. 4B; A₀ = 0.30, Fig. 5B), but also in the relatively greater reaction times in the left half of the reaction time plots (Figs. 3F, 4D, and 5D), this asymmetry is consistent with our previous studies in which stimuli were delivered to the crossed hands (Wada et al. 2004; Yamamoto and Kitazawa 2001a). Wada et al. (2004) found that this asymmetry is generally observed in right-handers but not in left-handers; given that all participants were right-handed in this study, the asymmetry might reflect the actual arm crossing of our right-handed subjects. On the other hand, asymmetry was not evident (Fig. 3C, A₀ = 0.40, Ar = 0.40) or reversed (Fig. 6A, A₀ = 0.10 < A₀ = 0.36) when the arms were not crossed but the tips of the sticks were positioned contralaterally; this may also reflect the brain’s different representations of the arms and the sticks.

Implications for neural mechanisms

When a monkey was trained to use a rake with a straight handle, the visual receptive fields of bimodal neurons in the intraparietal sulcus were elongated from the hand along the straight handle to the tip (Iriki et al. 1996). The data support the view that the connection from the hand to the tip is represented in the brain, as long as it is straight. Iriki et al. (2001) also reported that the receptive fields of such neurons could be confined to the tip of the rake when the image of the handle and
the hand was erased from visual feedback to the monkey. The bimodal neurons that have cutaneous receptive fields on the hand and visual receptive fields at the tip of the tool are good candidates for referring tactile signals to the tip. Under that assumption, we may be able to test several current issues. We may be able to test whether the visual receptive field is elongated along the L-shaped stick from the hand to the tip when it is placed without crossings, whether the visual receptive field is confined to the tip when the L-shaped sticks are positioned so that they make two crossings, and whether the visual receptive field is firmly established along the distal segment after extensive training for using the stick. These experiments may be possible with the monkey, because the monkey had been successfully trained to use not only a rake with a straight handle (Iriki et al. 1996) but also an L-shaped tool (Beck 1976).

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