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Proprioception and Stimulus-Response Compatibility

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Abstract

Sixteen subjects pressed a left or right key in response to lateralized visual stimuli, in uncrossed (left index finger on left key, right finger on right key) and crossed conditions (left finger on right key and vice versa), with varying finger separations. Visual, tactile, or "efference copy" cues about relative finger positions were unavailable. Subjects had to press the key on the same side as (compatible group) or opposite side to the stimulus (incompatible group). Separate proprioceptive judgements of the relative finger positions were obtained. Findings of an overall reaction time (RT) advantage for compatible instructions and for uncrossed hands were replicated. With decreasing finger separation the RT advantage for compatible instructions decreased, and the probability of responding with either hand increased. The compatibility effect disappeared completely at the 6-cm crossed position, not at the position that was hardest to judge proprioceptively. This suggests that two forms of neural activation are summed: automatic activation of the anatomically same-side limb, and an integrated, rule-based activation. The results further demonstrate that independent proprioceptive cues from each limb, unassociated with skin contact between the limbs, can mediate the determination of relative position for response selection in stimulus-response compatibility tasks.

Introduction

It is nearly half a century since the classic description of the general stimulus-response compatibility (SRC) phenomenon by Fitts and Seeger (1953), and some 25 years since Wallace (1971) demonstrated that the relative position of the limbs was of greater importance as a determinant of response selection than were their anatomical sides. In the latter study, reaction times (RTs) were shorter if the stimulus paired with the left-side response key was on the left, and that paired with the right-side key was on the right, than if it were vice versa. This task required subjects to respond on the basis of non-spatial stimulus properties (shape), but the spatial attributes largely determined RT—the Simon effect (after Simon & Rudell, 1967). When the hands were crossed, subjects responded more rapidly and with fewer errors when the stimulus was presented in the same relative position of the limb to be used in the response. "Pure" spatial SRC tasks, in which position is the stimulus feature that subjects are instructed to use, have also shown this effect (e.g. Anzola, Bertolini, Buchtel, & Rizzolatti, 1977; Brebner, Shephard, & Cairney, 1972; Klapp, Greim, Mendicino, & Koenig, 1979; Proctor & Dutta, 1993).

Despite the relative position effect being a robust and much replicated finding, the underlying mechanism is unclear. Why and how does the simple crossing of the limbs cause such a marked performance change? From a neuroanatomical point of view, crossing the limbs does not alter the fact that a lateralized visual stimulus is processed in the contralateral visual cortex—the hemisphere controlling the limb on the same side as the stimulus. Although the nervous system is obviously influenced by relative position information, it is unclear what central or sensory signals produce the observed effects. Previous experiments have confounded several distinct potential sources of relative position information: proprioceptive, cutaneous, and visual, as well as information arising from efference copy. In this study we explore the extent to which the relative position effect depends strictly on the proprioceptive inputs about relative limb positions. We also examine

whether the discriminability of the effector locations influences response selection.
Alternative Sources of Information About Relative Position

In most SRC studies involving crossed hands, subjects actively placed their hands in crossed or uncrossed positions in order to comply with instructions. Thus they knew the relative positions even without using any subsequent sensory information, both through the instructions and through a "corollary discharge" or "efference copy" mechanism. The relative position effect may, therefore, occur without the use of any sensory information. Only Wallace (1971, 1972) has employed conditions that exclude such centrally generated cues, by passively positioning the limbs in the required locations. As relative position effects still occurred, it appears that some form of sensory information can provide the necessary cues. But through which modality? Even when efference copy cues are unavailable, visual and proprioceptive cues generally are. Vision of the limbs is likely to be a decisive source if available, but if not (i.e. Wallace, 1972, Experiments 1 and 2), peripheral afferent information can still permit sensing of the relative limb positions. Such afference takes two forms. First is proprioceptive information arising from each limb independently, and from multiple sense organs, including muscle and joint receptors and cutaneous mechanoreceptors. Second, there is a special form of cutaneous input concerning relative limb position that will occur only in some situations. In addition to firing as a function of the position of individual joints (Edin & Johansson, 1995), skin receptors can signal whether or not the limbs are crossed by the presence or absence of mutual contact when one limb rests on the other (including thermal and mechanoreceptive cues).

Notwithstanding Wallace's (1972) claims that proprioceptive information alone mediates response selection, such specific tactile cues could certainly have contributed to relative position estimates in his studies, as one arm or hand was only laid on top of the other in crossed conditions. The current experiment sought evidence to determine whether proprioceptive inputs unconfounded by skin contact can mediate the relative position effect.
Discriminability of the Relative Positions of Stimuli and Effectors

A second issue is whether changes in the ambiguity of relevant sensory inputs systematically affect SRC task performance. Each of the possible sensory modalities obeys psychophysical principles such as Stevens' power law (1957), and therefore confusion could arise from small separation, and thus poor spatial discriminability, of either the stimuli or the effector positions. We consider each as follows.

When visual stimuli are presented at more eccentric locations (generally further left and right from midline), the easier it becomes to discriminate their relative positions, potentially leading to shorter latencies. With eccentricity manipulated only in a left-right dimension, Rabbitt (1967) found shorter RTs for more laterally located stimuli (at least for older subjects). On the other hand, both Nicoletti and Umiltà (1989, Experiment 1) and Hommel (1993b), found increases in response latencies with greater stimulus eccentricity—by as much as 101 msec in Hommel's (1993b) Experiment 2. Yet other studies have reported no influence of stimulus eccentricity (Simon & Wolf, 1963; Soetens, Deboek, Hueting, & Merckx, 1984). As Hommel (1993b) has observed, though, more eccentric visual stimuli may increase discriminability, but they are also further from the fovea and can thus incur substantial time costs in stimulus identification and localization.

In other paradigms, however, there is no confounding of discriminability with fovea-to-stimulus distance. Such is the case with auditory stimuli. Simon, Craft, and Small (1971, Experiment 2) observed that the increase in latencies for crossed (e.g. left stimulus, right response) compared to uncrossed (e.g. left stimulus, left response) mappings was larger when the possible locations were further from the median plane of the subject's head. For their task, the stimulus location was technically an "irrelevant" stimulus (the Simon effect).

The locations of responses, as well as those of stimuli, may be more or less discriminable. If the limbs are separated by a large distance, it should be easy to tell whether or not they are crossed, but sufficiently small separations should be much harder. Unfortunately, few studies have manipulated response locations, and in those cases other factors preclude a clear interpretation. For example, Michaels (1989) varied the eccentricity of hand position,

but the S-R mapping was nominally arbitrary because stimulus and response pairs were aligned perpendicular to one another. Response location separation has also been varied indirectly through the use of digits of each limb as opposed to digits of the same limb with either a constant (Hasbroucq & Possamai, 1995) or varying physical separation (Shulman & McConkie, 1973). Certainly, though, the simple notion that increased separation equates directly with discriminability is not upheld clearly. In a study by Heister, Schroeder-Heistel, & Ehrenstein (1990), the RT advantage of compatible over incompatible conditions was smaller when the separation (between the first and fifth digits) was 11 rather than 4.5 cm. In this case, the effects may result from the digits being in quite unusual anatomical positions.

In studies that have employed crossing of the hands, the degree of separation, where reported, has generally been quite large (and therefore easily detectable). Wallace (1972), for example, used a separation of 27 cm in one of his original experiments and 6.8 cm in another, and he found SRC effects in both. Whether crossed or uncrossed, there was no significant effect of separation when vision was available. Without vision, the advantage of a compatible over an incompatible pairing was less with the smaller separation, but only when the hands were crossed. It is not at all clear, though, whether a separation of 6.8 cm is small enough to introduce any uncertainty about relative position.

In order to establish directly how proprioceptive inputs influence the processing required in spatial SRC tasks, we conducted an experiment in which subjects responded to lateralized visual stimuli with key presses, with left and right index fingers in crossed and uncrossed positions and separated by varying distances. Subjects were forced to rely on proprioceptive information because vision of the limbs was occluded. In addition the limbs were moved into position by the experimenter (preventing any a priori knowledge about limb positions by means of efference copy resulting from active movement), and the head was kept in a fixed, midline position. Subjects had to rely on comparison of independent proprioceptive inputs from each limb because the limbs were never in contact. Psychophysical testing of relative position in the same subjects and same positions assessed the proprioceptive contribution to response selection processes in SRC tasks by removing the confound of the additional task requirements.

Methods

Subjects

Sixteen volunteer right-handed subjects (seven female, nine male), with a mean age of 24.6 (± 6.1) years, participated in both experimental procedures used in this study. All provided informed consent and were treated in compliance with the ethical standards of the American Psychological Association.

Apparatus

A microcomputer and custom software were used to control stimulus presentation and to time switch presses in the compatibility task (with a precision of 1 msec). A 14-inch, flat-screen, high-contrast monitor was used to display stimuli, at a distance of approximately 105 cm.

Subjects sat in an adjustable height chair at a table on which were mounted two identical rigid, horizontal, laminated surfaces, one 15.5 cm above the other. An adjustable chin- and head-rest ensured that the head was aligned with the body midline and with the centre of the screen.

A dark vertical drape prevented subjects from seeing the experimenter, who was seated across the table (below the level of the monitor), in the proprioceptive judgement task. For the compatibility task a rectangular aperture in this drape allowed vision of the computer. In both tasks, a horizontal opaque drape occluded vision of the entire upper extremity and the response switches.

The compatibility task used two microswitches (one for each hand), mounted on spring clips on the edge of the surfaces opposite the subject. These could be readily and silently moved between trials. A calibrated scale allowed the various finger and switch positions to

be located easily by the experimenter.

Procedure

The proprioceptive judgement and compatibility tasks were administered in two separate sessions, always in that order. After giving informed consent, the subject was given a description of the task and instructions for its conduct. Watches and jewellery were removed for the duration of testing.

Proprioceptive Judgement Task. Subjects had to make forced-choice judgements as to whether the index fingers of the two hands were crossed or uncrossed, in the lateral, horizontal plane. There were four uncrossed positions (index fingertips separated by 1.2, 3.6, 6.0, and 10.8 cm), and four crossed positions (same separations).¹ When the subject was comfortably seated two practice trials were given with the limbs placed in extreme crossed and uncrossed positions, approximately 40 cm apart, to ensure that the procedure was clear. On each trial, the subjects rested one arm on the top surface and the other on the bottom. Hands were positioned with the index fingers extended and the other digits flexed. Each trial began with the fingertips about 35 cm apart horizontally, approximately equidistant from the midline. The experimenter then moved the subject's hands in a quasi-random order so that the fingertips were placed in the appropriate positions for that trial. On a verbal prompt, subjects reported whether they felt the fingers to be crossed or uncrossed, the response being

Note: Four subjects were tested with a proprioceptive judgement protocol that used slightly different separations. Error rates for the standard positions were obtained separately for each of these subjects by linear interpolation. The procedure was identical in all other respects.

manually recorded. Subjects were instructed to use the centre of each fingertip as reference positions, so that, even if the fingers were perceived to be partially overlapping, a response of "uncrossed" should be given if the centre of the left fingertip were felt to be to the left of the centre of the right fingertip. Subjects' limbs were then moved back to resting positions. The passive movement of the hands by the experimenter included random changes in direction, sometimes moving in a lateral rather than a medial direction, sometimes overshooting the final position, so that starting positions, movement times, and distance cues would not be reliable position cues.

A total of 160 trials was administered. The first 80 involved 10 repetitions of each of the eight crossed/uncrossed, separation combinations. The order of their presentation was random without replacement, so that one set of eight combinations was completed before the next commenced. The second 80 trials followed a few minutes' rest. The limb positions were now switched so that the arm that had previously been on the top surface was now on the bottom, and vice versa. The arm to be on the top surface first was chosen at random.

Compatibility Task. In this second procedure, the same subjects had to respond as rapidly as possible to a visual stimulus, presented to the left or right of a vertical midline reference line, by pressing a left or right key. Half the subjects were allocated to a "compatible" group and were instructed to press the key on the same side as the stimulus, whether the index finger in that position belonged to the left or right hand. The other half ("incompatible" group) was told to respond by pressing the key opposite the stimulus, again, without regard to whether the index finger of the left or right hand was in that position.

After receiving instructions, subjects undertook a practice block of 15 trials, using both extreme crossed and uncrossed positions (approximately 40 cm separation). On each trial, subjects began with the hands and fingers in resting positions as in the previous task. For each block of 12 data trials, the experimenter moved the subject's hands to the appropriate positions (1.2, 3.6, 6.0, & 10.8 cm separation, crossed or uncrossed). The movements were made in the same way as for the proprioceptive judgement task except that at the final positions the fingertips rested on circular plastic pads (1 cm diameter) attached to the microswitches. Subjects were asked to press the switches once or twice before data collection.

To begin a trial, a warning tone was emitted along with the presentation of a short horizontal line crossing a vertical midline reference line at right angles, at the level where the subsequent left or right visual stimulus was to appear. Following a randomly varying foreperiod (1500-2000 msec), a visual stimulus (red filled circle) was presented 3 cm to the left or right of the reference line. Subjects had to respond by pressing the key appropriate to their instructions as rapidly as possible. After 12 trials, the subject rested in the starting position while the switches were moved to the positions for the next block. The order of the positions followed a predetermined random schedule for each subject.

As with the proprioceptive judgement task, a rest break of a few minutes occurred midway through testing, after which the limbs on the top and bottom surfaces were reversed. At the conclusion of testing, subjects were asked to state the compatibility rule they had been allocated, to ensure that they had attempted to act on this during the test session. All subjects correctly stated, in their own words, the compatibility rule that they had been given.

Data Reduction and Statistical Analysis

The two tasks were designed to yield data for the same set of crossed and uncrossed positions for the two tasks. To employ a standard measure, data from the proprioceptive judgement task were expressed as the percentage of trials that were correctly reported. Data from the compatibility task were expressed as the percentage of trials performed correctly given that subject's condition. This procedure ensured commensurability as it does not depend on limb position, condition, or on which side a stimulus was presented. For these data, a five-factor mixed-model analysis of variance (ANOVA) was used. The between-subjects factor was instruction (compatible or incompatible). Fully crossed within-subjects factors were task (proprioceptive judgement or compatibility), finger position (crossed or uncrossed), separation (1.2, 3.6, 6.0, or 10.8 cm), and vertical position (left hand above right, or right above left).

The reaction time data (compatibility task only) were analysed with a mixed-model four-factor ANOVA, identical to the one described previously, except that there was no task factor.

Results

Proprioceptive Judgement Task

Subjects tended to perceive the fingertips as less crossed than they actually were. The overall performance of subjects is shown in Figure 1a, in which the percentage of trials judged as uncrossed is plotted against the degree of actual separation in a continuum from uncrossed (widely separated) to crossed (widely separated). A typical ogival function can be seen, showing a high proportion of correct judgements at the extremes. The function is asymmetrical, however, and the actual point at which judgements were equally divided between crossed and uncrossed corresponded to about 3 cm crossed, indicative of the subjects' average perceptual bias. The data are shown separately for the two conditions in which the left or right hand was the limb on the top surface, but this vertical position factor was not significant, $F(1, 14) = 0.62, p > .4$, nor did it interact with task, $F(1, 14) = 0.47, p > .5$. Consequently, the remaining figures show data collapsed across the two levels of the vertical position factor.

Compatibility Task

The first variable considered is the frequency with which each limb was used. It should be noted, however, that although this variable is usually labelled "error rate", it is not an accurate term here. If subjects correctly perceive the relative position of the limbs and still use the wrong key, this constitutes a genuine error. If, however, their use of the wrong key is caused by a misperception of relative position, it is not an error of response selection. The 10.8 cm uncrossed position was correctly judged as uncrossed on 100% of trials in the preceding proprioception task, and in the compatibility task the error rates for this same position were 0% (for the compatible group) and 1.4% (for the incompatible group). This indicates that subjects properly understood and implemented the appropriate compatibility

instruction in a case where finger positions were unambiguous.

Figure 1b shows the percentage of trials on which subjects responded with the appropriate key for their compatibility condition. There was a clear tendency for subjects to behave as if the limbs were less crossed than they actually were. For example, perfect performance in the compatible condition would occur if, on 100% of trials in uncrossed positions, the limb anatomically ipsilateral to the stimulus were used. Similarly, this group should use the limb anatomically ipsilateral to the stimulus on none of the trials in crossed positions (i.e. the right limb, located to the left of the left hand, for a left-side stimulus). The idealized function for the incompatible group is the exact opposite.

The actual rate follows an ogival function rather than the idealized step change. More importantly, for the two crossed positions with the smallest separations, subjects in the compatible group responded with the finger anatomically ipsilateral and those in the incompatible group with the finger anatomically contralateral to the stimulus on the majority of trials. As before, the position at which subjects responded correctly 50% of the time serves as a measure of bias. This is approximately 6 cm crossed, double that manifest in the proprioceptive judgement task. This comparison is clearly seen in Figure 2a (in which results for the compatible and incompatible groups are combined).

The tendency to behave as if the limbs were less crossed than in fact they were was therefore evident in both tasks, but it was more marked in the compatibility task, as shown in the main effect of task, $F(1, 14) = 19.6, p < .001$. The interaction of task and hand position, $F(1, 14) = 27.1, p < .0005$, shows that the "error rates" were not much different between the tasks for uncrossed positions (performance being near perfect), but were much higher for the compatibility task than during proprioceptive judgements when the fingers were crossed. For this measure, there was neither a main effect of compatibility, nor did it feature in any significant interactions. For control purposes, subjects were tested with the right hand above the left and with the left above the right. This vertical position factor did not influence the results, alone or in combination with other variables. The degree of separation had a larger effect on finger selection when the fingers were crossed than when they were uncrossed, $F(3, 42) = 42.2, p < .000001$. This emphasizes what is apparent in Figure 2a—namely, that performance in both tasks was closer to that of an ideal performer in the uncrossed positions, changing only slightly with the degree of finger separation, but that it varied greatly with separation when crossed. At the extreme crossed position (10.8 cm apart), the appropriate limb was identified with high probability in both tasks.

Reaction Time. Group mean reaction times are shown in Figure 2b. There was a main effect of compatibility, $F(1, 14) = 4.6, p < .05$, compatible RTs averaging 343 msec and incompatible times 367 msec. The difference varied with the distance between the fingers. Most notably, the benefit of compatibility was clearly evident at extreme separations, was less at smaller separations, and was absent altogether at the 6-cm crossed position.

Specifically, pairwise comparisons (Fisher's Least Significant Difference Test) between corresponding compatible and incompatible RTs at each finger position/separation combination showed significant differences at the two most widely separated uncrossed positions, $p < .05$, and at the most widely separated crossed position. The size of the compatibility advantage (incompatible minus compatible) was greater for these cases than for the overall average (40, 35, and 47 msec, respectively, vs. 24 msec).

Figure 2b shows that, in general, RTs for the crossed positions were longer by an average of 24 msec than those for their uncrossed equivalents, confirmed by the main effect of hand position, $F(1, 14) = 29.1, p < .0001$. Again, the effect is most noticeable for the extreme separations, for which the difference is 55 msec.

In summary, these results show the compatibility effect to be reliable only when the fingers were widely separated. The effect is absent at the 6-cm crossed position—the location at which subjects used left and right fingers with almost equal probability—but not at the position that was most proprioceptively ambiguous.

Discussion

Effects of Varying Finger Separation

These results show that SRC effects are modulated by the clarity with which combined proprioceptive inputs from the two limbs signal the relative position of the fingertips. It is also apparent that the pure position-related proprioceptive cues arising separately from each limb can produce the crossed hands effect. At the extreme crossed and uncrossed positions, the findings of previous authors are replicated (Aglioti, Tassinari, & Berlucchi, 1996; Anzola et al., 1977; Brebner et al., 1972; Klapp et al., 1979; Proctor & Dutta, 1993;

Wallace, 1971, 1972). Not only does compatibility confer an advantage, but the overall times are longer in the extreme (10.8 cm) crossed position than in its uncrossed counterpart. This has been attributed to coding of the anatomical location, as well as the relative position of the limb, leading to increased times when these are in conflict (Nicoletti, Umiltà, & Ladavas, 1984; Umiltà & Nicoletti, 1990). Here we can see that this phenomenon is actually part of a continuum of effects that vary with the ambiguity or otherwise of the combined proprioceptive inputs.

We also observed a sizeable performance bias. First, even on straightforward psychophysical testing, subjects tended to perceive the fingers as less crossed than they actually were. The cause of this bias is unknown. Subjects may unintentionally have used information not only from the positions of the index fingertips, but also from those of more proximal parts of the limb (i.e. the whole digit and possibly some part of the hand). The latter were uncrossed in some situations where the fingertips were crossed. On the other hand, Riggio, Gawryszewski, and Umiltà (1986) showed that subjects were clearly capable of using information about the distal part of the extremity, even when this was a stick extending beyond the hand position. Whatever its cause, the size of this bias doubled in the SRC task. In consequence, subjects typically responded with the "wrong" finger on a majority of trials when the fingers were crossed and less than 6-cm apart, whatever their instruction set. This is despite having performed more accurately at these positions during proprioceptive judgements—especially in the 3.6 cm condition. We believe that this significant shift reveals the manner in which proprioceptive inputs are incorporated into response selection, and we outline this later, after first addressing alternative explanations.

Although it is theoretically possible that subjects perceived the relative positions differently in the two tasks, this seems highly improbable given that the positions were the same. The possibility exists, of course, that the additional shift is the consequence of a deliberate strategy. The subject might apply the rule "when in doubt, use the limb on the same (anatomical) side as the stimulus". Such a strategy, however, would not give rise to the results actually observed. Specifically, it predicts that the frequency of use of the same side limb, anatomically, would peak at the position closest to that of greatest proprioceptive ambiguity (3.6 cm crossed), and not at 6 cm crossed as it does. In fact, at 6 cm crossed, subjects made correct proprioceptive judgements nearly 70% of the time. Second, any deliberate strategy would invoke a substantial time cost, which should be maximal at the point of greatest proprioceptive ambiguity. The RT data actually show a peak for compatible conditions at 6 cm crossed and for incompatible conditions at 10.8 cm crossed.

Neither result is consistent with a deliberate strategy explanation. As Figure 1a shows, subjects judged this position correctly almost 100% of the time in the proprioception task and thus cannot be said to be in doubt concerning the relative positions of the fingers in the compatibility task. The difference in performance between the two tasks for this position is evident in Figure 2a. The persistence with which the anatomically same-side limb is favoured even for an obviously crossed position is inconsistent with a deliberate strategy hypothesis.

Automatic Activation

We suggest that the current results support the notion that response selection in SRC tasks includes some automatic activation of circuits associated with the limb that is on the same anatomical side as the relative position of the stimulus. Later, we explain how this obligatory process can introduce the additional bias in the compatibility task, compared to

proprioceptive judgements. Crucially, we see automatic activation as occurring without any reference to the relative position of the limbs or to the compatibility rule in effect for that trial. This concept of automatic activation has been outlined by Kornblum, Hasbroucq, and Osman (1990), who in turn make use of Posner's (1978) criteria of automatic processes as those that "may occur without intention, without giving rise to conscious awareness, and without producing interference" (p. 91). This hypothesized process is also quite similar to that proposed by Hommel (1993a) for non-goal-related stimulus properties in the Simon effect. Indeed, there is much accumulated evidence for some form of automatic activation (Proctor, Lu, Wang, & Dutta, 1995).

Rule-based Activation

We hypothesize a second type of activation that must incorporate three elements: (a) visual information about relative stimulus position, (b) proprioceptive information about relative limb positions, and (c) the prevailing compatibility rule, and we will refer to this as a rule-based activation. These three elements must be combined neurally. We favour a model in which the proprioceptive information arising from each limb is combined to produce a signal that is related to the relative position of the limbs and whose strength is related to the degree of separation. The compatibility rule is invoked only as a final "check", with the response that is activated being switched (thus costing time and increasing errors) if an incompatible rule is to be applied. However, these signals are actually combined, all three are logically required if the task is to be carried out correctly.

Combining Automatic and Rule-based Activation

Certain aspects of our results can be explained by a response selection mechanism in which these two forms of activation are summated. Consider, for example, four different trials for a subject in a compatible condition responding to a right-side stimulus. In the first, the subject's left and right index fingers are 10 cm uncrossed, so a right index finger movement is the correct choice. Both forms of activation are congruent, leading to a low probability of error and a short reaction time. On a second trial, the limbs are 10 cm crossed, so the anatomically left limb should be used, and it is, indeed, selected. However, as rule-based activation and the automatic activation are now at odds, the probability of an error is higher and the RT longer than for a corresponding uncrossed position. These two positions resemble conditions used in most previous experiments (Aglioti et al., 1996; Anzola et al., 1977; Brebner et al., 1972; Klapp et al., 1979; Proctor & Dutta, 1993). On a third trial, however, the limbs are crossed by 3 cm. Our psychophysical data suggest that the average subject perceives them to be perfectly aligned vertically, so that neither limb is preferentially selected by rule-based activation. The automatic activation, however, favours the anatomically right-side limb, which is then chosen, but with a reduced probability and a longer reaction time. Finally, on a fourth trial, the limbs are 6 cm crossed. In this position our results suggest that proprioceptive inputs indicate quite strongly that the limbs are crossed. In consequence, rule-based activation would lead to the use of the anatomically left-side limb (located on the right). However, the automatic activation of the right-side limb competes with this, and the two limbs are chosen with almost equal frequency. RTs are at their maximum and the compatibility effect disappears.

This analysis, if correct, sheds light on the proposal that spatial coding (relative position coding) is hierarchically higher than spatio-anatomical coding (Ehrenstein, Schroeder-Heister, & Heister, 1989; Heister, Ehrenstein, & Schroeder-Heister, 1986; Heister, et al., 1990). We see spatio-anatomical coding, which we call automatic activation, as being continuously present but summated with spatial coding. Thus it will only dominate when it is stronger than the activation resulting from (visual) stimulus position and (proprioceptive) relative position inputs—that is, spatial coding.

The fact that this automatic activation favours the limb on the same anatomical side as the stimulus could have a relatively simple neural processing basis. For the simple case in which subjects look straight ahead and stimuli are presented to the left or right of midline, a left-side stimulus would fall on the nasal and temporal retinal hemifields of the left and right eyes, respectively. It would receive visual processing mostly in right occipital cortex, which in turn projects to right-side areas of frontal and parietal cortex involved in movement selection and execution. We note that compatibility effects still occur for stimuli

in different parts of the same visual hemifield, suggesting that the neural processing is actually more complex and that spatial distinctions may still arise from within the visual cortex of one hemisphere. There is some evidence that the stimulus-response compatibility rule is put into effect by neurones in the primary motor cortex (Requin & Riehle, 1995), with the cingulate gyrus (Taylor, Kornblum, Minoshima, Oliver, & Koeppel, 1994) and dorsal premotor cortex (Crammond & Kalaska, 1994) also implicated. In addition, Iacobini, Woods, and Mazziotta (1996) report increased regional blood flow in parts of the superior parietal cortex for an incompatible mapping in a two-choice task resembling the current one, relative to a compatible mapping. It is quite plausible that a fairly constant bias towards the same-side limb could emerge from lateralized visual cortical inputs to these regions. The current observations also fit well with the results of Eimer (1995), who has demonstrated that lateralized readiness potentials (LRPs) appear within about 200 msec of a lateralized visual stimulus onset, even though the position of this cue is irrelevant, and with those of Stauder, Hassainia, and Precourt (1996) who found LRP peaks to be unaffected by a decision rule used to choose the responding hand. Eimer, Hommel, and Prinz (1995) further suggest that automatic activation produced by irrelevant spatial information is relatively short-lived and independent of any activation related to the relevant aspect of the stimulus. Furthermore, in a conventional crossed/uncrossed spatial SRC task, Aglioti et al. (1996) have adduced evidence that the normal operation of the corpus callosum attenuates the automatic activation of the same-side limb. Specifically, they report that two patients with complete callosal defects exhibited not only the normal effects of spatial compatibility and crossed hands, but also a strong RT advantage for the hand anatomically ipsilateral to the stimulus, unlike controls.

Finally, these results hint at a trade-off between proprioceptive signal clarity and speed of responding. RTs are highest when sensory ambiguity is high—though shifted by the proposed automatic activation. In a manner reminiscent of signal detection theory (Green & Swets, 1966) we envisage that response selection will be curtailed rapidly when proprioceptively mediated relative position is obvious, but sampling of these inputs will last longer as ambiguity increases. We further note that, as the "switching" entailed in the crossed hands effect can evidently arise from comparison of the separate proprioceptive inputs from each limb, any factors influencing even one limb's perceived position may alter both the probability of choosing a given limb in such SRC tasks, and the time course of response selection.

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FIG. 1. A: Percentage of trials judged as uncrossed at each separation, during psychophysical testing. Data are shown separately for the left hand above the right, and the right hand above the left. B: Probability of using finger anatomically ipsilateral to stimulus for compatible and incompatible groups in the SRC task.

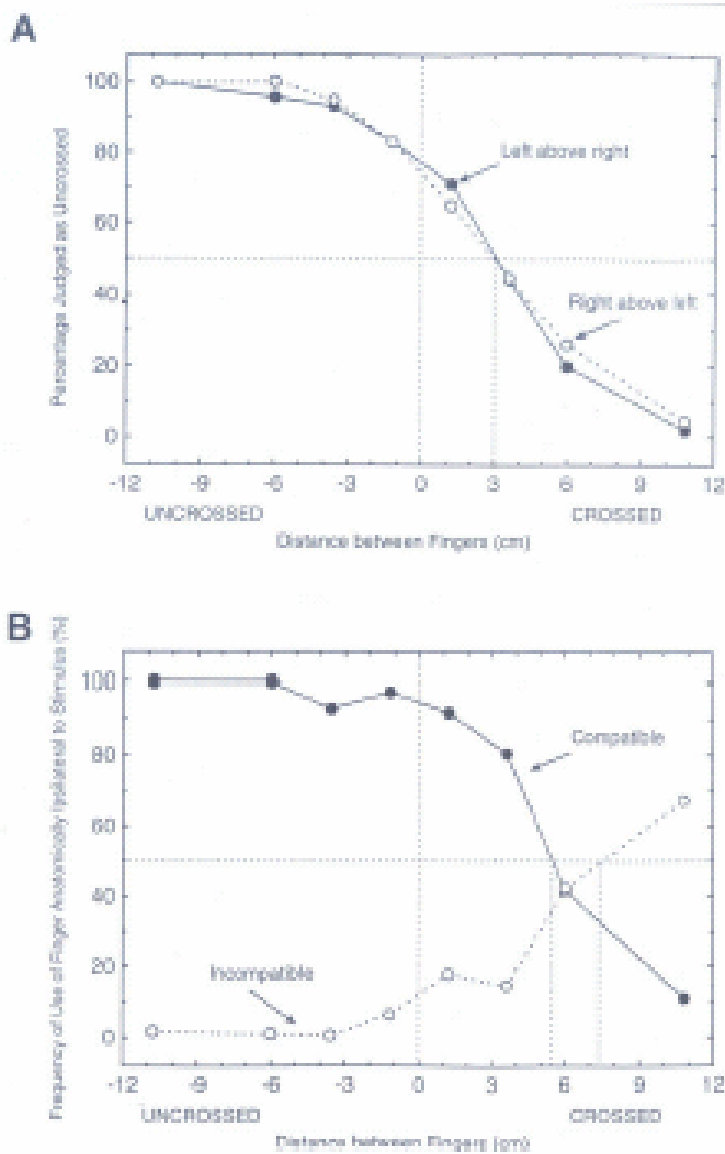
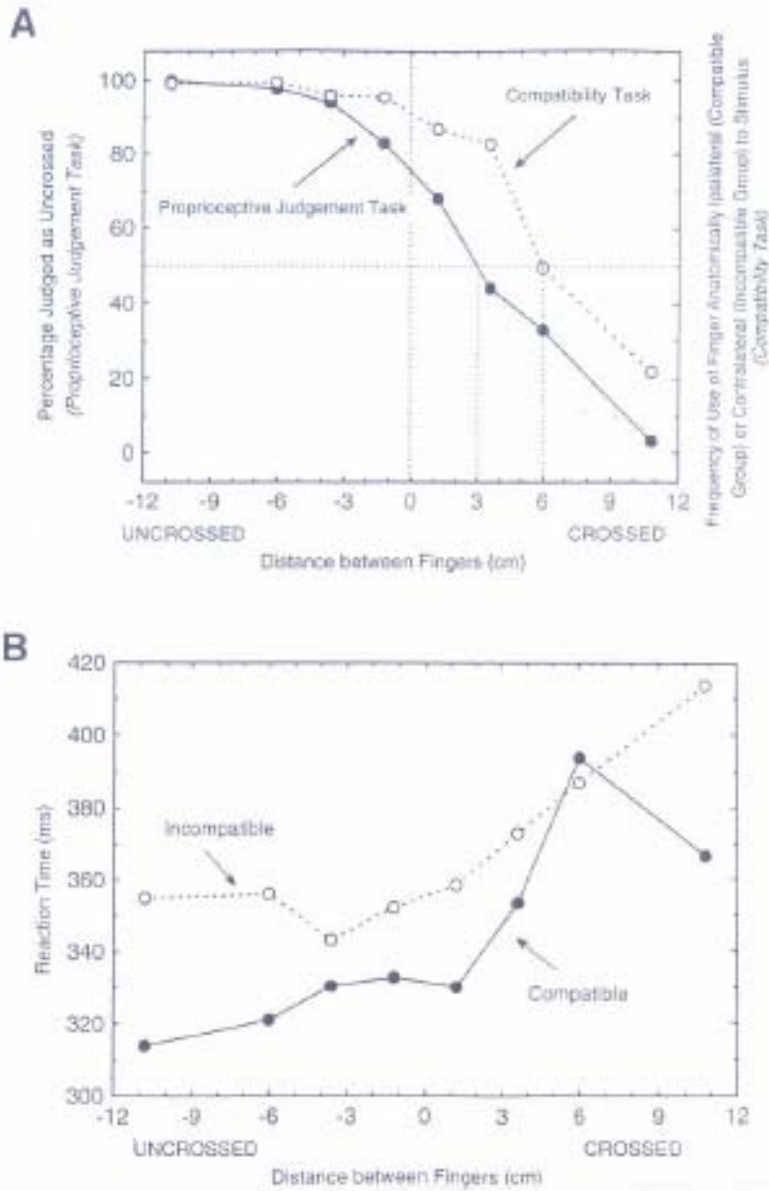


FIG. 2. A: Percentage of trials judged as uncrossed for psychophysical test and for the SRC reaction time task. Data are averaged over compatible and incompatible groups. B: Reaction times in SRC task for compatible and incompatible groups.



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