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Report

Others' Actions Reduce Crossmodal Integration in Peripersonal Space

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Summary

Specific mechanisms integrate visual-tactile information close to the body to guide voluntary action [1, 2] and to enable rapid self-defense in peripersonal space [3–5]. In social interactions, others frequently act in one's peripersonal space, thereby changing the relevance of near-body events for one's own actions. Such changes of stimulus relevance may thus affect visual-tactile integration. Here we show that crossmodal processing in peripersonal space is reduced for perceptual events that another person acts upon. Participants performed a visual-tactile interference task [6] in which spatially incongruent visual distractors in the peripersonal space are known to interfere with judging the location of a tactile stimulus [7–10]. Participants performed the task both alone and with a partner who responded to the visual distractors. Performing the task together reduced the crossmodal interference effect on tactile judgments, but only if the partner occupied the participant's peripersonal space (experiment 1) and if she responded to all, rather than only a subset, of the visual distractors (experiment 2). These results show that others' actions can modulate multisensory integration in peripersonal space in a top-down fashion. Such modulations may serve to guide voluntary action and to allow others' actions in a space of self-defense.

Results and Discussion

Participants performed the crossmodal congruency (CC) task [6, 11], both alone and together with another person (their "partner"). In this task, participants hold a foam cube in each hand that houses a tactile stimulator on the top and on the bottom. Participants respond to the elevation (up or down) of tactile stimulation by operating a foot switch while visual distractors are presented synchronously at the same or opposite elevation as the tactile stimulus (see Figure 1A). Despite the instruction to ignore visual distractors, participants' responses are faster and more accurate when visual distractors occur at the same elevation as tactile stimulation (congruent trials) than when distractors occur at opposite elevations (incongruent trials).

The performance difference between incongruent and congruent trials is known as the crossmodal congruency effect (CCE). The CCE is larger when distractors occur near the tactile stimulus than when distractors occur further away, for example near the nonstimulated hand [7, 9, 10, 12, 13]. The CCE is also enhanced when distractors are presented near objects that the brain presumably integrates into the body schema, like rubber hands [6, 14] and tools [8, 15], and when distractors occur near the image of one's own back during a whole-body illusion [16]. The CCE is therefore considered a reliable measure of multisensory processing in the peripersonal space [11], i.e., the space close around one's body.

To investigate whether another person's actions modulate the extent to which crossmodal integration occurs, we had participants perform the CC task alone, as well as together with a partner who performed a complementary task (see Figure 1B, right). The partner faced the participant, holding the opposite side of the foam cubes (see Figure 1A, left). In the partner condition, participants performed exactly the same task as in the individual condition while the partner judged the elevation of visual distractors (experiment 1a, peripersonal, with task; see Figure 1C, left). Thus, the partner resided in the participant's peripersonal space and acted upon visual events that are automatically integrated with tactile events when the task is performed alone. Because the CCE is larger for same-side than opposite-side distractors [11, 17], we report only same-side trials (see Supplemental Data for opposite-side results). The CCE was significantly reduced when participants performed the task with a partner compared to when they performed the task alone (see Figures 2A and 2B; $t(12) = 2.43$, $p = 0.032$, in a two-sided paired sample t test).

To assess whether this social modulation of visuotactile integration requires the partner's presence within the participant's peripersonal space, we repeated the experiment with new participants. This time, the partner sat outside of the participant's peripersonal space, resting her hands on her lap (experiment 1b, extrapersonal, with task; Figure 1C, middle). As before, however, the partner responded to the elevation of the visual distractors. Here the CCE did not differ between the alone condition and the partner condition (see Figures 2A and 2B; $t(12) = -0.23$, $p = 0.83$). A further experiment tested whether the partner must perform a task on the visual distractors in peripersonal space in order for the social modulation of visuotactile integration to occur. Now the partner held the cubes together with the participant, but she did not respond to the visual distractors (experiment 1c, peripersonal, no task; Figure 1C, right). Again there was no significant change of the CCE in the partner condition compared to the alone condition (see Figures 2A and 2B and Table S1; $t(12) = -1.54$, $p = 0.15$).

An analysis of variance (ANOVA) over the three experiments with between-subjects factors partner condition (peripersonal with task versus extrapersonal with task versus peripersonal without task) and social context (alone versus with partner) showed no significant main effects but showed a significant interaction between the two factors ($F(2,36) = 4.12$, $p = 0.025$). This result demonstrates that social modulation of visuotactile integration occurs only if the partner performs a task in the participant's peripersonal space. Consistent with previous findings that the CCE results mainly from

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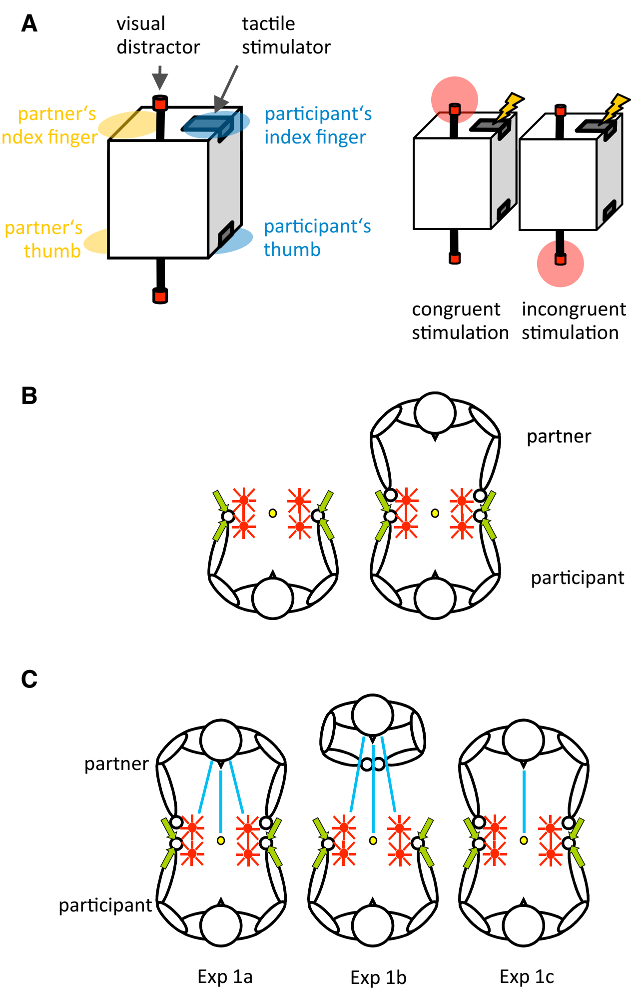

Figure 1. Task Setup and Design

(A) Stimulus devices (left) and stimulus arrangements (middle and right). Participants held two foam cubes, one in each hand, with the index finger and thumb (right). A tactile vibrator was located underneath each of these fingers. When the partner held the cubes together with the participant, their fingers did not touch (red ovals indicate participant's fingers, blue ovals indicate partner's fingers). LEDs were attached to the cube in close proximity to the tactile vibrators. In each trial, the tactile and the visual stimulus were either presented at the same relative elevation (middle) or at differing relative elevations (right). See Results and Discussion and Experimental Procedures for details.

(B) Illustration of the social manipulation of the experiment. All participants performed the task both alone and with a partner. Green arrows symbolize locations of tactile stimulation; red dots with rays symbolize visual distractors.

(C) Experimental conditions in the order described in the Results and Discussion. Blue lines symbolize the partner's task, with lines leading to the visual distractors indicating that the partner responded to these distractors; the rest is as in (B). In experiment 1, the partner was in the participant's peripersonal space and responded to the distractors. In experiment 2, the partner sat farther away (in extrapersonal space for the participant) and responded to the distractors. In experiment 3, the partner was again in the participant's peripersonal space but did not perform a task. See Results and Discussion and Experimental Procedures for details.

impaired performance in incongruent trials [7, 17], the social modulation of the CCE seen here was due mainly to an improvement in incongruent distractor trials (see Figure 2B, white bars), indicating that participants could ignore discordant stimuli better when their partner acted upon them.

Two further experiments tested whether crossmodal processing of visual events in peripersonal space depends on the partner's specific task rules for each stimulus. Alternatively, it may be crucial that the partner covers all visual events in a person's peripersonal space independently of the specific task rules. Experiment 2a was identical to experiment 1a (peripersonal, with task) except that the visual distractors had two different colors (red or blue in different trials). The partner responded to distractors of both colors. As in experiment 1a, the CCE was lower when the task was performed with a partner rather than individually ($t(10) = 2.30$, $p = 0.045$; see Figures 3A and 3B), and the reduction of the CCE occurred mainly in incongruent distractor trials (see Figure 3B, white bars). Thus, the social modulation of visuotactile integration generalizes to situations with variable visual distractors.

In experiment 2b, the partner responded only to visual distractors of one color and did not respond to distractors of the other color. An ANOVA with the within-subject factors social context (alone versus with partner) and stimulus relevance (stimuli relevant to the partner versus stimuli irrelevant to the partner) revealed no significant main effects or interaction (all $p > 0.52$; see Figures 3A and 3B). Thus, the social modulation of visuotactile integration occurred only when the partner responded to all visual distractors that occurred in the participant's peripersonal space. Accordingly, an ANOVA with the within-subject factor social context (alone versus with partner) and the between-subject factor experiment (2a versus 2b) revealed a significant interaction ($F(1,27) = 7.86$, $p = 0.009$).

The results of the present experiments demonstrate that the task a partner performs in a person's peripersonal space can affect visuotactile integration. In particular, crossmodal integration was reduced for visual events that the partner responded to. However, the assumption that partners represent each other's tasks [18] and actions [19] is not sufficient to explain the current findings [20]. First, the participant's performance was only affected when the partner performed her task in peripersonal space (experiments 1a versus 1b). Second, the social modulation of visuotactile integration did not occur when only a part of the visual events was covered by the partner's task rules (experiments 2a versus 2b). Rather, it was necessary that the participant knew that the partner's task covered all visual events that occurred in peripersonal space.

Several potential confounds can be ruled out. First, overlapping response mappings (participant and partner responded with the same button presses for up and down responses) cannot account for the social modulation of the CCE, because experiment 1b had overlapping response mappings and no social modulation was observed. Second, holding the foam cubes together cannot explain the social modulation of the CCE, because partners held the foam cubes together in experiments 1c and 2b and, again, no social modulation was observed. Although participants could hear neither stimulators nor response devices, synchronization of response timing between participant and partner may have contributed to the observed effects. However, there were no significant single trial correlations between partners' and participants' reaction times (RTs) in any of the four experiments requiring the partner to respond (all $p > 0.75$). Similarly, the difference in CCE between the alone and partner conditions did not correlate significantly with the difference in RT between participants and partners (all $p > 0.16$). Thus, response synchronization cannot explain the social modulation of the CCE.

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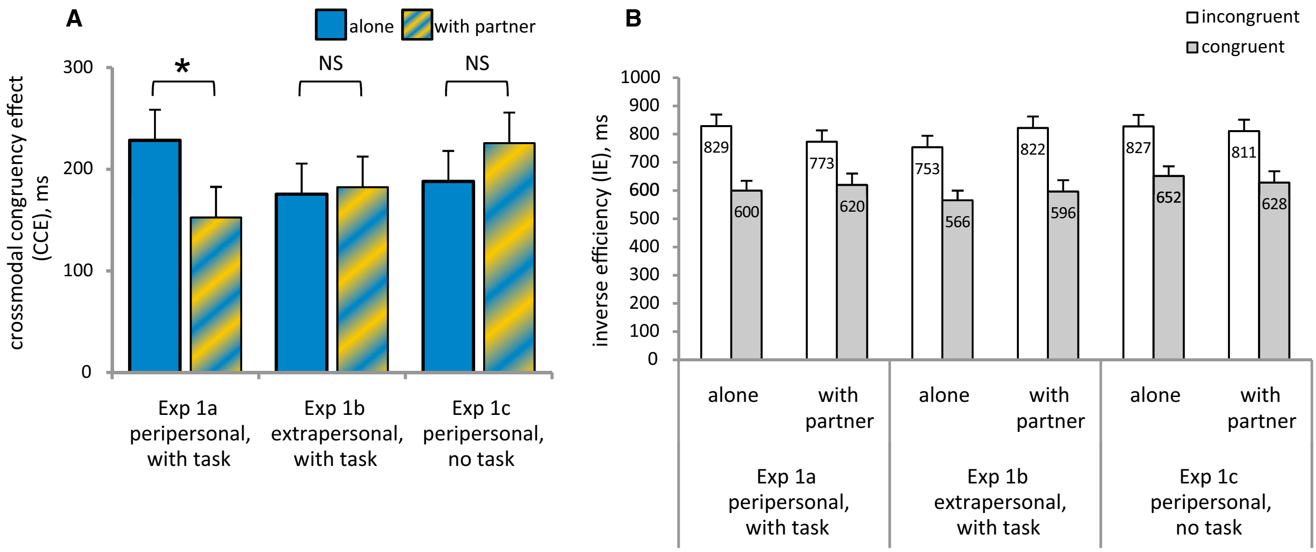

Figure 2. Results of Experiments 1a, 1b, and 1c

(A) Crossmodal interference, assessed by the crossmodal congruency effect (CCE), i.e., the difference between incongruent minus congruent conditions (see B). The dependent measure is the inverse efficiency (IE, reaction time/percentage of correct responses [10, 38]). Different participants took part in each experiment. The CCE was lower when a partner performed a task involving the visual distractors, but only when she resided in the peripersonal space of the participant. *$p < 0.05$. Error bars denote standard error of the mean.

(B) IE data of experiments 1a, 1b, and 1c, separately for incongruent and congruent conditions. Each bar in (A) results from subtracting gray bars from their neighboring white bars in (B). Note that changes in the CCE are due mainly to changes of performance in the incongruent trials.

It has been discussed whether the CCE observed in nonsocial setups results from response conflict or from the dominance of vision in multisensory integration [7, 17]. Although previous research suggests that representing a partner's task can induce response conflict [19], this assumption cannot explain the present findings. Representing the partner's response should have increased the conflict between vision and touch in incongruent trials. The CCE should therefore have been larger rather than smaller in the partner condition compared to the alone condition. The reduced CCE in the partner condition of experiments 1a and 2a can be better explained as a top-down modulation of multisensory integration, so that representing a partner's task changed the relative contributions of the visual and tactile modalities to tactile judgments. In particular, knowing that a partner acts upon visual events close to one's body reduced the influence of visual information. Such adjustments in weighing information from different modalities have been observed for different levels of attention [21–23] and for differences in reliability of sensory information [24, 25]. For nonsocial versions of the CC task, top-down influences have been demonstrated for different proportions of congruent and incongruent trials [26]. The finding that the CCE was only reduced when all visual events were relevant to the partner's task is in line with the interpretation of the social modulation of the CCE as a top-down influence on multisensory integration. It suggests that the weight for the visual modality is changed only when the partner's task is known to cover all visual events in one's peripersonal space.

The top-down modulation resulting from a partner's actions can be interpreted in two ways. On the one hand, the representation of peripersonal space has been suggested to serve as the body's safety zone [27]. The CCE is largest when visual distractors occur in the peripersonal space of the body [7, 10–12] or when they occur near a rubber hand [6] or body shadow [9]. Neuroimaging studies have revealed that frontal and parietal regions are involved in peripersonal, tactile-visual integration in humans [28, 29]. The CCE has, therefore, been linked to multisensory neurons in the premotor and parietal cortex of the macaque monkey [10, 26, 29]. These neurons integrate spatially coinciding signals from touch with visual events occurring close to the body [3–5, 30, 31] but do not respond to visual stimulation in extrapersonal space. Cell responses are highest when visual stimuli approach the tactile receptive field [5], and electrical stimulation of neurons in this circuit evokes defensive behaviors [32]. In our experiments, the partner's engagement with the visual distractors may have decreased their potential threat in peripersonal space, allowing a downregulation of the visual modality.

On the other hand, areas representing the peripersonal space may contribute also to goal-directed actions [1, 2]. Some visuotactile neurons respond during voluntary, goal-driven movements [33, 34]. In fact, the CCE is modulated by reaching [35] and grasping [2, 35] actions. Thus, when the partner in our experiments was engaged with the visual distractors, this may have rendered the visual stimuli less likely as action targets for the participant, leading to the reduction of interference observed in experiments 1a and 2a. Both interpretations remain speculative, because the current experiments were not designed to test these alternatives. Irrespective of these considerations, however, the present results highlight the close relationship between the spatial representation of the body [36], multisensory integration, and social interaction [37].

Experimental Procedures

Participants

Each participant took part in only one experiment. Thirty-nine participants were randomly assigned in equal proportions to experiments 1a, 1b, and 1c, respectively (11, 9, and 11 female; mean age 22.4, 25.3, and 24.7 years).

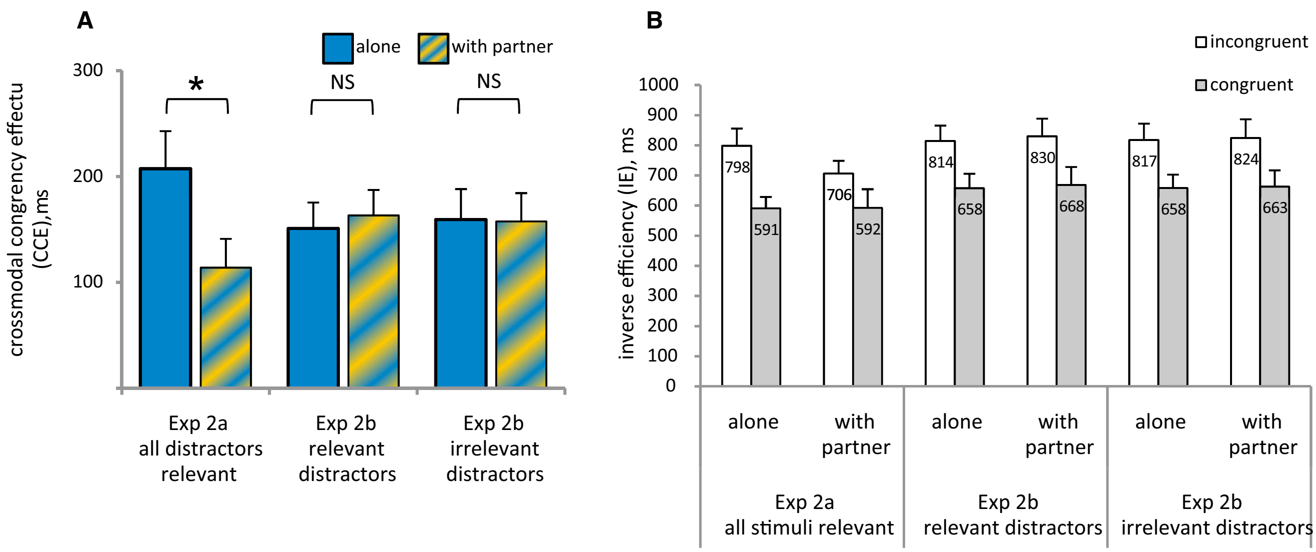

Figure 3. Results of Experiments 2a and 2b

(A) CCEs as IE values. The CCE was reduced, as in experiment 1a, when the partner covered all visual distractors. The CCE was not modulated when the partner only handled a subset of the stimuli (labeled as "relevant"), defined by the color of the distractor. *$p < 0.05$. Error bars denote standard error of the mean.

(B) IE data of experiments 2a and 2b, separately for incongruent and congruent conditions. As in experiment 1, modulation of the CCE is due predominately to a performance change in the incongruent condition of experiment 2a.

Eleven participants (8 female, aged 19–46, mean 27.5) took part in experiment 2a, and 18 participants (11 female, aged 19–40, mean age 26.7) took part in experiment 2b. Most participant-partner dyads were not acquainted. All participants were healthy and had normal or corrected-to-normal vision. Four participants were left-handed, and all others were right-handed. The experiment was conducted according to the guidelines of the Declaration of Helsinki (http://www.wma.net/en/30publications/10policies/b3/index.html, accessed on May 21, 2010).

Apparatus

Participants were seated facing each other. One participant's task involved judgments about tactile stimulation ("participant" hereafter), whereas the other participant's task involved judgments about visual stimulation ("partner"). A fixation LED was attached in eye height to both sides of a stick placed between the participants. The participant held a foam cube (6.0 × 5.0 × 4.5 cm) in each hand with her index finger and thumb. The minimum distance between the cubes was 30 cm. A tactile vibrator (Oticon bone conductor BC 461-0/12) was located directly underneath each finger. Multicolor LEDs were attached near each vibrator (direct distance 5 cm), visible to both participants. For tactile stimulation, tactile vibrators were driven with 167 Hz for three 50 ms bursts, separated by 50 ms each. Stimulus strength was adjusted to feel equal at all stimulation sites (see [10]). Visual stimulation consisted of three 50 ms flashes separated by 50 ms and always preceded tactile stimulation by 30 ms. This particular stimulus arrangement has been reported to maximize the crossmodal congruency effect [7].

Participant and partner responded using foot switches placed underneath the right foot, with one button under the toes and one under the heel. When participant and partner sat close together (to hold the foam cubes together), their feet were about 30 cm apart (person to person). When the partner sat far away, distance between the feet was about 1 m. To mask noise from stimulators and response pedals, participants wore earplugs and headphones emitting white noise. Although we were not interested in the partner's performance, partners wore ear plugs to create the impression (for both participant and partner) that their task was as important as the participants' task. Catch trials assured that participants did not close their eyes and encouraged fixation (about 5% of the overall number of trials, randomly distributed across the experiment; see Supplemental Experimental Procedures and [10]).

Design and Procedure

The standard experimental procedure for investigating the CCE (see e.g., [6, 10, 11]) was adapted to permit the interpersonal manipulations of the present experiment. In each trial, a tactile stimulus was presented at one of four locations. Participants indicated whether this stimulus had occurred up (at the index finger) or down (at the thumb), irrespective of the hand stimulated. Assignment of up and down judgments to toe and heel foot responses was counterbalanced across participants. A visual distractor was presented synchronously with the tactile stimulus on the same hand. This distractor could be congruent (e.g., visual and tactile up) or incongruent (e.g., visual down, tactile up). To allow comparison with earlier studies, the distractor occurred at the same or the opposite hand in experiments 1a and 1c (see Supplemental Data). Each combination of stimuli was equally likely and was repeated 28 times during the experiment. Trial duration varied randomly from 2500 to 2800 ms and was independent of participants' response speed.

All participants performed the experiment alone, as well as together with a partner. The order of alone and partner conditions was counterbalanced. When performing together, both participant and partner were informed about each other's task. The partner gave foot responses to the elevation of the distractors (except in experiment 1c). The up/down-to-toe/heel response assignment was always the same for participant and partner.

The variable of interest was the size of the CCE in the alone condition and the partner conditions. Reaction time and error scores were combined into one measure, inverse efficiency, by dividing reaction time by the percentage of correct trials per condition, controlling for possible speed accuracy trade-offs [10, 38]. In all experiments, performance in congruent trials was significantly better than performance in incongruent trials (all $p < 0.001$), confirming that the basic congruency manipulation was successful. The critical interactions of partner condition × social context are statistically equivalent whether congruent and incongruent conditions are analyzed as a factor or whether they are combined into one measure (see Supplemental Data for more detailed information).

Supplemental Information

Supplemental Information includes Supplemental Data, Supplemental Experimental Procedures, and three tables and can be found with this article online at doi:10.1016/j.cub.2010.05.068.

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Supplemental Data

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Supplemental Data

ANOVA Including Opposite-Hand Trials of Experiments 1a and 1c

Experiments 1a and 1c included opposite-hand distractors to verify that the CCE seen in our experiments behaved as in previous experiments, with a large CCE for same-hand distractors, but a small CCE for opposite-hand distractors. We present here the results for these additional conditions. Data of Experiment 1a are shown in Table S1. A 2x2 ANOVA with CCE (i.e., difference between incongruent minus congruent trials) as dependent measure and within-subject factors Social Context (alone vs. with partner) and Distractor Side (same vs. opposite hand as tactile stimulus) revealed a significant main effect of Social Context [$F(1,12) = 6.99$, $p = 0.021$] and of Distractor Side [$F(1,12) = 50.55$, $p < 0.001$]. The interaction was not significant [$F(1,12) = 3.50$, $p = 0.086$.

Data for Experiment 1c are shown in Table S2. The ANOVA with within-subject factors Social Context (alone vs. with partner) and Distractor Side (same vs. opposite hand) revealed a significant effect of Distractor Side [$F(1,12) = 54{,}61$, $p < 0.001$), but neither the main effect of Social Context [$F(1,12) = 2.49$, $p = 0.140$] nor its interaction with Social Context [$F(1,12) = 1.43$, $p = 0.254$] were significant.
Our analyses collapsed over incongruent and congruent trials, using their difference, the CCE, as dependent measures. ANOVA results for all other factors are unchanged by this simplification. For example, the three-way interaction of Social Context x Distractor Side x Congruency in an ANOVA including incongruent and congruent trials as a factor is identical to the two-way interaction of Social Context x Distractor Side when using the CCE (i.e., the difference computed from the Congruency factor) as dependent measure. Similarly, the interaction of Social Context x Congruency reduces to the main effect of Social Context. Including factor Congruency did not change any of our conclusions. In all experiments, Congruency was highly significant ($p < 0.001$) and (when opposite-hand trials were included) interacted with Distractor Side ($p < 0.001$).

Supplemental Experimental Procedures

Design and Performance of Secondary Task (Catch Trials)

Participants had to perform a secondary task (referred to as catch trials) to encourage central fixation. In catch trials, a green LED attached directly underneath the participants' fixation light was flashed three times, and no tactile stimulus occurred. Participants had to respond immediately to this visual stimulus (foot response, either heel or toes, balanced over participants and balanced with respect to the response assignment of the main task).

RT for this secondary task was comparable over Experiments (i.e., different groups of participants), and did not differ between alone and partner conditions. Table S3 lists RTs and the p-value obtained from repeated measurement t-tests (comparing alone vs. partner conditions) for each experiment. An ANOVA over all five experiments with within-subject factor Partner Condition (alone vs. with partner) and between-subjects factor Experiment revealed no significant main effects and interaction (all $p > .50$). RTs were in the range of the primary, tactile task. Because the inter-trial interval was randomized, participants could not respond in a timely manner based on detecting the omission of a tactile stimulus in the catch trials. Performance in the catch trials was close to perfect (means in all conditions > 99% correct) and was therefore not analyzed.

Table S1. Inverse Efficiency Values (Reaction Time/Percentage of Correct Responses) for All Conditions of Experiment 1a, Including Same versus Opposite-Hand Distractor Trials

			Mean	Standard Error
Alone	same hand	incongruent	829	32
		congruent	600	28
	opposite hand	incongruent	695	29
		congruent	667	30
With partner	same hand	incongruent	773	30
		congruent	620	44
	opposite hand	incongruent	683	35
		congruent	672	31

Table S2. Inverse Efficiency Values (Reaction Time / Percentage of Correct Responses) for All Conditions of Experiment 1c, Including Same versus Opposite-Hand Distractor Trials

			Mean	Standard Error
Alone	same hand	incongruent	753	42
		congruent	566	36
	opposite hand	incongruent	662	36
		congruent	607	42
With partner	same hand	incongruent	822	45
		congruent	596	46
	opposite hand	incongruent	692	38
		congruent	633	48

Table S3. Reaction Times and Standard Error of the Mean (in Brackets) in ms for the Secondary Task (Speeded Response to Flashing Light) for All 5 Experiments

Experiment	Alone	With Partner	t Test (p)
1a	764 (27)	796 (18)	0,235
1b	725 (27)	744 (35)	0,530
1c	791 (57)	785 (33)	0,902
2a	773 (30)	778 (31)	0,805
2b	769 (25)	762 (31)	0,801

The last column lists the p-value from the t-test comparing alone and partner conditions.