

Direct coupling of haptic signals between hands

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Edited by Randolph Blake, Vanderbilt University, Nashville, TN, and approved December 1, 2014 (received for review October 14, 2014)

Although motor actions can profoundly affect the perceptual interpretation of sensory inputs, it is not known whether the combination of sensory and movement signals occurs only for sensory surfaces undergoing movement or whether it is a more general phenomenon. In the haptic modality, the independent movement of multiple sensory surfaces poses a challenge to the nervous system when combining the tactile and kinesthetic signals into a coherent percept. When exploring a stationary object, the tactile and kinesthetic signals come from the same hand. Here we probe the internal structure of haptic combination by directing the two signal streams to separate hands: one hand moves but receives no tactile stimulation, while the other hand feels the consequences of the first hand's movement but remains still. We find that both discrete and continuous tactile and kinesthetic signals are combined as if they came from the same hand. This combination proceeds by direct coupling or transfer of the kinesthetic signal from the moving to the feeling hand, rather than assuming the displacement of a mediating object. The combination of signals is due to perception rather than inference, because a small temporal offset between the signals significantly degrades performance. These results suggest that the brain simplifies the complex coordinate transformation task of remapping sensory inputs to take into account the movements of multiple body parts in haptic perception, and they show that the effects of action are not limited to moving sensors.

touch | haptics | perception | sensorimotor integration | kinesthesia

Motor and kinesthetic signals arising from the movement of the eyes in the head, and translation of the eyes and ears in space due to head and body movements, have been shown to play an important role in visual (1–3) and auditory (4–6) perception. However, because of the small number of sensory surfaces in these modalities, and the rigid constraints on their movement, the number of kinesthetic degrees of freedom is limited. In active touch or the haptic modality (7–13), the large number of sensory surfaces, and the nearly unlimited ways these surfaces can move, lead to the question of how movement can be represented and associated with the cutaneous or tactile signals. To study how tactile and kinesthetic cues are combined to haptically perceive object shape and size, we created a novel haptic stimulus in which these cues were completely dissociated. This stimulus consisted of simulated triangles felt through a narrow slit, as in anarthoscopic perception in vision (14–16) or haptic perception (17), and as illustrated in Fig. 1.

The tactile signal consisted of a line that expanded or contracted on the index finger, delivered using a tactile display composed of pins that could vibrate independently, as shown in Fig. 1A. In one condition (SAME), the display was mounted on a slider that experimental participants slid along a track perpendicular to the tactile expansion or contraction, as shown in Fig. 1B. The slider's position was used to update the tactile display to simulate stationary triangles of various lengths, oriented toward or away from the participant, felt through a virtual slit that moved with the finger. Would participants perceive an extended triangular shape, rather than the proximal stimulus consisting of expansion or contraction, and if so, which orientation would they perceive? For example, a backward-pointing triangle could result from a tactile expansion coupled with a forward movement (as

shown in Fig. 1B, where forward motions and orientations—away from the participant—are shown as upward), or a contraction coupled with a backward movement—and vice versa for a forward-pointing triangle (Fig. 1E). Thus, the directions of the tactile stimulus and of the finger movement are insufficient by themselves to yield veridical perception of triangle orientation, and must be combined in an exclusive-or function (Fig. 1E) to yield veridical perception of object orientation. There are no purely tactile shape cues: the triangle's edges are not slanted in our tactile stimulus (in contrast to the edges of an actual triangle behind a slit). Therefore, from the functional point of view, the only way to obtain triangle orientation is for the nervous system to make use of the exclusive-or rule on some level. Below we will show that this rule is applied perceptually rather than through cognitive inference.

Crucially, we separated tactile and kinesthetic stimuli in the different (DIFF) condition. Participants moved the slider with one hand, and received the tactile stimulation through the stationary fingertip of the other hand (Fig. 1C). The position of the moving was measured and used to update the tactile display as in the SAME condition. Finally, in the immobile (IMMOB) condition, neither hand moved, and the durations of the tactile expansions and contractions were the same as in the other conditions (Fig. 1D). Thus, in both the DIFF and IMMOB conditions, we simulated a moving triangle felt through a stationary slit. In all conditions, participants reported both the perceived orientation and size of the triangle using a visual probe at the end of each trial. Participants closed their eyes during the movement and tactile stimulation, and therefore could not see the display during the crucial part of each trial. In the movement conditions (SAME and DIFF) the direction and speed of finger movement varied from trial to trial. Each of the three conditions was performed in separate blocks for different hands, with the blocks in random order.

Significance

When we actively explore objects by touch, the brain receives two types of signals, tactile sensory inputs and signals about the exploratory movement, which must be combined to perceive the shape and location of objects in space. Whereas these signals usually come from the same body part, we have developed a technique to separate them, directing the tactile signals to one hand and the movement signals to the other. We find that separated and synchronized signals are combined as if they arose from the same hand. Our results suggest that to solve the difficult problem of multidimensional signal combination in touch perception, the brain uses a simplified, source-independent representation of movement.

Author contributions: L.D., V.H., and M.W. designed research; V.H. and M.W. constructed the experimental apparatus; L.D. created the experimental software and performed research; L.D. and M.W. analyzed data; and L.D. and M.W. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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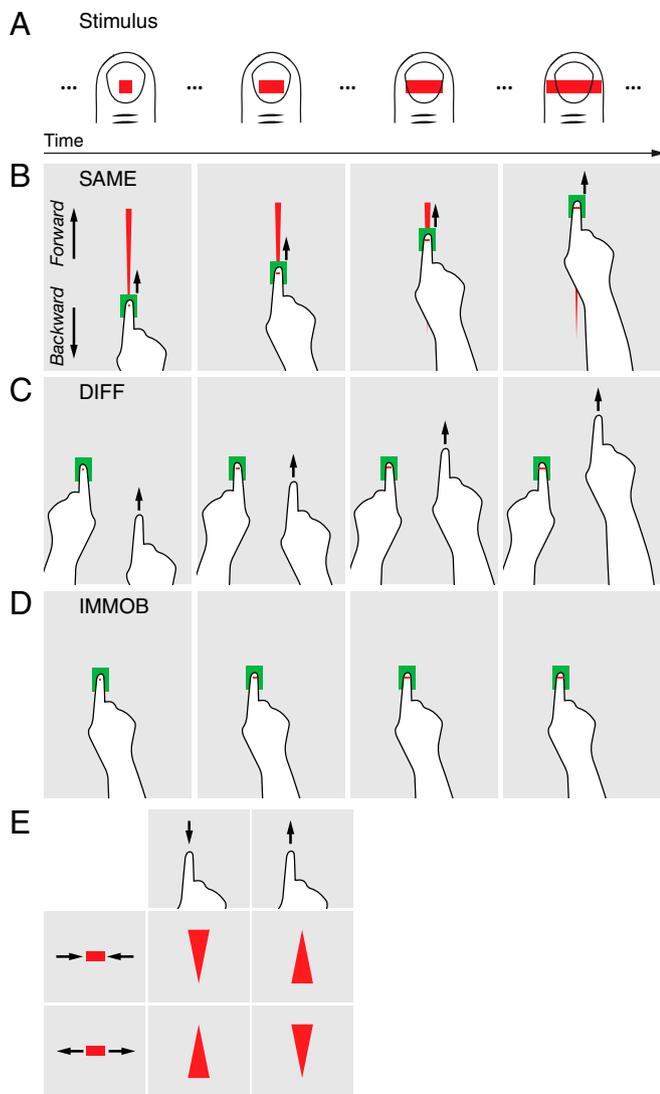


Fig. 1. Tactile stimuli and movement conditions. (A) An example of the tactile stimulus, here an expanding bar. The stimulus is shown as a series of “snapshots,” with the time running to the *Right*—the actual stimulus was continuous. The red rectangle represents the vibrating pins. (B) SAME condition: the same hand moves and experiences the tactile consequences of the movement. The hand moves the tactile display (green rectangle) mounted on the slider. In this example, a forward movement (away from the participant, upward in the figure) together with an expanding bar simulates a backward-pointing triangle (shown in red), felt through a slit. (C) DIFF condition: one hand moves, while the other hand, immobile, receives the tactile stimulus. The tactile signal (expanding bar) and kinesthetic signal (forward movement) are the same as in the previous example. Will the observer perceive simply an expanding bar or triangle in space? If a triangle is perceived, in which direction will it point? (D) IMMOB condition: the tactile signal is presented alone, with no movement. The expanding or contracting bar’s width as a function of time is a replay of a previous trial. (E) Correct spatial orientation of the triangle in the SAME condition, as a function of the movement direction (forward or backward) and the tactile stimulus (expansion or contraction). This truth table is an exclusive-or function, which has null correlations with its two input signals. Using either of the two signals alone will result in chance performance.

Results

In the SAME condition, participants’ perceptual processing had to integrate the direction of tactile motion (expansion or contraction) and finger movement (forward or backward) using the exclusive-or logical function: relying on either of the signals

alone would yield performance at chance level, or 50% correct. Mean performance on orientation discrimination in SAME condition was 85% correct (SD 13%), significantly above chance ($t_{26} = 6.16, P < 0.0001$; Fig. 2), and also above 50% in each individual participant. Thus, even in the absence of purely tactile shape cues, such as sloping edges that would indicate the orientation of the triangle, object orientation could be perceived by correctly integrating tactile and kinesthetic signals. Subjectively, most participants readily reported perceiving an extended triangle in space, rather than the proximal tactile stimulus.

In deriving the “correct” triangle orientation (Fig. 1E), we made the tacit assumption that the triangle is stationary in an observer-independent reference frame; a triangle moving faster than the finger in the same direction as the finger would have the opposite orientation. The fact that our participants largely reported this correct orientation implies that they also made the assumption of object stationarity, as has been found in active vision (18–20) (see ref. 3 for a review), and more indirectly in haptic perception (21).

When movement was separated from tactile sensation in the DIFF condition, we had three hypotheses concerning how these signals would be integrated. First, observers could feel the proximal tactile stimulus for what it was—an expanding or contracting line—rather than integrating it with the movement signal and experiencing a triangle, and performance on the orientation task would be at chance (the “no-transfer” hypothesis). Second, the motion of the moving hand would be directly transferred or coupled to the stationary, feeling hand, as if the two moved in exactly the same way (the “direct-transfer” hypothesis). Thus, for the case pictured in Fig. 1C, the direct-transfer hypothesis predicts the perception of a triangle with its apex pointing backward, as in Fig. 1B. Third, observers could respond as if the moving hand slid the triangle under the stationary feeling hand (the “indirect-transfer” hypothesis). For the case of Fig. 1C, the indirect-transfer hypothesis predicts that subjects will perceive a forward-pointing triangle; in general, the direct- and indirect-transfer hypotheses always predict opposite perceptions of triangle orientation.

We scored responses in the DIFF condition as correct if they were in agreement with the direct-transfer hypothesis, so that performance above chance would support the direct-transfer hypothesis, below chance, the indirect-transfer hypothesis, and chance performance, the no-transfer hypothesis. The results are shown in Fig. 2. Mean percentage correct was 83% (SD 12%), significantly above chance ($t_{26} = 7.26, P < 0.0001$), and above chance individually in every participant. These results exclude both the no-transfer and indirect-transfer hypotheses and strongly support the direct-transfer hypothesis. In fact, there was no significant difference between the rate of correct responses in the SAME condition and the rate of responses in DIFF, in agreement with the direct-transfer hypothesis ($t_{26} = 0.97, P = 0.34$), as well as a highly significant within-participant correlation between performance in the SAME and DIFF conditions (Pearson $R = 0.80, P < 0.0001$, bootstrap). We found a higher fraction of correct responses for larger objects (90% for size 16 cm, for example, across SAME and DIFF conditions) than for smaller objects (75% for size 4 cm), which participants reported as seeming very small (see below) and sometimes having a rather indistinct shape. An ANOVA revealed the size factor as being significant ($F_{1,26} = 59.6, P < 0.0001$) but there was no significant difference between SAME and DIFF conditions. In summary, when we separated the tactile sensation from the movements that usually accompany haptic perception, our participants perceived at least one aspect of object shape—orientation—as if the two signals came directly from the same hand.

Because participants also reported perceived object size, we could test how haptic object perception depends on continuous metric properties of movement such as spatial extent, and how this dependence survives the separation of signals in the DIFF condition. Size could be judged from the Euclidean distance

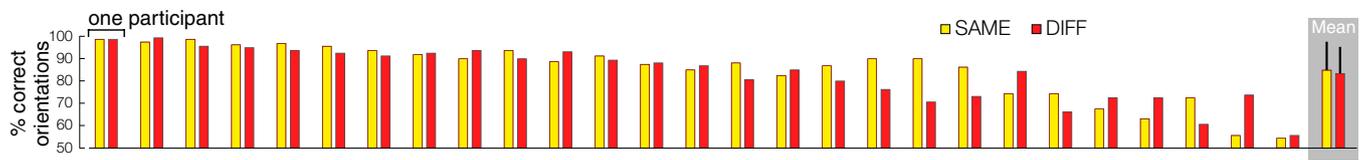


Fig. 2. Percentage of triangles perceived with the correct orientation. The correct orientation, in both the SAME and DIFF conditions, is defined by the truth table in Fig. 1E. Results are shown for individual experimental participants, with mean results shown on the *Right*. Error bars represent between-participant SDs.

between the spatial positions when touching the two extremities of the triangle. However, larger triangles may also be perceived as larger only because, on average, the stimulus had longer duration (22–26). We therefore analyzed reported sizes simultaneously as a function of simulated size and stimulus duration. In the DIFF condition the duration cues are available only to the feeling hand, whereas the distance cues are available only to the moving hand. Thus, the possible integration of distance cues in size judgments in the DIFF condition would be another strong sign of the combination of tactile and kinesthetic cues from disparate sources.

Reported size, as a simultaneous function of displayed size and contact duration, is shown in Fig. 3A and B for SAME and DIFF conditions. The same data are shown in Fig. 3C and D, as a function of displayed size and categorized by duration. In both conditions, perceived size seems to depend on the displayed size, which is not surprising, but also on duration: for a fixed displayed size, longer contact durations lead to larger perceived size. However, participants seem to have had a somewhat weaker dependence on size, and a stronger dependence on duration, in the DIFF than in the SAME condition. It should also be noted that size was quite severely underestimated: median ratio of reported to simulated size was 0.37 and 0.31 in SAME and DIFF conditions, respectively. This underestimation is reminiscent of the compression found in anorthoscopic perception in vision (14, 16, 27–29).

We performed a linear regression of reported size as a function of displayed size and stimulus duration. The model did not include an interaction term, because preliminary analyses revealed no significant interaction (as can be seen in Fig. 3C and D). All variables were standardized to zero mean and SD of one, and all regressions were performed separately for each participant in each condition. Fits were performed using the least trimmed squares method (30) with a 95% threshold. The resulting coefficients correspond to the weights of spatial and temporal information in the perception of object size, and are shown in Fig. 4. In both the SAME and DIFF conditions, size coefficients were significantly positive (SAME: mean 0.48, SD 0.17, $t_{26} = 15.1$, $P < 0.0001$; DIFF: mean 0.34, SD 0.15, $t_{26} = 11.6$, $P < 0.0001$). Duration coefficients were also significantly positive in both conditions (SAME: mean 0.35, SD 0.19, $t_{26} = 9.40$, $P < 0.0001$, DIFF: mean 0.46, SD 0.19, $t_{26} = 12.77$, $P < 0.0001$). Size coefficients were significantly higher in the SAME condition ($t_{26} = 5.03$, $P < 0.0001$), whereas duration coefficients were higher in DIFF condition ($t_{26} = 3.92$, $P < 0.001$). Both coefficients were correlated between the SAME and DIFF conditions within participants: for example, participants having a higher dependence on size in SAME also tended to have a higher dependence on size in DIFF (Pearson $R = 0.60$ for size and 0.66 for duration, both $P < 0.001$ by bootstrap).

These results quantitatively confirm the qualitative observations of Fig. 3, namely, that participants use both spatial and temporal information in judging size in both the SAME and DIFF conditions. The dependence on duration, with longer durations leading to longer perceived lengths, has been found in a number of previous studies (22–26). However, there is a somewhat greater weight put on spatial information in the SAME condition, and

greater weight on temporal information in the DIFF condition. Because in DIFF spatial information is available only to the moving hand and not to the feeling hand, the significant contribution of spatial information to size judgments demonstrates that metric as well as discrete information across separate hands can be coupled in haptic perception. The between-participant correlations of weights in the SAME and DIFF conditions show that haptic size judgments are quantitatively similar when signals are separated across the two hands as when they originate in the same hand. However, the significantly smaller weight of the spatial variable in DIFF (mean 0.34) compared with SAME (0.48) suggests that size estimates in the DIFF condition may actually depend on a weighted average of the kinesthetic variables arising from the two hands, with about 70% coming from the moving hand and 30% from the immobile hand that receives the tactile signal.

In the immobile condition, where there was no spatial information, perception of object size could only rely on duration. We performed a linear regression of the perceived size as a function of duration (Fig. 4B, light blue bars). The regression coefficient was significantly positive (mean 0.76, SD 0.15, $t_{26} = 26.5$, $P < 0.0001$), which indicates that sizes were not reported randomly, but rather strongly depended on duration, as if participants assumed motion with a fixed speed (31).

Studies of interlimb transfer of learning have reported asymmetries between the right and the left hand (32–34) and preferred versus nonpreferred hand (34–36). In SAME and DIFF conditions, we tested the preferred and nonpreferred hands in separate blocks to check if haptic cue integration depended on

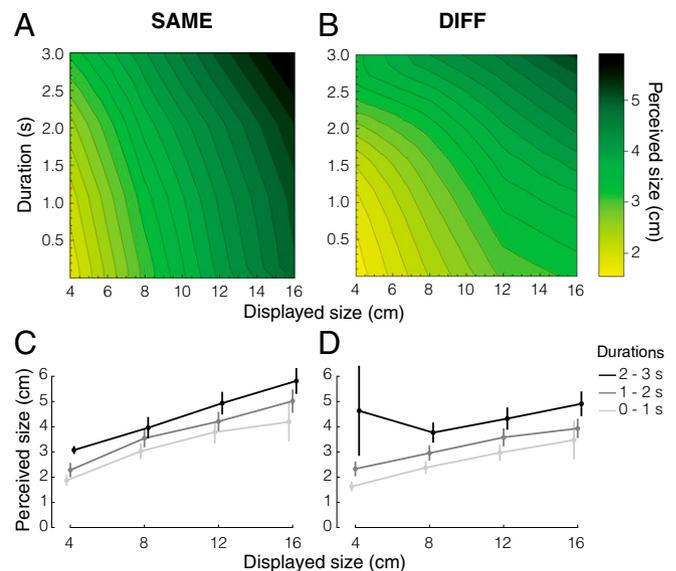


Fig. 3. Perceived object size as a function of displayed size and duration. (A) Reported triangle size, averaged over all participants, as a function of displayed size and contact duration, in the SAME condition. (B) Same thing, in the DIFF condition. (C) Same data as in A, shown as mean reported size as a function of displayed size and by categories of contact duration, in the SAME condition. (D) Same thing, in the DIFF condition.

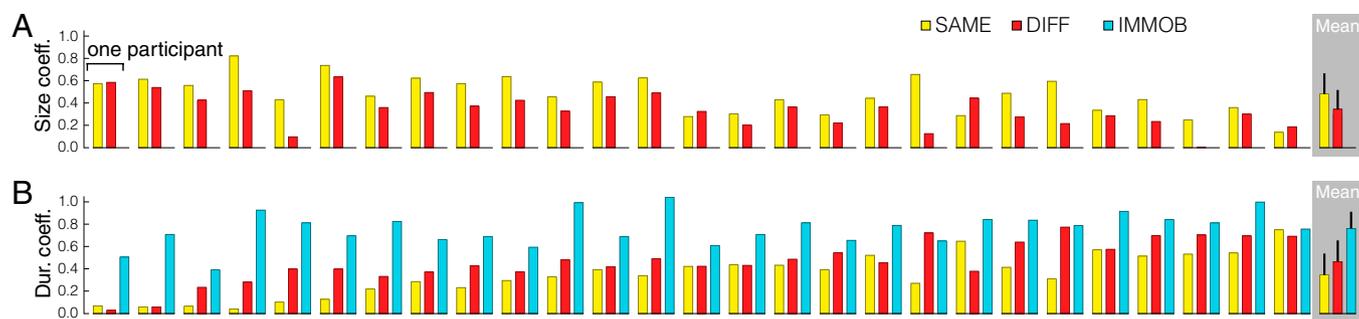


Fig. 4. Weights of displayed size and duration in the perception of object size. The weights were calculated as coefficients in the linear regression of perceived size versus displayed size and duration. Results are shown for individual experimental participants, with mean results shown on the *Right*. Error bars represent between-participant SDs. (A) Weights of displayed size in the SAME and DIFF conditions. (B) Weights of duration in the SAME, DIFF, and IMMOB conditions.

this factor. In the linear regression of reported size on spatial and temporal variables, the weight of the spatial factor in the SAME condition was higher when the preferred hand moved (0.53, SD 0.18) than when the nonpreferred hand moved (0.46, SD 0.18), and this difference was marginally significant ($t_{25} = 2.15, P < 0.05$). We found no significant effect of the preferred hand in the DIFF condition, nor any absolute advantage of either the right or left hand.

In the experiment that we have just reported, the instructions were to report the triangle orientation that was perceived. However, the response could instead have been consciously deduced from the combination of tactile stimulus and movement direction (Fig. 1E). Subjectively, the impression of triangle orientation and size clearly seem like perception rather than deduction to the authors. To objectively determine if the responses were perceived or deduced, we performed a supplementary experiment with 10 new participants. After an initial block in the SAME and DIFF conditions, we added an asynchronous condition, in which the same tactile stimulus was displayed, but after—rather than during—the movement, while the hand was immobile. The tactile stimulus began with a median delay of 676 ms following the end of the hand movement. The individual tactile and kinesthetic signals were the same in the synchronous and asynchronous conditions. Therefore, if participants deduce—rather than perceive—the triangle’s orientation, they should report the same orientation in the two conditions, because the small delay should not impede reasoning or working memory (37–39). If, on the other hand, participants report what they perceive, they should not be able to identify the correct orientation in the asynchronous condition, because the asynchrony exceeds the integration time of perception (40–42). In the synchronous condition, the mean rate of correct responses was 0.94 and significantly above chance (SD 0.07, $t_9 = 19.6, P < 0.0001$), whereas in the asynchronous condition, it was 0.56 and not significantly different from chance (SD 0.14, $t_9 = 1.42, P = 0.19$), with performance significantly different in the two conditions ($t_9 = 7.42, P < 0.0001$). Here, when we refer to correct responses, we mean those that follow the rule in Fig. 1E in the SAME condition, and the direct-transfer version of that rule in the DIFF condition. (We found very similar results in the SAME and DIFF conditions and no significant differences between them, so results are given across the two conditions.) Therefore, in the asynchronous condition, participants were unable to correctly report triangle orientation, neither through perception—as they were instructed—nor through deduction—if this was the strategy they used.

To ensure that this result was not due to any difficulty in deducing the triangle’s orientation with a temporal asynchrony between the movement and the stimulation, participants then repeated the above conditions, but with explicit instructions to

base their responses on the rule in Fig. 1E, which was carefully explained, rather than any perceptual impressions. In contrast to the perception condition above, we found high levels of performance in both the synchronous (mean rate of correct responses 0.97, SD 0.05) and asynchronous (0.87, SD 0.16) conditions. Performance in the asynchronous condition was significantly improved when participants were instructed to deduce than when they were instructed to perceive ($t_9 = 5.27, P < 0.001$).

Thus, we have shown that the introduction of a small asynchrony between the hand movement and tactile stimulus—which should impede perception, but not explicit reasoning or deduction—leads to a catastrophic drop in performance on the orientation task, with performance becoming indistinguishable from chance. Furthermore, participants are able to do the asynchronous task when instructed to explicitly use the combination rule. Therefore, we have shown that the drop in performance in the asynchronous condition is not due to any difficulty in explicitly deducing triangle orientation. Taken together, these results show that performance in the synchronous SAME and DIFF conditions is due to perception, rather than to explicit deduction and reasoning.

Discussion

In this study, we have separated tactile and kinesthetic signals, the two input channels underlying haptic perception, by splitting them between different hands. To accomplish this, we developed a technique, akin to anorthoscopic perception in vision, in which a simulated object—here a triangle—is felt through a virtual slit; this manipulation effectively decouples tactile and kinesthetic signals into two separate streams. When the two streams are applied to the same hand, the triangle’s orientation is generally perceived correctly, and its perceived size scales with both its simulated, veridical size and with the stimulus duration. When the tactile stream is applied to one hand and the kinesthetic to the other—when one hand feels while the other moves—the two streams are combined into the percept of a single object, as if they came from the same hand. Our paradigm allows us to distinguish between two types of combination: direct transfer, in which the movement signal from the moving hand is transferred directly to the stationary hand that receives the tactile stimulus, and indirect transfer, in which the moving hand is assumed to transport an object felt as the tactile stimulus by the stationary hand, as in a typical act of bimanual coordination. Our results strongly support direct-transfer and contradict the indirect-transfer hypothesis. Although no participant spontaneously reported feeling that his or her stationary hand moved, orientations were reported as if the stationary hand moved.

In addition to the combination of discrete signals (finger movement direction, tactile expansion or contraction, triangle orientation), we have also shown that continuous tactile and kinesthetic

signals combine across the two hands. By simultaneously varying speed and object size in our mobile conditions, we have shown here that the spatial information (available only to the moving hand) and the temporal information (available only to the feeling hand) are combined as if they originated from the same hand. We did find that the weight of the spatial variable was significantly smaller in the split-hand than in the same-hand condition. This difference implies that lengths or speeds may be estimated in the split-hand condition as a weighted average between the two hands, with about 70% of the contribution from the moving hand and 30% from the immobile hand receiving the tactile signal. In summary, we have shown that the observer's movement can affect the perceptual interpretation of sensory signals, even when the sensory surface is not the body part undergoing the movement.

An important question about these results is whether they are due to perception or to the experimental participants' explicitly deducing and consciously applying rules such as the one for orientation (Fig. 1E). We performed a second experiment in which we introduced an asynchronous version of the stimulus that would have impeded perception but not reasoning. We found near-chance performance in the asynchronous condition, but not when participants were instructed to explicitly apply the combination rule for triangle orientation—with no significant difference between same- and split-hand conditions. The results on size perception also support the idea that signal combination was perceptual rather than cognitive, because observers have little access to the metric details of their movement trajectories (43, 44). Taken together, we can conclude that the signal combination that we report here—both within the same hand, and across hands—is due to perceptual rather than cognitive processes.

Our results can be seen as a previously unidentified form of interlimb coordination. Previously, interlimb coordination has been studied from either the purely motor or purely perceptual point of view. On the motor coordination side, it has been shown that there is not only tight coupling between the movements of paired limbs (34–37), but also peripheral (38) and central (39) activation of the opposite limb. On the perceptual side, some studies have shown at least partial combination of signals across the two hands (45, 46), whereas others (47, 48) have found no evidence for optimal signal combination (46). Here we have demonstrated a truly sensorimotor form of interlimb coordination, in which motor or kinesthetic signals from one limb are combined with sensory signals from the other limb into one unified haptic percept.

When combining sensory tactile and movement-related kinesthetic signals, haptic perception faces a unique challenge: the potentially large number of degrees of freedom of the kinesthetic signal, due to multiple tactile sensory surfaces that can move independently. Given our results, we may speculate that haptic perception deals with this high dimensionality by collapsing multiple movements into one central representation. It may not matter that the kinesthetic signal arises from the “wrong” hand, because the haptic system may only be able to represent a single motion signal, regardless of its source. The mechanism for such simplification may arise from effector-independent representations of actions in the motor system, for which there is a large amount of neurophysiological evidence (49, 50). An analogous case is known in vision, where the deflection of one eye is combined with retinal data from the other eye in spatial localization (51). In haptic perception, a possibly related phenomenon is the recent observation that synchronized sensations at multiple fingers can be perceptually collapsed into the percept of a single object (52). The haptic interfaces in many sensory-substitution devices supply sensory feedback to a different part of the body from the one driving the camera and receiving kinesthetic signals, and therefore tacitly rely on movement signal transfer (53–56). Consequently, the signal transfer that we have documented in this study is of both fundamental and applied interest.

Methods

Apparatus. The tactile stimulus was produced using a Latero Tactile Display (Tactile Labs) (57). This display has an area of 1.2 cm² and consists of 8 × 8 pins that can be moved independently in one direction parallel to the surface, with a maximum amplitude of about 0.1 mm and bandwidth of about 100 Hz. Movement was monitored using a 23-cm-long low-friction linear slider. The slider was equipped with an optical coder connected to a dedicated electronic counter, which allowed us to retrieve the position of the platform with a precision of better than 0.1 mm and negligible latency.

Stimuli. In all conditions, the participant placed his or her left or right fingertip on the tactile display. In the SAME condition, the tactile display was mounted on the slider; the participant moved the display and received the tactile stimulus with the same hand. In the DIFF condition, the display was not mounted on the slider, but placed 30 cm to the left or right. The participant moved the slider with one hand, while receiving tactile stimulus in the other, stationary hand. In the IMMOB condition, the slider was not used; the subject received a tactile stimulus sequence that played back a trial in one of the other conditions.

The tactile stimulus was a bar consisting of two of the eight rows of the tactile display (therefore about 3 mm thick), that expanded from zero to full width (eight pins, about 0.95 cm wide), or contracted from full width to zero, in a direction perpendicular to the slider's rail. At each moment, the bar's width was defined by the active pins, which oscillated at 70 Hz. To avoid spatial aliasing, we gradually tapered the amplitude of the pins' oscillations at the edges of the bar. The expansion or contraction simulated an isosceles triangle whose axis lay parallel to the slider, by measuring the slider's position in real time and using it to calculate the real-time bar width, in an update loop executing at 500 Hz. The simulated triangles were 4, 8, 12, or 16 cm long, and their maximum width was equal to the display width, about 0.95 cm. The triangle was centered on the slider with a random jitter between –2 and +2 cm from trial to trial (to decrease the reliability of absolute hand position cues in triangle size judgments). Triangle sizes and expansion or contraction were chosen randomly and were independent of the direction of the participant's movement in the SAME and DIFF conditions. In the DIFF condition, the slider was used to measure the position of the moving hand; this position was used to update the tactile display in the same way as in the SAME condition. In the IMMOB condition, each trial's stimulus parameters (expansion or contraction of the tactile stimulus, duration of the stimulus, and time to stimulus onset) were randomly chosen from an already displayed trial in the SAME or DIFF condition.

Procedure. Participants sat facing the tactile display, the slider, and a keypad and a computer monitor that were used for entering responses. On each trial in the SAME or DIFF conditions, the participant performed a continuous forward or backward movement over the full length of the slider, with the eyes closed, with the instruction to keep movement speed as constant as possible. The direction of movement was alternated from one trial to the next. The tactile stimulus was displayed during part of this hand movement. When the movement was over, the participant opened his or her eyes and reported the size and the orientation of the perceived triangle by adjusting a triangle displayed on the monitor using two keys of the keypad. After the response was submitted, the participant was automatically instructed to move faster or slower on the next trial, with the goal of sampling in the range of 4–10 cm/s.

The experiment was composed of six blocks (the SAME, DIFF, and IMMOB conditions, each performed with the right hand receiving the tactile stimulus and with left hand), repeated two times. Block order was random. Each block was composed of 40 trials. The overall number of trials was 480.

To familiarize participants with the tactile stimulation, there was a training phase with the same stimuli and task as in the main experiment, in which participants performed five trials in each of the three conditions, each performed once with each of the hands. These six training blocks were presented in random order, but the IMMOB condition was never presented.

The entire experiment lasted ~2 h.

Participants. Twenty-seven volunteers (mean age 24) participated in the experiment and were compensated 10 € per hour. Of these, 11 were males, 15 were right handed, 11 left handed, and one ambidextrous following the Edinburgh Handedness Inventory (58). Twenty were naïve and the rest were experienced psychological observers, but naïve concerning the hypotheses of the study.

Supplementary Experiment. The experiment, in which participants reported only triangle orientation and not size, was divided in two halves. In the first, participants were instructed to report the orientations they perceived. In the second half, they were instructed to deduce the orientation, strictly following the rule illustrated in the table in Fig. 1E. Before the start of the second half, all four cases of the table were explained to participants until they felt comfortable with the rule. Each half consisted of four blocks of 40 trials. The first pair of blocks in each half were similar to the main experiment: the tactile stimulus was displayed during the movement (synchronous condition). In the second pair of blocks, the stimulus was displayed after the end of the movement (asynchronous condition): as soon as the hand stopped moving, we virtually replayed the hand's movement and stimulated the unmoving hand as for a normal, synchronous trial. Thus, the duration of the stimulus depended on the velocity of the preceding movement (as in the synchronous trials), as did the delay between the end of the movement and the tactile stimulus. In each pair of blocks, the first one was done with the left hand moving and receiving the tactile stimulus (SAME condition) and the second one with the right hand

moving and the left hand receiving the stimulus (DIFF condition). Because we did not measure perceived size or its dependence on movement speed or duration in this experiment, we used only two triangle sizes (8 cm and 16 cm) and did not give participants trial-by-trial instructions concerning movement speed; instead, participants were instructed to move slowly to maximize accuracy. At the start of the experiment, participants repeated the first block (SAME, synchronous, perception) until reaching 80% correct responses, to ensure that, if they did learn an explicit rule (which we showed was not the case), that the rule would be the correct one. Six of the 10 participants met this criterion on their first attempt and the remaining 4 on their second attempt. The experiment lasted approximately 2 h. Ten volunteers (mean age 25, four males) participated in the experiment.

ACKNOWLEDGMENTS. We thank Irene Fasiello for her participation in the preliminary stages of this research. This study was supported by the European Research Council (FP7) ERC Advanced Grant (PATCH) to V.H. and M.W. (no. 247300).

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