

Current Biology

A Rapid Tactile-Motor Reflex Automatically Guides Reaching toward Handheld Objects

Highlights

- Tactile inputs about changes in target location yield rapid movement corrections
- These corrections account for the direction and magnitude of target displacement
- Tactile-motor corrections are as rapid as visuomotor corrections
- The latency of tactile-motor corrections is insensitive to the number of targets

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In Brief

Pruszynski and colleagues document a tactile-motor reflex that rapidly and automatically corrects target-directed reaching movements after target displacements sensed by touch. This newly uncovered sensorimotor control mechanism may support dexterous object manipulation and tool use.



A Rapid Tactile-Motor Reflex Automatically Guides Reaching toward Handheld Objects

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SUMMARY

The ability to respond quickly and effectively when objects in the world suddenly change position is essential for skilled action, and previous work has documented how unexpected changes in the location of a visually presented target during reaching can elicit rapid reflexive (i.e., automatic) corrections of the hand's trajectory [1–12]. In object manipulation and tool use, the sense of touch can also provide information about changes in the location of reach targets. Consider the many tasks where we reach with one hand to part of an object grasped by the other hand: reaching to a berry while holding a branch, reaching for a cap while grasping a bottle, and reaching toward a dog's collar while holding the dog's leash. In such cases, changes in the position of the reach target, due to wind, slip, or an active agent, can be detected, in principle, through touch. Here, we show that when people reach with their right hand to a target attached to the far end of a rod contacted, at the near end, by their left hand, an unexpected change in target location caused by rod rotation rapidly evokes an effective reach correction. That is, spatial information about a change in target location provided by tactile inputs to one hand elicits a rapid correction of the other hand's trajectory. In addition to uncovering a tactile-motor reflex that can support manipulatory actions, our results demonstrate that automatic reach corrections to moving targets are not unique to visually registered changes in target location.

RESULTS

In our main experiment, participants ($n = 12$) reached with their right hand to contact (i.e., touch) a small ball attached to the far end of a 30 cm long rod oriented horizontally in the mid-sagittal plane (Figure 1; also see the [Supplemental Experimental Procedures](#)). When the hand moved 5 cm from the start position, located close to the body near the midline, the rod could some-

times unexpectedly rotate in the horizontal plane about its near end. The duration of the rotation was always 50 ms. In the visual condition, the participant could see the changes in target location and could make visually guided corrections during the reach to achieve the goal of contacting the target. In the touch condition, shutter glasses were used to occlude vision from the time at which the participant's right index finger contacted the start position until the displacement of their finger first exceeded 22.5 cm from the start target, which allowed participants to make terminal reach corrections based on vision (if needed). The participant lightly held the tip of their left thumb on an edge attached to the near end of the rod. Thus, in the touch condition, the orientation of the edge provided veridical information about the direction to the target relative to the tip of the left thumb. Because edge rotation deformed the skin but did not cause movement of the left thumb, correcting for a target displacement with the right hand required using tactile information from the left thumb about the orientation of the rod.

When the target did not move, which happened on half the trials, participants made smooth reaches toward the target in both the touch and vision conditions (Figures 2A, 2B, S1, S2A, and S2B, black traces). For these baseline trials, participants' mean reach time from leaving the start position to contacting the target was 340 ± 37 ms (mean \pm SD) for touch trials and 313 ± 34 ms for vision trials. When the target did unexpectedly move, which happened on the other half of the trials, participants made appropriate corrections and continued to make contact with the target, showing significant lateral deviations from their unperturbed trajectory in the direction of the new target location on 92% and 95% of touch and vision trials, respectively (Figures 2A, 2B, S1, S2A, and S2B, red and blue traces). Trials with inappropriate corrections, where participants either did not correct when the target moved or did so but in the wrong direction, were distributed throughout the experimental session, suggesting that such errors did not relate to learning and/or fatigue. In terms of total reach time, a two-way repeated-measures ANOVA revealed no effect of sensory condition ($F_{1,11} = 1.5$, $p = 0.16$) but a main effect of target displacement ($F_{4,44} = 7.5$, $p < 0.001$), which arose because reach times were slightly longer for larger and leftward target displacements (reach times, mean \pm SD: $-20^\circ = 425 \pm 138$ ms; $-10^\circ = 389 \pm 47$ ms; $+10^\circ = 328 \pm 45$ ms; $+20^\circ = 413 \pm 119$ ms).

Not only were the corrective responses in the appropriate direction, but the magnitude of these responses scaled to the

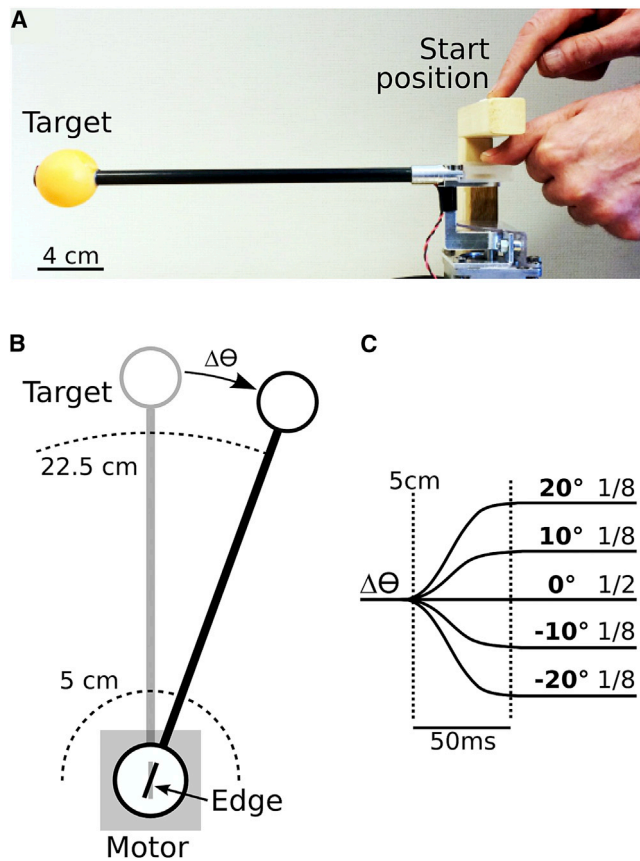


Figure 1. Apparatus and Experimental Methodology

(A) Side view of the apparatus. On perturbation trials, the object rotated (and thus the reach target moved) when the finger had moved 5 cm from the start position. On touch trials, vision was occluded until the finger had moved 22.5 cm from the start position.

(B) Schematic top view of the apparatus.

(C) On half of the trials, the object did not rotate. On the other half of the trials, the object moved over 50 ms with a sigmoidal trajectory to one of four possible target locations with equal probability.

size of the target displacement for both touch and vision trials (Figure 2C). We quantified this scaling by determining the lateral position of the hand 100 ms after the right fingertip reached 22.5 cm from the start position, and thus before visual information provided at the very end of the reach could contribute to corrections in touch trials. A two-way repeated-measures ANOVA revealed a main effect of target displacement ($F_{4,44} = 424$, $p < 0.001$) but no effect of sensory condition ($F_{1,11} = 0.005$, $p = 0.95$). However, an interaction between these two factors ($F_{4,44} = 33.5$, $p < 0.001$) revealed that the sensitivity of the adjustments was higher for vision trials than for touch trials (Figure 2C). Importantly, corrective responses triggered by either touch or vision were sensitive to the magnitude of target displacement as Bonferroni-corrected comparisons showed that corrective responses were greater for $\pm 20^\circ$ target displacements than for $\pm 10^\circ$ target displacements for both sensory conditions (touch: $F_{1,11} = 36.3$, $p < 0.001$; vision: $F_{1,11} = 314.0$, $p < 0.001$). (See Figure 5C in [10] for a previous demonstration of such scaling in vision.) A similar pattern of results was obtained

when considering only the first three trials performed under each experimental condition, suggesting that the presence of rapid corrective responses did not require extensive practice (main effect of target displacement: $F_{4,44} = 404$, $p < 0.001$; main effect of sensory condition: $F_{1,11} = 0.03$, $p = 0.8$; interaction between target displacement and sensory condition: $F_{4,44} = 35.8$, $p < 0.001$).

We further examined the robustness of the rapid corrective responses by performing a similar analysis for each participant individually using a two-way ANOVA. For all 12 participants the corrective responses were reliably ($p < 0.05$) scaled by the target displacement, and for eight participants there was a significant ($p < 0.05$) interaction between sensory condition and target displacement. For both touch trials and vision trials, eight participants showed significantly ($p < 0.05$) greater corrective responses for the larger target displacements.

Consistent with many previous studies, fast corrective responses to target movements were observed for vision trials [1–12]. Strikingly, we found that responses were similarly fast for touch trials. Inspection of the behavioral data revealed that the hand started to move toward the new target location approximately 110 ms after the onset of target movement (i.e., perturbation onset) in both sensory conditions (Figure 2B). Measured as changes in shoulder muscle activity (Figures 3A, 3B, S2B, and S2C), the median response onset latencies for individual muscle samples were 87 and 88 ms for visual and tactile trials, respectively (Figure 3C). A two-way repeated-measures ANOVA failed to reveal an effect of sensory condition ($F_{1,11} = 2.5$, $p = 0.15$) or magnitude ($\pm 10^\circ$ versus $\pm 20^\circ$) of target displacement ($F_{1,11} = 0.29$, $p = 0.60$) on the muscle onset latency. A similar factorial analysis revealed that the magnitude of muscle activity averaged between 75 and 100 ms post-perturbation varied with the target displacement ($F_{3,33} = 21.3$, $p < 0.01$; Figure 3D). In agreement with the kinematic data, a reliable interaction between sensory condition and target displacement ($F_{3,33} = 4.94$, $p < 0.01$) signified a greater sensitivity of the muscle responses to the magnitude of target displacement for vision trials than for touch trials (Figure 3D). A similar pattern of results was obtained when we analyzed the magnitude of muscle activity for each participant individually. A two-way ANOVA constructed for each participant revealed that all 12 participants showed a reliable ($p < 0.05$) main effect of target displacement, and ten showed a significant ($p < 0.05$) interaction between sensory condition and target displacement.

In an additional experiment, which our participants ($n = 12$) completed in the same session as the main experiment, we tested whether corrective responses are hastened if the target is always displaced to the same final position. With only one possible displacement, the nervous system could, at least in principle, prepare a response in advance of the perturbation and simply respond to the detection of a sensory event without first having to analyze the direction and magnitude of displacement associated with the event [13]. Alternatively, a similar response latency would indicate that a relatively direct sensorimotor mapping—implemented as part of the reach motor program—mediates the reflex responses, obviating the need of additional neural processing for flexibly adapting the responses to specific perturbation parameters [9, 14]. As in our main experiment, we presented participants with touch-only and vision-only

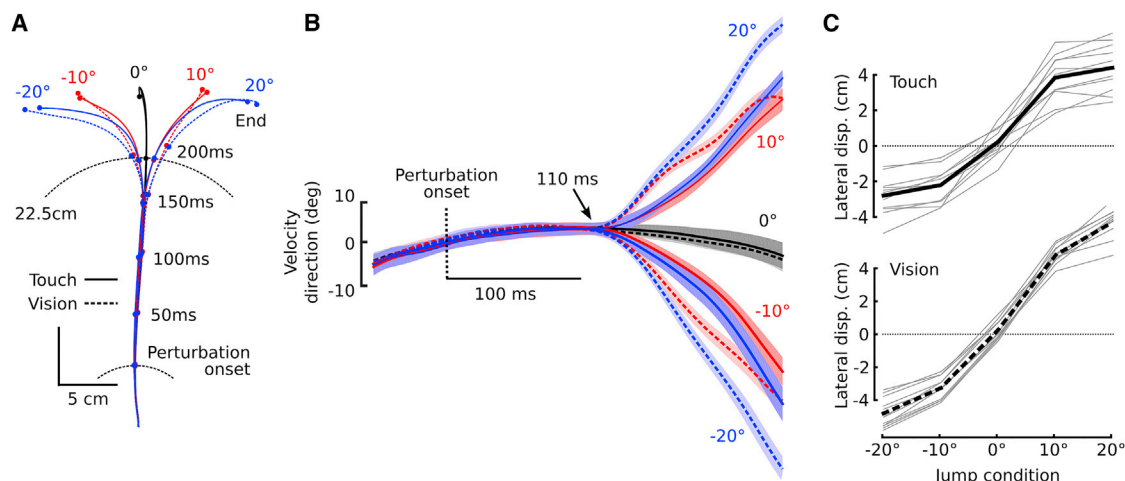


Figure 2. Behavioral Results

(A) Spatial hand position averaged across participants. Small dots on each trace provide timing information relative to the instant the finger moved 5 cm from start position, i.e., the point of onset of target movement on perturbation trials.

(B) Velocity vector direction averaged across participants. Data are aligned as in (A). Shaded areas represents ± 1 SEM.

(C) Lateral displacement of the finger 100 ms after it had moved 22.5 cm from the start position. Gray traces represent averages across trials within single participants. Black traces represent averages across participants.

See also Figures S1 and S2.

conditions but with only one target displacement of $+20^\circ$, which occurred on half of the trials. As observed in our main experiment, the participants made straight and accurate reaches during the unperturbed trials and very rapid corrections on perturbations tri-

als, for both the vision and touch conditions (Figures 4A, S3A, and S3B). Critically, paired *t* tests comparing the response latencies in our main experiment and the additional experiment failed to reveal an effect of the target displacement alternatives (four

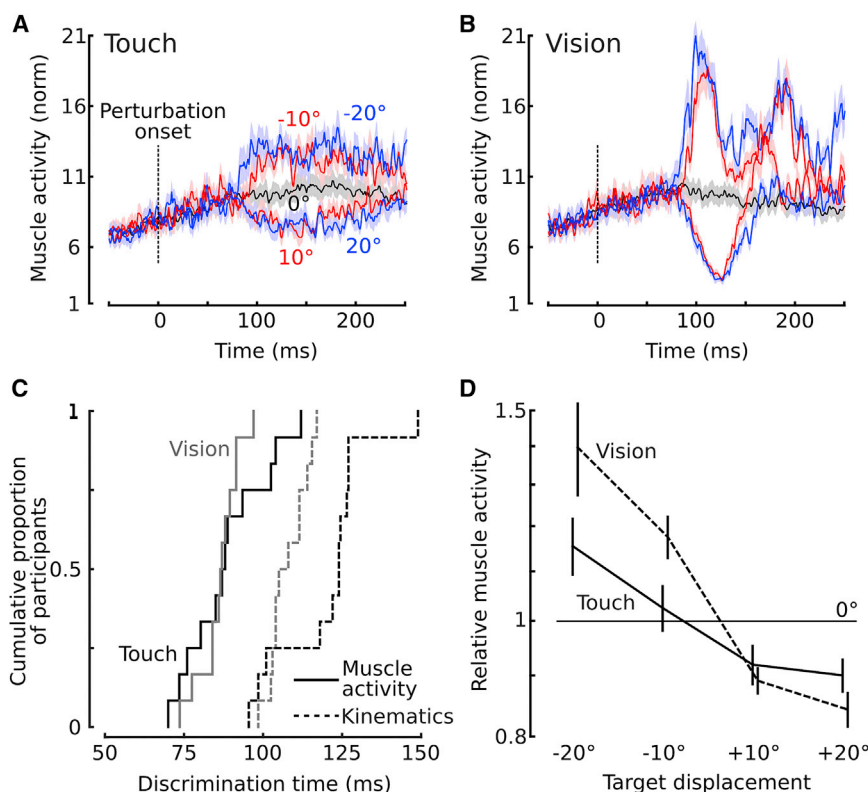


Figure 3. Muscle Activity.

(A) Pectoralis major muscle activity averaged across participants for touch trials. Data are aligned as in Figure 2A. Shaded areas represent ± 1 SEM.

(B) Same format as (A) but for vision trials.

(C) Time when muscle activity and kinematic responses began to diverge according to a time-series receiver operating characteristic (ROC) analysis for target displacements of equal magnitude but opposite direction (for details, see the Supplemental Experimental Procedures). Time is relative to perturbation onset for each individual muscle sample. Data are pooled from $\pm 10^\circ$ and $\pm 20^\circ$ conditions.

(D) Magnitude of muscle activity averaged between 75 and 100 ms after perturbation onset relative to unperturbed trials as a function of target displacement. Error bars represent ± 1 SEM.

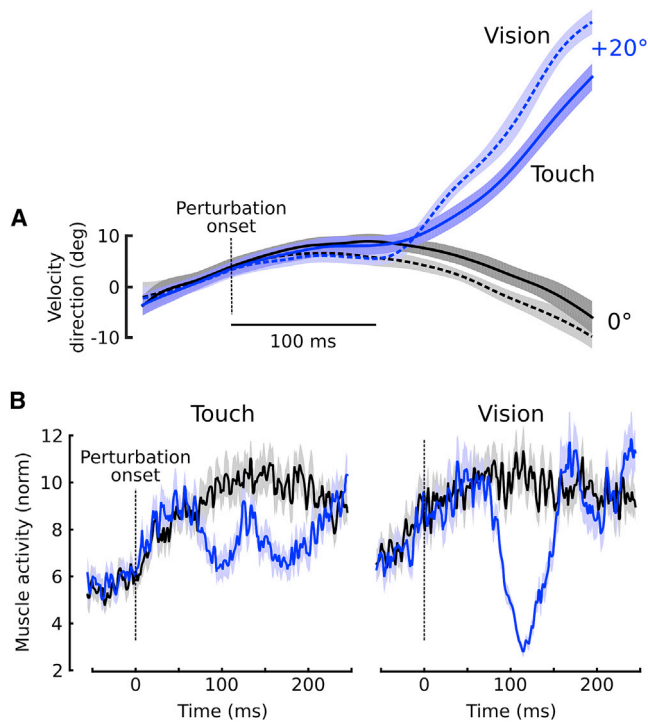


Figure 4. Responses when Final Target Position Is Fully Predictable
 (A) Same format as Figure 2B but for experiment 2, where participants could predict the target's final position on perturbation trials.
 (B) Same format as Figures 3A and 3B but for the labeled conditions associated with experiment 2.
 See also Figure S3.

versus one) for either vision (paired t test, $t_{11} = 1.2$, $p = 0.26$) or touch ($t_{11} = 0.8$, $p = 0.46$) trials (Figure 4B; Figures S3C and S3D).

DISCUSSION

Our study documents a previously unknown tactile-motor reflex that can rapidly and automatically compensate for changes in a target's position during object handling. That is, tactile information about disturbances in the position of a handheld object can automatically correct the movement of the other hand when it reaches for a particular location on the object. Complementing previous work on visuomotor corrections to sudden target displacements [1–12], we found that tactile-motor corrections, as well as visuomotor corrections, quickly account for the direction and amplitude of target displacement.

Although our experiments do not specifically address the underlying sensorimotor pathways, the general similarity between tactile and visual reflex corrections suggests that they are mediated by overlapping neural circuits most likely involving the brainstem [9, 15] and the posterior parietal cortex [16, 17], where commissural connections unifying lateralized sensory representations of space relative to the body's midline occur for vision, as well as touch. Moreover, the rapidity of these corrections, apparent in muscle responses within 90 ms of target displacement and yielding kinematic effects within 110 ms, is consistent with recent work showing that detailed geometric and spatial in-

formation can be extracted very early in the tactile [18–20] and visual [21] processing pathways.

Whereas information about the change in target position is veridically available through vision during the visuomotor reflex, tactile inputs indirectly provide this information in the corresponding tactile-motor reflex. In our experiment, the tactile inputs provide information only about the direction to the target relative the left thumb and, as such, determining the target's position in space requires prior knowledge about the length of the rod. Therefore, compared to the visuomotor reflex, the rapid mapping between tactile inputs and target displacements may draw on an additional already implemented (i.e., learned) transformation where the tactile signals from the hand are assigned as arising from a spatial location that represents the task-relevant source of the signal (i.e., the tip of the rod). Previous research has shown that experience with objects and tools is incorporated into the collection of processes that continuously register the posture of one's body parts in space and are used for spatial organization of action, the so-called body schema [22–24], as well as the activity of neurons involved in processing somatosensory and visual information [25]. Moreover, tools that reverse the most common mappings between hand actions and their visual consequences can be incorporated effectively into on-line visuomotor control such that delayed responses normally associated with such a reversal are ameliorated [26]. Although our present results suggest that establishing rapid tactile corrections in the context of a simple object does not require extensive practice, an important avenue for future research is to determine how visuomotor and tactile-motor reflex corrections compare and interact when learning to handle novel objects and tools.

Previous research examining tactile-motor control mechanisms underlying object manipulation has focused on processes supporting grasp stability [27, 28]. When lifting and moving an object using a precision grip, tactile information about the properties of the contact interface—including angles, shapes, and the slipperiness of contacted surfaces—provided when the digits first contact the object, leads to rapid updating (within ~90 ms) of the coordination of fingertip forces when these properties differ from what is expected [29–32]. Accidental slips at the contact interface result in similarly rapid updating of force coordination [29, 30]. The current results provide a significant advance because they show that tactile inputs can also provide spatial information about sites on handheld objects remote from the contacted area, which can be used to guide actions toward these sites.

The tactile-motor reflex we document likely plays a central role during the many bimanual object manipulation actions that we perform on a daily basis. Such actions typically engage the two hands in an asymmetrical but coordinated manner, with one hand holding an object while the other hand performs various tasks on the handheld object, including reaching toward and contacting a target location on the object [33, 34]. We often perform such tasks when vision and visual attention are directed elsewhere, for example, when using a spoon to extract food from a handheld cup while chatting with a friend or watching television. In this setting, the tactile-motor reflex described here can support goal attainment (e.g., successfully inserting the spoon in the cup) in the event of an unexpected change in the position of an object (i.e., the cup), which could arise from motor noise,

external forces perturbing the object or the hand holding the object, or object slip due to insufficient grip forces.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and three figures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.01.027>.

AUTHOR CONTRIBUTIONS

J.A.P., R.S.J., and J.R.F. designed the experiments. J.A.P. collected and analyzed the data. J.A.P., R.S.J., and J.R.F. prepared the manuscript.

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