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

Authors

J. Andrew Pruszynski, Roland S. Johansson, J. Randall Flanagan

Correspondence

andrew.pruszynski@uwo.ca

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

J. Andrew Pruszynski,^{1,2,4,*} Roland S. Johansson,² and J. Randall Flanagan³

¹Department of Physiology and Pharmacology, Department of Psychology, Robarts Research Institute, Brain and Mind Institute, Western University, London, ON N6A 5B7, Canada

²Department of Integrative Medical Biology, Umea University, 901 87 Umeå, Sweden

³Centre for Neuroscience Studies and Department of Psychology, Queen's University, Kingston, ON K7L 3N6, Canada

⁴Twitter: @andpru

*Correspondence: andrew.pruszynski@uwo.ca

http://dx.doi.org/10.1016/j.cub.2016.01.027

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; $+10^{\circ} =$ $328 \pm 45 \text{ ms}; +20^{\circ} = 413 \pm 119 \text{ ms}).$

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.

Motor

(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 ±20° 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) Pectorals 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 timeseries 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 information 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 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.

ACKNOWLEDGMENTS

This work was supported by the Swedish Research Council (Project 22209), the Strategic Research Program in Neuroscience at the Karolinska Institute, and the Natural Sciences and Engineering Council of Canada. J.A.P. received a long-term fellowship from the Human Frontier Science Program. We thank Anders Bäckström, Carola Hjältén, Per Utsi, and Göran Westling for their technical and logistical support.

Received: November 10, 2015 Revised: December 22, 2015 Accepted: January 12, 2016 Published: February 18, 2016

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- 792 Current Biology 26, 788–792, March 21, 2016 ©2016 Elsevier Ltd All rights reserved

Current Biology, Volume 26

Supplemental Information

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FIGURE S1



Figure S1 (related to Figure 2). Single trial data for Experiment 1.

(A,B) Same format as Fig. 2A,B. Each trace represents a single touch trial from Participant #2. Trials taken in order from near the end of the experiment.

(C,D) Same format but for vision trials.

FIGURE S2



Figure S2 (related to Figure 2). Results for representative participant in Experiment 1. (**A**,**B**) Same format as Fig. 2A,B but for a representative participant (#2). (**C**,**D**) Same format as Fig. 3A,B but for a representative participant (#2).

FIGURE S3





SUPPLEMENTAL EXPERIMENTAL PROCEDURES

Participants

A total of 12 healthy right-handed individuals (19-34 years old) participated in two experiments. Participants provided written informed consent in accordance with the Declaration of Helsinki. The ethics committee of Umeå University approved the study.

Experimental procedures

Participants stood at a table (90 cm high) and made right-handed reaches from a central start location to a spherical target (diameter = 4 cm) located 30 cm in front of them (Fig. 1A). Their goal was to touch the target with their right index finger. The target was mounted on the distal end of a rod, the proximal end of which was connected to a vertically oriented shaft of a rotational motor (Fig. 1A,B). On a subset of trials, the motor could rotate the rod such that the participant needed to adjust their hand trajectory to successfully touch the displaced target. Target movements were triggered when the distance between the finger position and the start position first exceeded 5 cm. The duration of the target movement was always 50 ms. Participants could initiate a reach whenever they liked after keeping their index finger at the start position for 1-1.5 s (as indicated by an auditory cue). Participants were instructed to reach at a consistent speed and received auditory feedback if their reach time, defined as the time required for the finger to go from 5 cm to 22.5 cm relative to the start position, was not between 100 and 300 ms. Participants reliably met this constraint.

In the present experiments, we manipulated the magnitude and direction of target displacements (Fig. 1C) and, critically, the modality of sensory inputs upon which the participant could make corrective responses.

Experiment 1: Corrective responses to perturbations of varying direction and magnitude

Participants (n = 12) made reaching movements guided by either vision or touch. In vision trials, participants could see the target throughout the duration of the trial. In touch trials, participants had their vision occluded during the main portion of the reach by shutter glasses (PLATO, Translucent Tech., Toronto, Canada), but lightly held their left thumb on a raised edge attached to the near end of the rod. The edge (width at top = 0.5 mm; height = 8 mm; length = 28 mm) was aligned with the long-axis of the rod and centered on the rotational axis of the motor. The shutter glasses were open at the start of the trial allowing participants to prepare their movement while seeing the target at its unperturbed location. The shutter closed when the participant's right index finger contacted the start position but reopened when the distance between the finger and the start position exceeded 22.5 cm, which allowed participants to make terminal reach corrections based on vision (if needed).

For both vision and touch trials, half the trials were unperturbed so that participants reached straight to the presented target (0°). In the other half of trials, the target moved either left- or rightwards at one of two different magnitudes (i.e. $\pm 10^{\circ}$, $\pm 20^{\circ}$) with equal probability (Fig. 1C). Participants performed a total of 160 perturbed trials (2 sensory conditions x 4 target displacements x 20 repeats) and 160 unperturbed trials (2 sensory condition. Each block included 20 unperturbed trials and 5 perturbed trials for each direction and magnitude. Blocks were randomized across the experimental sessions and counterbalanced across individuals. Within each block, the various target

displacements were randomly interleaved such that the participant could not predict the presence, direction or magnitude of a target displacement.

Note that a control experiment, where participants performed the touch trials of Experiment 1 but touched the motor housing rather than the edge, showed that general auditory and/or vibratory cues from the device could not be used to guide corrective responses. That is, participants were unable to reliably reach to the goal target on perturbation trials when touching the motor housing.

Experiment 2: Corrective responses when final target position is fully predictable

This experiment was run in the same session as Experiment 1. Participants (n = 12) made reaching movements guided by either vision or touch. Half the trials were unperturbed and, in the other half of trials, the target moved to the right at one magnitude (i.e. $+20^{\circ}$). Participants performed 50 perturbed trials (2 sensory conditions x 1 target displacement x 25 repeats) and 50 unperturbed trials (25 per sensory condition). These trials were grouped in 2 blocks of 50 trials, each based on a single sensory condition. Each block included 25 unperturbed trials and 25 perturbed trials. Blocks were counterbalanced across individuals. Within each block, the perturbation trials were randomly interleaved such that the participant could not predict the presence of a target displacement but could perfectly predict the final location of the target on perturbation trials because there was only one possible target displacement.

Data analysis

We measured the position of the participant's right index finger in three dimensions at 120 Hz with a miniature electromagnetic position-angle sensor (FASTRAK; Polhemus, Colchester, VT) glued to the nail. We acquired muscle activity using electromyography (bandwidth 20–450 Hz) using bipolar electrodes (DE-2.1, Delsys, Boston, MA) placed on the skin above the bellies of two shoulder flexors (pectoralis major, biceps long head) and two shoulder extensors (posterior deltoid, triceps long head) of the right arm. We focused our analysis on the pectoralis major muscle. Similar results were evident for the biceps. Signals from the extensor muscles gave limited information since their activity was markedly inhibited during the reaching movement around the time of target displacement.

Kinematics and muscle activity were digitized and collected by the same system at a sampling rate of 1000 Hz (S/C Zoom, Umea, Sweden). All incoming data was filtered (3rd-order, two-pass, Butterworth with passpand 20-450 Hz) and temporally aligned on the time when the right index finger first passed 5 cm from the start position, which was the trigger for onset of object rotation and target movement in perturbation trials. We analyzed the trajectory of the finger motion in the horizontal plane. Preliminary analyses showed no obvious effect of sensory condition or type of target displacement on hand elevation. To analyze how hand kinematics evolved over time as a function of target displacement and sensory condition, we calculated the direction of the velocity vector by numerical differentiation of the finger position signals in the horizontal plane.

Muscle activity was full-wave rectified and normalized to the mean background activity when the participant held their right index finger at the start position (500 ms window before they received the cue that they could begin reaching). To quantify muscle activity during the fast corrective responses, we analyzed mean activity between 75

and 100 ms after perturbation onset. We chose this epoch because responses at these latencies are automatic, that is, faster than standard measures of voluntary reaction time. The effect of sensory condition and target displacement on the muscle activity was assessed using a repeated-measures ANOVA.

We used the receiver-operator characteristic (ROC) technique to determine the time point when kinematics or muscle activity first differed as a function of target displacement for each sensory condition. For each time step (1 ms), we generated an ROC curve to calculate the probability that an ideal observer could discriminate between kinematics or muscle activity for target displacements of equal magnitude but opposite direction (Exp. 1) or between the perturbed $(+20^{\circ})$ and unperturbed (0°) trials (Exp. 2). Areas under the ROC curve with values of 0 and 1 represent perfect discrimination, whereas a value of 0.5 represents chance performance. For kinematic data, we estimated the timing of the initial separation by first calculating when the ROC data remained above a threshold of 0.75 or below 0.25 for at least 5 consecutive time steps and then looking back in time for the first data sample that fell on the other side of 0.5 (i.e. < 0.5 if threshold = 0.75; > 0.5 if threshold = 0.25). We used the same approach for muscle activity data but with thresholds of 0.4 and 0.6 to account for relatively noisy nature of single-trial muscle activity. Because such quantitative methods are sensitive to the signal-to-noise ratio of the underlying signals [S1], we confirmed that our findings were qualitatively similar across a range of thresholds and that the outputs of our quantitative method matched manual inspection of the underlying data. We compared our estimates of initial separation times using a repeated-measures ANOVA with sensory condition and target displacement as factors (Exp. 1) or with a paired t-test between sensory conditions (Exp. 2). All statistical tests were deemed significant if p < 0.05.

SUPPLEMENTAL REFERENCES

 Oostwoud Wijdenes, L., Brenner, E., and Smeets, J. B. J. (2014). Analysis of methods to determine the latency of online movement adjustments. Behav. Res. Methods 46, 131–139.