Experimental Brain Research (2019) 237:839–853
https://doi.org/10.1007/s00221-018-5448-3

RESEARCH ARTICLE

Rapid online corrections for upper limb reaches to perturbed somatosensory targets: evidence for non-visual sensorimotor transformation processes

Gerome A. Manson[1,2] · Jean Blouin[1] · Animesh S. Kumawat[2] · Valentin A. Crainic[2] · Luc Tremblay[2]

Received: 17 August 2018 / Accepted: 30 November 2018 / Published online: 5 January 2019

Abstract

When performing upper limb reaches, the sensorimotor system can adjust to changes in target location even if the reaching limb is not visible. To accomplish this task, sensory information about the new target location and the current position of the unseen limb are used to program online corrections. Previous researchers have argued that, prior to the initiation of corrections, somatosensory information from the unseen limb must be transformed into a visual reference frame. However, most of these previous studies involved movements to visual targets. The purpose of the present study was to determine if visual sensorimotor transformations are also necessary for the online control of movements to somatosensory targets. Participants performed reaches towards somatosensory and visual targets without vision of their reaching limb. Target positions were either stationary, or perturbed before (~450 ms), or after movement onset (~100 ms or ~200 ms). In response to target perturbations after movement onset, participants exhibited shorter correction latencies, larger correction magnitudes, and smaller movement endpoint errors when they reached to somatosensory targets as compared to visual targets. Because reference frame transformations have been shown to increase both processing time and errors, these results indicate that hand position was not transformed into visual reference frame during online corrections for movements to somatosensory targets. These findings support the idea that different sensorimotor transformations are used for the online control of movements to somatosensory and visual targets.

Keywords Reaching · Online-control · Somatosensory targets · Sensorimotor transformations · Double-step

Introduction

When performing movements to visual targets, the motor system can successfully correct to changes in target location (Day and Lyon 2000; Johnson et al. 2002; Sarlegna and Mutha 2015; Smeets et al. 1990). These corrections can occur when perturbations are not consciously detected or when there is no vision of the reaching limb (Goodale et al. 1986; Heath 2005; Komilis et al. 1993; Pélisson et al. 1986; Reichenbach et al. 2009; Saunders and Knill 2003). When the reaching limb is not visible, somatosensory information about the limb's position and visual information about the new target location can be used to perform trajectory amendments. However, because movements to visual targets are hypothesized to be planned in a visual reference frame (Ambrosini et al. 2012; Buneo and Andersen 2006; Thompson et al. 2012, 2014), previous studies have argued that the reaching limb's position must first be converted into extrinsic visual coordinates prior to the initiation of corrections (Prablanc and Martin 1992; Reichenbach et al. 2009). It is unknown if such online sensorimotor transformation processes also occur for reaches to non-visual targets. The purpose of the present study was to investigate the sensorimotor transformation processes involved in the online control of reaching movements to somatosensory targets performed without vision of the reaching limb.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00221-018-5448-3) contains supplementary material, which is available to authorized users.

✉ Gerome A. Manson
gerome.manson@utoronto.ca

1 CNRS Laboratory of Cognitive Neurosciences, Aix-Marseille University, 3 place Victor-Hugo, 13331 Marseille, France

2 Centre for Motor Control, University of Toronto, 55 Harbord Street, Toronto M5S 2W6, Canada

Online-visuomotor transformation processes for movements to visual targets

Previous studies have found that rapid reaches to perturbed visual targets are less accurate and have longer correction latencies when there is no vision of the reaching limb compared to when there is vision of the limb. For example, Komilis et al. (1993) conducted a study wherein participants reached to visual targets that were perturbed either at movement onset or at peak velocity. Movements were performed with or without vision of the reaching limb and endpoint accuracy was assessed. Similar to previous studies (e.g. Goodale et al. 1986), the authors found that participants were able to achieve very accurate endpoints in response to target perturbations at movement onset, regardless of whether their limb was visible or not. However, for perturbations at peak velocity, movements that were performed without vision of the limb were slower and slightly less accurate than movements performed with vision of the limb (see also Heath 2005). Reichenbach et al. (2009) also noted that the amount of time required to initiate a correction (i.e. the correction latency) was longer (+ 10 ms based on EMG and + 30 ms based on limb kinematics) when participants performed reaches to visual targets that were perturbed shortly after movement onset without vision of their limb compared to when they performed reaches with the vision of their limb. It was reasoned that, when the limb is not visible, corrections are programmed based on the updated visual target location and visual estimates of the current limb position derived using efferent information and somatosensory inputs from the reaching limb (see also Bard et al. 1999). Reichenbach and colleagues concluded that when the limb is not visible, additional time is required for the transformation of somatosensory information about the limb position to a visual estimate prior to the programming of the correction. Together, the results of these studies support the idea that a common visual reference frame is used for the online control of actions irrespective of the sensory modality used to encode hand position (see also Buneo and Andersen 2006).

Sensorimotor transformation processes for movements to somatosensory targets: planning and online control

The idea that a common visual reference frame is used for the online control of goal-directed actions is based primarily on studies involving movements to visual targets. Very little is known about online sensorimotor control processes that occur during reaching movements to somatosensory targets. Research on movement planning, however, has revealed that the reference frame used to plan movements to somatosensory targets could be visual (Blangero et al. 2005; Jones and Henriques 2010; Pouget et al. 2002) or non-visual (Bernier et al. 2007, 2009; Blouin et al. 2014; McGuire and Sabes 2009; Sarlegna and Sainburg 2007; Sober and Sabes 2005).

Both Pouget et al. (2002) and Jones and Henriques (2010) found that when participants shifted their gaze position prior to reaching to somatosensory targets, participants' endpoint errors were biased in the opposite direction of the gaze-shift (see also Blangero et al. 2005). The effects of a change in gaze position on movement endpoint bias was similar to the effects observed when participants performed movements to visual targets (see Bock 1986; Henriques et al. 1998). Thus, these studies concluded that movements to somatosensory targets were also planned in a visual coordinate system (see also Mueller and Fiehler 2014).

In contrast, other studies have found that movements to somatosensory targets can be planned in a non-visual coordinate system. For example, Sarlegna and Sainburg (2007) found that altering visual information about the initial hand position had no effect on endpoint errors when participants reached to somatosensory targets (see also Sober and Sabes 2005). Because both the limb and the target can be represented in somatosensory coordinates (see Battaglia-Mayer et al. 2003), and because movements were unaffected by visual perturbations, the authors concluded that the computation of the movement vector was performed in a non-visual reference frame when reaching to somatosensory targets. Other studies have also suggested that using non-visual sensorimotor transformations for movement planning to somatosensory targets may avoid errors which are associated with the conversion from a somatosensory coordinate system to a visual coordinate system (Sarlegna et al. 2009).

Although sensorimotor transformations in both visual and non-visual coordinate systems have been found for the planning of movements to somatosensory targets, the type of sensorimotor transformation employed for online trajectory amendments remains unclear. In the present study, the latency and magnitude of online trajectory corrections to perturbed visual and somatosensory targets were assessed to investigate the sensorimotor transformation processes used for the online control of an unseen reaching limb. It was hypothesized that if a visual reference frame is employed, longer correction latencies and smaller corrections should be observed for reaches to somatosensory targets as compared to reaches to visual targets. This is because somatosensory cues from both the perturbed somatosensory target position and reaching limb would have to be converted into visual coordinates prior to the initiation of corrections. For movements to visual targets, only the reaching limb position would require a conversion into a visual coordinate system.

In contrast, if corrections are programmed in a non-visual reference frame then we would expect faster and more accurate corrections in response to somatosensory target perturbations compared to visual target perturbations. Corrections in a non-visual reference frame would be programmed using the new target and limb position in somatosensory coordinates, without the need for a reference frame transformation.

Methods

Participants

Fourteen participants (10 women, aged 20–33 years $M = 25$, $SD = 4$) took part in the experiment. All participants were right-handed (assessed by the Edinburgh handedness questionnaire, adapted from Oldfield 1971), self-declared neurologically healthy, and had normal or corrected-to-normal vision.

Written informed consent was obtained prior to the experimental protocol and the University of Toronto's Office of Research Ethics approved all procedures. Including the informed consent, breaks, snacks, and debriefing, the experiment lasted approximately 3 h and participants were compensated with $20 CAD.

Apparatus

A drawn representation of the experimental setup is shown in Fig. 1. The experiment was conducted in a completely dark room, where participants were seated comfortably on a kneeling chair facing a protective cage made of a clear polymer. Participants placed their head on a headrest that was positioned on the outside of the cage and interacted with the experimental materials located inside the cage through a window (80 cm high). A small microphone (FBA_4330948551, Phantom YoYo) that was used for the vocal response time protocol (see below) was placed at the bottom left of the headrest position.

Inside the cage was a Selectively Compliant Assembly Robot Arm (SCARA; Epson E2L853, Seiko Epson Corp.) that was used to position both the visual and the somatosensory target stimuli (see Manson et al. 2014 for details on the robotic device). Located directly below the robot was a table with a custom-built aiming apparatus placed on its surface. Participants saw all the visible stimuli through the clear ploymer cage.

The aiming apparatus included a black tinted Plexiglas aiming surface (60 cm wide by 45 cm long by 0.5 cm thick) mounted 12 cm above a wooden base. Underneath the aiming surface, there was a textured home position (2 cm by 2 cm). On the top of the aiming surface was a blue light emitting diode (LED, 2 mm diameter) that served as the gaze

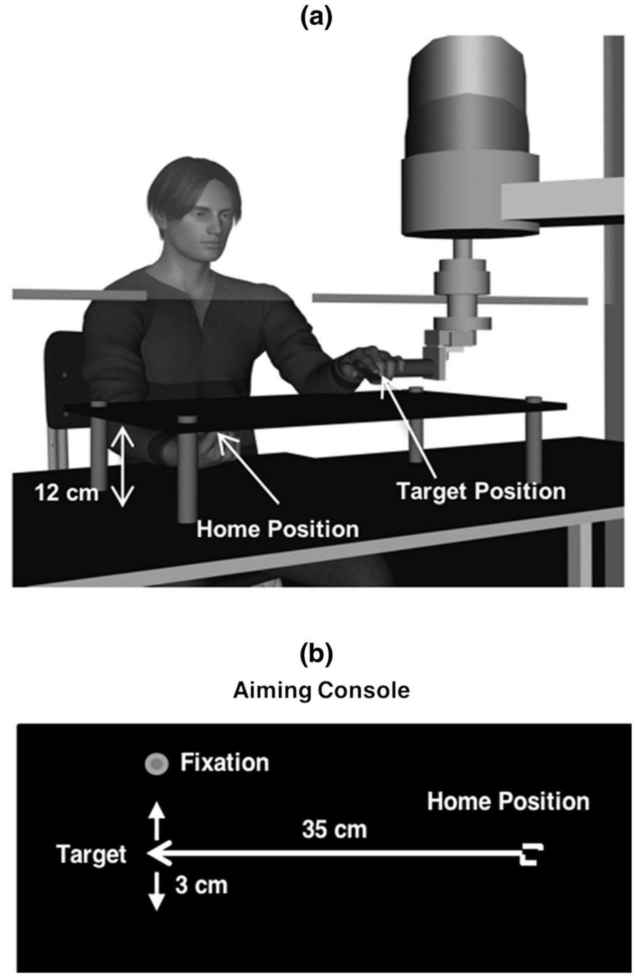

Fig. 1 A drawn representation (not to scale) of the experimental setup in the Somatosensory target condition is shown in **a**. **b** Drawn representation (not to scale) of the aiming console and stimuli positions. Participants sat facing the aiming apparatus in a dark room. A robotic device was used to deliver target perturbations in both somatosensory (left finger) and visual (LED) target conditions. Participants performed reaching movements from the home position located on their left to the target position located close to their midline

fixation point. The LED was aligned with the participant's midline and was located ~ 65 cm from the participant's eye position.

In the robot's neutral position (i.e., for no-perturbation trials or at the start of the perturbed trials), the custom end-effector attached to the robot arm was positioned 0.5 cm above the aiming surface and 35 cm to the left of the home position. In the somatosensory target condition, participants grasped the robot's end effector with their left hand and they were instructed to depress an attached micro-switch (B3F-1100, OMRON) with their index finger. The micro-switch served as both a reference for the somatosensory target location and a safety mechanism that would immediately shut off the robot's motors if the button was released (note: no participants released the switch during the study). In the visual target condition, a green LED (~6 mm diameter) was attached to the robot's end effector at the same position as the fingertip in the somatosensory target condition (i.e., at the microswitch location).

The participant's reaching fingertip and the robot's end effector were both affixed with an infrared light emitting diode (IRED). An Optotrak Certus (Northern Digital Inc.) motion tracking system recorded the position of both IREDs at a sampling rate of 200 Hz. A custom MATLAB (The Mathworks Inc.) program was used to gather data from the Optotrak and microphone, as well as to send outputs to the aiming console and the robotic effector. A piezoelectric buzzer (SC628, Mallory Sonalert Products Inc.) was used to provide brief auditory cues to the participants.

Procedure

Participants completed the experimental tasks over two sessions, one for each target modality. The presentation of target modality was counterbalanced across participants, and the time between sessions was between 5 and 14 days ($M = 10.5$ days) for most participants.

Each session consisted of two protocols: a vocal response time protocol, and a reaching protocol. In the first protocol, participants were asked to make a vocal response to the perturbation of the target stimulus. In the second protocol, participants were asked to reach to the target stimulus as accurately as possible within a movement time bandwidth (i.e., 450–600 ms from movement start to movement end). Participants were given the instructions for the reaching protocol only once they had completed the vocal response time protocol.

Vocal response time protocol

The goal of the vocal response time protocol was to examine whether the modality of the target alters the time taken to detect the onset of target motion. For the somatosensory target session, participants responded to perturbations of their left limb placed on the robot's end effector. For the visual target session, participants responded to the perturbation of the target LED placed on the same position. During both sessions, participants placed their right index finger on the home position located underneath the aiming surface (see Fig. 1).

At the beginning of each trial, the fixation light was turned on. After the experimenter verified that participants were on the home position, the trial was started. After a random foreperiod, the robot perturbed the visual or somatosensory target either 3 cm toward or away from the participants, or 3 cm to the left of them (i.e., catch trials). The duration ($M = 200$ ms, SD = 3.8) and velocity of the target perturbations were the same in both the vocal response time protocol and the reaching protocol. Participants were instructed to verbally respond with "Yo!" as soon as the target stimulus moved either toward or away from their body, and to not respond when the target moved to their left (i.e., "catch trials"). Note that participants did react on 0.02% of the catch trials; however, none of the participants reacted to more than one catch trial. Following the recording of the vocal response, the fixation light turned off and the robot returned to the neutral position. Vocal response times were computed as the time difference between the onset of target displacement (i.e., when the velocity of the robot surpassed 30 mm/s) and the response time recorded by the microphone.

Reaching protocol

After participants completed the vocal response time protocol, the experimenter explained the reaching protocol and trial procedures. The reaching protocol consisted of four phases: familiarization, perception of target position in the pre-test, reaching trials, and perception of target position in the post-test. All four phases were performed for both target modalities.

There were two kinds of reaching trials: no-perturbation and perturbation reaching trials. In the no-perturbation trials, participants performed movements from the home position to the neutral target position within a movement time bandwidth of 450–600 ms. Each trial began with the illumination of the fixation LED. In the visual target session, the target LED was also illuminated at the same time as the fixation LED. Four hundred milliseconds after the fixation LED was turned on, an auditory go signal (50 ms beep) cued participants to begin their reaching movement. The time instant at which finger velocity raised above or fell below 30 mm/s for more than 10 ms marked the movement start and end, respectively. Once the reaching movement was completed, participants received auditory feedback about their movement time and the fixation LED was turned off. The auditory feedback indicated to the participants whether their movement time was within the time bandwidth. Participants were presented with two short (50 ms) beeps if their movement time was within the bandwidth; one long (100 ms) beep if their movement time was shorter than the lower limit of the bandwidth; or three short (50 ms) beeps if their movement time was longer than the upper limit of the bandwidth. The beeps also served as a signal to move back to the home position to begin the next trial.

In the perturbation trials, the target was shifted 3 cm away from or towards the participant either 300 ms before the go signal, or ~100 ms or ~200 ms after the movement onset. These perturbation signal times ultimately occurred at 450 ms (SD = 73 ms) before, or 93 ms (SD = 4 ms) or 190 ms (SD = 4 ms) after movement onset. (see Fig. 2 for velocity

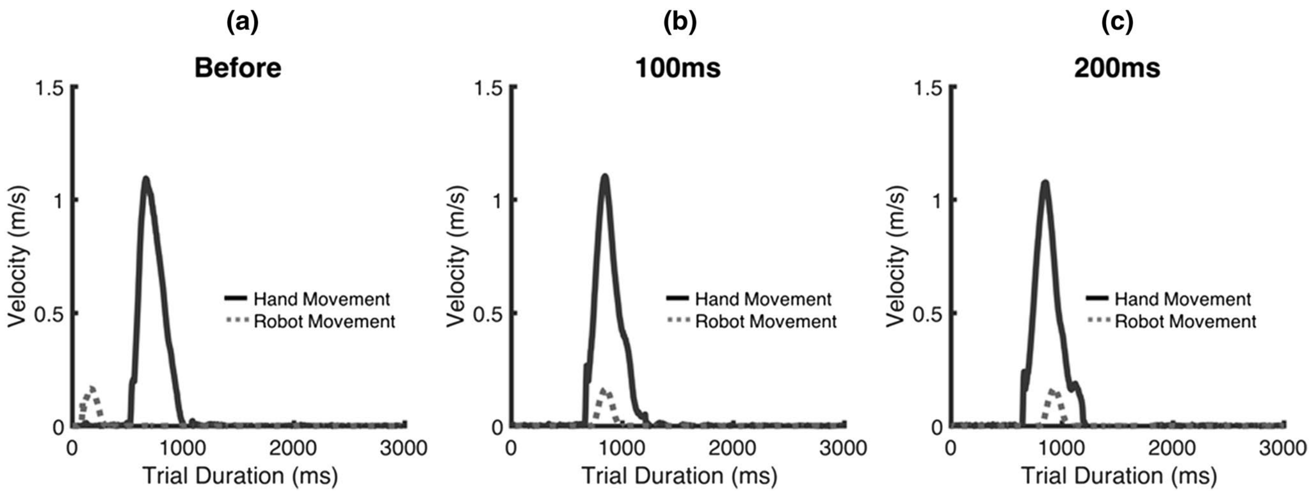

Fig. 2 Examples of velocity profiles of the reaching hand and the robotic effector (Target) for each perturbation time. **a** Shows a perturbation occurring before movement onset; **b** Shows a perturbation occurring ~ 100 ms after movement onset, and **c** shows a perturbation occurring ~ 200 ms after movement onset

profiles of hand and robot movements in each perturbation condition). The change of target position required a change in movement direction (with consideration that movements are planned as a vector defined in terms of amplitude and direction; Buneo and Andersen 2006; Dadarlat et al. 2015; Desmurget et al. 1998). Offline analyses showed that the 100 ms perturbation time occurred prior to peak velocity, at a time during which visual information has been found to be important for online corrections (Kennedy et al. 2015; Tremblay et al. 2017). The 200 ms time roughly corresponded with the peak velocity of the aiming movements. This time may be too late to use visual feedback effectively (e.g. Kennedy et al. 2015) but may still be viable for the use of somatosensory information (Goodman et al. 2018; Redon et al. 1991). Perturbations before movement onset were included as a control condition to compare the corrections that resulted from planning and online control processes between somatosensory and visual conditions.

Participants were asked to reach to the position of the target stimulus (e.g., the surface area of the finger on the button, or target LED) as if projected onto the underneath of the aiming surface. When performing movements to visual targets, participants placed their non-reaching limb on the side of the kneeling chair. To perform the reaching task, participants performed an "underhanded" reaching movements, primarily with muscles in their shoulder joints. Participants were asked to perform their movements without sliding their finger on the aiming surface. Their wrists remained supinated throughout the trajectory. To discourage wrist movements, participants also wore a wrist orthotic (Champion-C218, Champion Health and Sports Supports, Cincinnati, USA). Participants performed 180 reaching trials for each target modality (360 trials total). These trials consisted of 90 no-perturbation trials and 90 perturbation trials (15 trials in each of the 6 perturbation conditions). None of the perturbation conditions were repeated more than twice consecutively.

Familiarization

After receiving the instructions for the reaching task, participants performed 30 trials to familiarize themselves with the experimental task, the auditory feedback, and the movement time bandwidth. Participants were presented with 18 no-perturbation trials followed by 12 perturbation trials (2 trials in every perturbation condition).

Perception of target position pre- and post-test

To record the perceptions of the target position, participants were asked to reach to where they perceived each target position was as if it were projected onto the underneath surface of the Plexiglas. Participants first reached to the center target and adjusted their index finger until they felt it matched the target's position. Participants then verbally indicated when their hand was on the target position, and this position was recorded. Once the reaching hand was returned to the home position, the robotic effector was moved to the 'away' target position and the procedure was repeated. Finally, the entire sequence was repeated for the 'toward' target position. Participants' perceived target locations were recorded twice during each session: once after the completion of the familiarization trials (i.e. pre-test) and again after the completion of the reaching trials (i.e. post-test). The perceived target locations recorded during these trials were used for endpoint error calculations (see constant and variable errors in the "Results" sections).

Data analysis

Vocal response time protocol

All vocal response time trials, target perception trials, and trajectory data were processed and analyzed using a custom MATLAB program. For vocal response time data, trials with a response time more than three standard deviations higher or lower than the participant's mean were removed. These accounted for 5.2% of all vocal response trials. Vocal response data were submitted to a two-perturbation direction (away, toward) by two-target modality (somatosensory, visual) repeated-measures ANOVA.

Reaching protocol

Trials with movement times, reaction times, or endpoint errors that were more than three standard deviations from the mean were excluded from the analyses. This resulted in the exclusion of 4.5% of all reaching trials. The main dependent variables for this experiment were constant error, variable error, correction magnitude, and the latency of online corrections.

Constant and variable errors

Constant error was calculated as the bias in endpoint position relative to the participant's averaged perceived target position (calculated using the pre- and post- target perception trials). Constant error was computed for both the amplitude and the direction axes (hereafter referred to as amplitude constant errors and direction constant errors, respectively). Variable errors were computed by calculating the standard deviation of these constant errors (hereafter referred to as amplitude variable error and direction variable error).

For amplitude constant errors, positive values indicated an overshoot relative to the target location, whereas negative values indicated an undershoot relative to the target location. Similarly, for direction constant errors, positive values represent an over-correction relative to the new target's position, whereas negative values represent an under-correction relative to the new target's position.

Amplitude and direction constant and variable errors were submitted to separate two-target modality (somatosensory, visual) by two-perturbation direction (away from the body and toward the body) by three-perturbation time (before, 100 ms, 200 ms) repeated measures ANOVAs.

Correction magnitude

Correction magnitude was calculated as the average of the absolute difference between the average end position of the perturbation trials (e.g. before, 100 ms, and 200 ms) and the average end position of the no-perturbation trials. This measure was only computed for the direction axis (i.e. axis of the perturbations). It is worth noting that there were no differences in overall endpoint variability between somatosensory and visual target conditions in the no-perturbation conditions $t(13) = -1.35$ $p = 0.20$ (see "Results" Sect. Comparison of no-perturbation trials, and Table 2. Correction magnitudes were submitted to a two-target modality (somatosensory, visual) by two-perturbation direction (away, toward) by three-perturbation time (before, 100 ms, and 200 ms) repeated measures ANOVA.

Latency of online corrections

The method of determining the latency of online corrections was adapted from Oostwoud Wijdenes et al. (2013). Using this method, correction latency was computed based on a linear extrapolation of the differences in the average acceleration profiles in the movement direction axis (axis of the perturbation) between no-perturbation and perturbation trials (see also Veerman et al. 2008). When tested on simulated data, this extrapolation method was deemed to be an accurate and precise method for detecting correction latencies (Oostwoud Wijdenes et al. 2014).

Accelerations profiles in the movement direction axis were computed by a double differentiation of the displacement data obtained from sampling the finger IRED and subsequently low pass-filtering these time-series with a second-order recursive bidirectional Butterworth filter at 50 Hz. For each participant, the difference in the average acceleration profiles were computed between the no-perturbation and the 100 ms perturbation trials, and the no-perturbation and the 200 ms perturbation trials. These difference profiles were then used to compute the correction latencies.

The no-perturbation trials used for the computation of the average acceleration profile were selected based on the distribution of movement times used to compute the respective profile in the perturbation condition. The number of control trials used to compute the average trajectories thus varied for each condition within each participant. The number of control trials used ranged from 25 to 85 ($M = 59$ trials, $SD = 14$). Overall, movement times between perturbation trials ($M = 544$ ms, $SD = 17$) and control trials ($M = 543$ ms, $SD = 16$) were not significantly different, as indicated by a paired-samples t test, $t(13) = 0.86$, $p = 0.41$.

To determine response latency, the maximum acceleration value occurring after perturbation was first identified. Second, a line was drawn between the points on the acceleration profile corresponding to 25% and 75% of the maximum acceleration. Response latency was defined as the difference between the time of perturbation and the time instant when this line crossed zero (i.e., y value of zero; see Oostwoud Wijdenes et al. 2013, 2014; Veerman et al. 2008) and Fig. 3 for a graphical representation of the method applied to participants' data from the present study.

Correction latencies were submitted to a two-target modality (somatosensory, visual) by two-perturbation time (100 ms, 200 ms) by two-perturbation direction (away, toward) repeated-measures ANOVA. Note that corrections to the target perturbations that occurred before movement onset likely occurred during movement planning and are, therefore, not reflective of online control processes. Furthermore, accurate correction latencies for the "before" perturbation time are unlikely to be detected by this method. Because of the above-stated reasons, the before perturbation condition was not included in the statistical design.

It is also worth noting that for this analysis, the absolute values of correction latency were not as important as the between-modality differences. In the present study, because of technical limitations between the syncing of the Optotrak and robotic apparatuses, reaching data were sampled at a frequency (200 Hz) lower than what was used in previous studies (500 Hz: Oostwoud Wijdenes et al. 2011, 2014). Also, this was the first time such a method was applied to reaching movements performed with a supinated wrist posture to a somatosensory target. Thus, some contrasts between our values and those commonly found in the literature were expected.

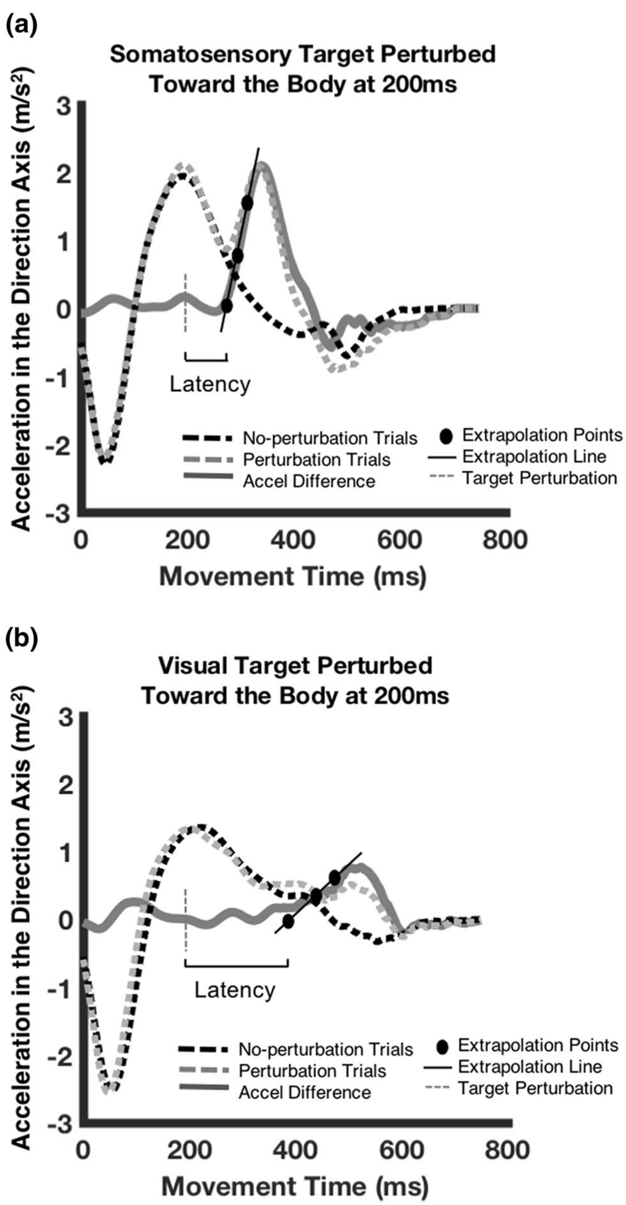

Fig. 3 The extrapolation method for determining the latency of online corrections. For each participant, average acceleration profiles in the direction axis were computed for both perturbation and no-perturbation trials. The acceleration difference between these profiles (Accel Difference) was then plotted to calculate correction latency. Correction latencies were computed by drawing a line (Extrapolation Line) between 75% and 25% of the maximum difference in the Accel Difference profile (Extrapolation points) and extrapolating the line to the first zero crossing. The time between the perturbation and the zero crossing was defined as the correction latency. **a** shows this method applied to averaged data for somatosensory target perturbations and **b** shows the method applied to averaged data for visual target perturbations

Comparison of no-perturbation trials

To examine the effect of target modality on reaching performance and kinematics, paired samples t-tests were performed (effect sizes reported with Cohen's d_z) on reaction time, movement time, total movement amplitude, amplitude and direction constant and variable errors, as well as on time to, and time after peak velocity. Note that for these comparisons, direction constant errors were defined using a coordinate system relative to the home and target positions. Negative values indicated deviations closer to the body with respect to the target, and positive values indicated endpoints further away from the body with respect to the target.

Statistics and post-hoc tests

All statistical analyses were performed using the Statistical Package for Social Scientists (SPSS: IBM Inc. version 20). For all t-tests and repeated-measures ANOVAs, alpha was set to $p = 0.05$. For clarity and brevity, only the significant main effects and interactions were reported. Also, when main effects could be solely explained by a higher order interaction, only the break-down of the interaction was reported. The Hyunh-Feldt correction was used to correct the degrees of freedom (corrected to 1 decimal place) when the assumption of sphericity was violated. The Tukey's

Honestly Significant Differences (HSD) test was used to decompose all significant interactions.

Results

Vocal response protocol

For perturbation detection times, the analysis yielded a significant main effect of stimulus modality, $F(1,13)=5.04$, $p<0.05$, $\eta_P{}^2=0.28$, and a significant stimulus modality by perturbation direction interaction, $F(1,13)=5.56$, $p<0.05$, $\eta_P{}^2=0.30$, HSD = 22 ms. Overall, somatosensory targets perturbations were detected faster ($M=452$ ms, SD = 95) than visual targets perturbations ($M=486$ ms, SD = 104). Breaking down the interaction between modality and perturbation direction revealed that, when the stimulus was perturbed away from the body, there was a larger difference in detection times between somatosensory and visual stimuli (somatosensory away: $M=445$ ms, SD = 100; visual away: $M=491$ ms, SD = 102) than when the stimuli were perturbed toward the body (somatosensory towards: $M=459$ ms, SD = 92; visual towards: $M=481$ ms, SD = 108).

Reaching protocol

Normalized trajectory profiles for each condition in the reaching protocol are displayed in Fig. 4. Also, a summary of the average temporal and kinematic characteristics of the movements produced in each condition are shown in Table 1, and a summary of the movement endpoint characteristics are displayed in Table 2.

Comparison of no-perturbation trials

First, no-perturbation trials were analyzed to determine whether the sensory modality of the target had significant effects on the different reaching variables. The analyses revealed significant effects of target modality on the reaction time, $t(13)=2.98$, $p<0.05$, $d_z=0.8$ movement amplitude, $t(13)=4.12$, $p<0.001$, $d_z=1.1$ and direction constant error, $t(13)=-3.15$, $p<0.01$, $d_z=0.8$. Participants took more time to initiate movements to somatosensory targets (mean reaction time = 330 ms, SD = 60) compared to visual targets (mean reaction time = 253 ms, SD = 71). Also, movements had larger total movement amplitudes when participants reached to somatosensory targets ($M=35.2$ ms, SD = 3.4) as compared to visual targets ($M=31.2$ ms, SD = 5.0). Finally, the analysis of direction constant error revealed that participant's endpoints were distributed further away from the body when reaching to visual targets ($M=1.31$ cm, SD = 1.19) compared to somatosensory targets ($M=0.16$ cm, SD = 1.07).

Constant and variable errors

For direction constant error, the ANOVA yielded a significant main effect of perturbation time, $F(2,26)=40.85$, $p<0.001$, $\eta_P{}^2=0.76$, HSD = 0.41 cm, and a significant modality by perturbation time interaction, $F(2,26)=11.94$, $p<0.001$, $\eta_P{}^2=0.48$, HSD = 0.64 cm. Breaking down the two-way interaction revealed that participants showed smaller direction constant errors in response to target perturbations in both the 100 ms and 200 ms perturbation conditions when they reached to somatosensory targets as compared to when they reached to visual targets. No difference in direction constant error between target modalities was observed in response to perturbations before movement onset (see Fig. 5a; Table 2). For the trials with target perturbations, the analyses yielded no significant main effects or interactions for amplitude constant and amplitude variable errors (Fs > 0.09 and ps > 0.098).

For direction variable error, the analysis yielded a significant main effect of perturbation direction, $F(1,13)=16.80$, $p<0.001$, $\eta_P{}^2=0.62$; perturbation time, $F(2,26)=21.00$, $p<.001$, $\eta_P{}^2=0.56$, HSD = 0.20; and a target modality by perturbation direction interaction, $F(1,13)=11.54$, $p<.01$, $\eta_P{}^2=0.47$, HSD = 0.25 cm. Participants' endpoint variability was significantly higher when they reached targets perturbed 200 ms after movement onset ($M=1.71$ cm, SD = 0.62) compared to when they reached to targets perturbed 100 ms after movement onset ($M=1.51$ cm, SD = 0.56). Direction variable errors were also significantly higher in response to both 100 ms and 200 ms perturbations than in response to perturbations before movement onset ($M=1.20$ cm, SD = 0.39). Breaking down the target modality by perturbation direction interaction revealed that, when moving to a somatosensory target, participants' direction variable errors were significantly lower when the target was perturbed towards the body ($M=1.16$ cm, SD = 0.37) compared to when the target was perturbed away from the body ($M=1.66$ cm, SD = 0.56). There were no differences between perturbation directions for reaches to visual targets (global $M=1.62$ cm SD = 0.58).

Correction magnitude

The analysis of correction magnitude yielded a significant main effect of target modality, $F(1,13)=70.07$, $p<0.001$, $\eta_P{}^2=0.84$ perturbation time, $F(2,26)=39.81$, $p<.001$, $\eta_P{}^2=0.75$ HSD = 0.63 cm, perturbation direction, $F(1,13)=7.71$, $p<.05$, $\eta_P{}^2=0.37$ and a target modality by perturbation time interaction, $F(2,26)=10.04$, $p<.001$, $\eta_P{}^2=0.44$, HSD = 0.55 cm. Participants exhibited larger corrections in response to targets perturbed toward the body ($M=3.83$ cm, SD = 1.47) compared to targets perturbed away from the body ($M=3.42$ cm, SD = 1.20). Decomposing the target modality by perturbation time

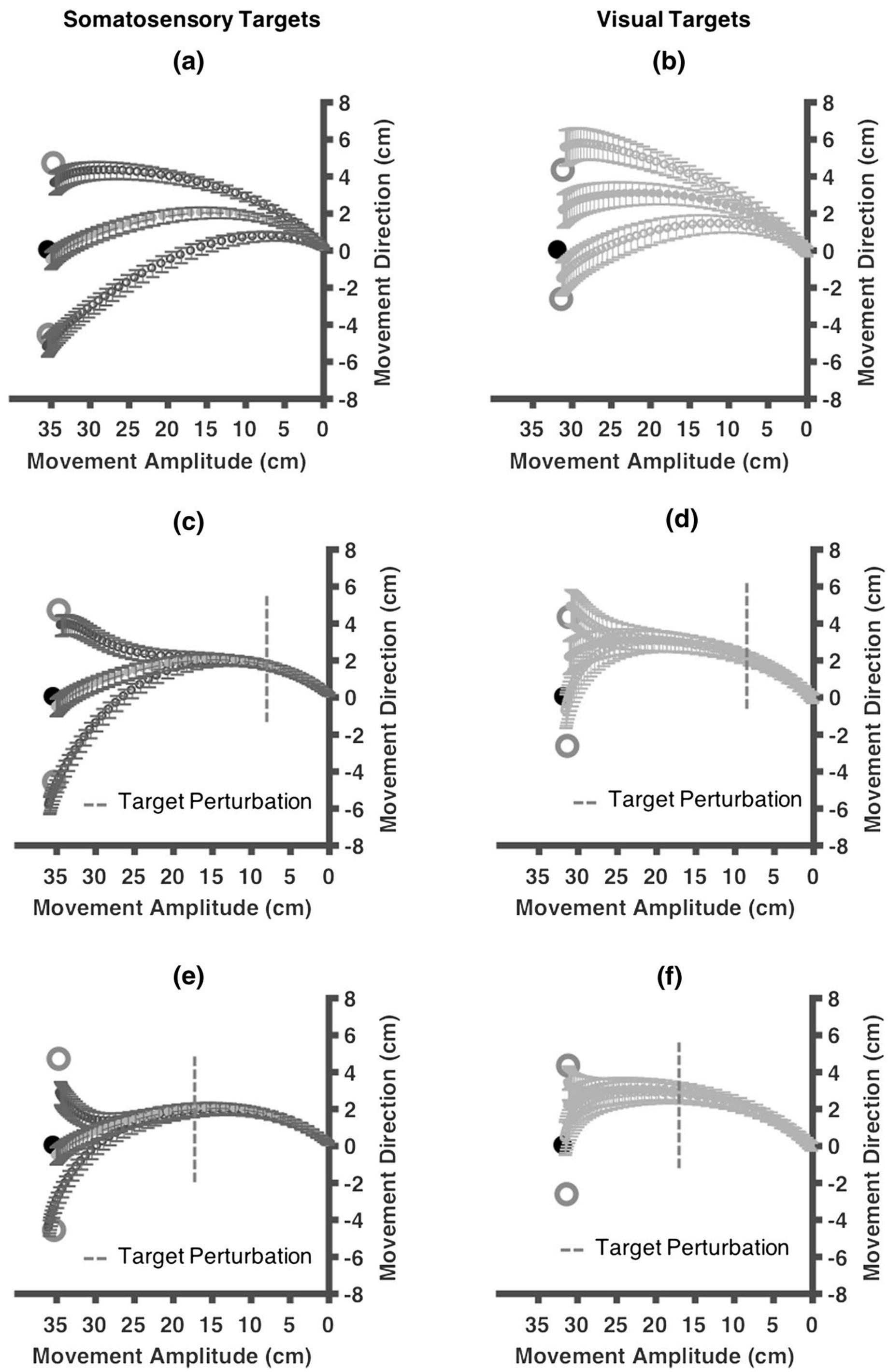

Fig. 4 Average reaching trajectories for each condition in the reaching protocol. **a**, **b** Depict perturbations occurring before movement onset. **c**, **d** Depict perturbations 100 ms after movement onset. **e**, **f** Depict perturbations occurring 200 ms after movement onset. Trajectories were normalized with each point representing 2% of movement duration. Error bars indicate the between-subject standard deviation of spatial position

interaction revealed that, overall participants performed larger corrections in response to somatosensory target perturbations compared to visual target perturbations and that, compared to the before condition, the increase in correction magnitudes observed in the 200-ms condition was significantly larger for movement to visual targets (1.63 cm increase) compared to movements to somatosensory targets (0.64 cm increase: see Fig. 5b).

Latency of online corrections following target perturbation

The analysis of correction latencies yielded a significant main effect of target modality, $F(1,13) = 501.00$, $p < .001$, $\eta_P^2 = 0.96$, perturbation direction, $F(1,13) = 18.11$, $p < .001$, $\eta_P^2 = 0.58$ and a target modality by perturbation direction interaction, $F(1,13) = 11.62$, $p < .01$, $\eta_P^2 = 0.47$, HSD = 30 ms. The main effect of target modality revealed

Table 1 Mean and standard deviation for the temporal and kinematic variables of movements to somatosensory (somato) and visual targets

Variables	Targets	Perturbation conditions						
		No perturbation	Before		100 ms		200 ms	
			Away	Toward	Away	Toward	Away	Toward
Reaction Time (ms)	Visual	253 (71)	119 (69)	105 (62)	254 (75)	253 (93)	257 (77)	257 (77)
	Somato	330 (60)	127(83)	135 (75)	326 (48)	324 (60)	332 (61)	320 (68)
Movement Time (ms)	Visual	521 (22)	518 (27)	506 (32)	559 (40)	544 (32)	533 (24)	559 (30)
	Somato	522 (14)	515 (20)	519 (32)	554 (22)	525 (33)	550 (30)	536 (30)
Robot-hand start difference (ms)	Visual	–	−449 (71)	−435 (69)	91 (2)	91 (2)	192 (1)	191 (2)
	Somato	–	−453 (85)	−459 (73)	95 (3)	95 (4)	193 (2)	192 (2)
Time to peak velocity (%)	Visual	39 (5)	36 (5)	37 (4)	37 (5)	37 (5)	37 (6)	37 (4)
	Somato	38 (5)	36 (5)	37 (5)	36 (5)	40 (7)	37 (6)	38 (6)
Time after peak velocity(%)	Visual	61 (5)	64 (5)	63 (4)	63 (5)	63 (5)	63 (6)	63 (4)
	Somato	62 (5)	64 (5)	63 (5)	64 (5)	60 (7)	63 (6)	62 (6)
Peak velocity (m/s)	Visual	1.12 (0.18)	1.13 (0.18)	1.24 (0.20)	1.12 (0.14)	1.11 (0.18)	1.13 (0.18)	1.11 (0.18)
	Somato	1.31 (0.17)	1.33 (0.19)	1.45 (0.21)	1.27 (0.18)	1.34 (0.15)	1.28 (0.17)	1.30 (0.18)

Table 2 Mean and standard deviation (in cm) for the accuracy variables of movements to somatosensory (somato) and visual targets

Variables	Targets	Perturbation conditions						
		No perturbation	Before		100 ms		200 ms	
			Away	Toward	Away	Toward	Away	Toward
Movement amplitude	Visual	31.2 (5)	30.9 (5)	31.4 (4.6)	30.9 (4.8)	31.6 (4.8)	31.2 (5.0)	31.6 (4.8)
	Somato	35.2 (3.4)	34.7 (3.5)	35.7 (3.4)	34.6 (3.6)	36.1 (3.4)	34.7 (3.5)	36.2 (3.4)
Amplitude constant error	Visual	−0.43 (2.22)	−0.02 (1.97)	0.19 (2.33)	0.02 (1.83)	0.40 (2.47)	0.23 (1.91)	0.39 (2.50)
	Somato	0.38 (1.49)	0.48 (2.14)	0.66 (2.18)	0.38 (2.12)	1.07 (2.30)	0.44 (1.97)	1.14 (2.45)
Direction constant error	Visual	1.32 (1.20)	0.47 (1.82)	−0.10 (1.63)	−0.14 (2.02)	−0.80 (2.11)	−1.62 (1.45)	−2.03 (2.03)
	Somato	0.16 (1.07)	−0.33 (1.30)	−0.07 (1.69)	−0.06 (1.21)	0.60 (1.33)	−1.03 (1.35)	−0.73 (1.24)
Amplitude variable error	Visual	1.47 (0.35)	1.60 (0.92)	1.48 (0.71)	1.55 (0.93)	1.23 (0.30)	1.51 (0.63)	1.43 (0.78)
	Somato	1.55 (0.49)	1.53 (0.61)	1.55 (0.38)	1.62 (0.52)	1.60 (0.63)	1.65 (0.67)	1.55 (0.54)
Direction variable error	Visual	1.39 (0.35)	1.20 (0.37)	1.28 (0.47)	1.56 (0.64)	1.64 (0.41)	1.71 (0.55)	1.82 (0.48)
	Somato	1.28 (0.23)	0.99 (0.28)	1.34 (0.38)	1.12 (0.28)	1.70 (0.69)	1.37 (0.55)	1.94 (0.76)
Correction magnitude	Visual	–	3.46 (0.94)	3.71 (0.81)	3.08 (0.97)	3.10 (0.70)	1.83 (0.57)	2.08 (0.72)
	Somato	–	4.18 (0.99)	4.68 (1.53)	4.45 (0.86)	5.34 (1.23)	3.53 (0.90)	4.06 (1.02)

that correction latencies in response to somatosensory target perturbations were significantly shorter ($M=68$ ms, SD = 20) than correction latencies to visual target perturbations ($M=188$ ms SD = 46). Breaking down the interaction revealed that, for visual targets, correction latencies were significantly shorter when the target was perturbed away from the body ($M=164$ ms, SD = 30) as compared to when the target was perturbed towards the body ($M=213$ ms, SD = 46). There were no significant differences in correction latency between directions for movements to somatosensory targets (see Fig. 6).

A supplementary analysis was performed to investigate if the differences between modalities in correction latencies could be explained by the differences in perturbation detection times. It was found that the differences in vocal response time between visual and somatosensory target modalities ($M=34$ ms, SD = 61) were much lower than differences between modalities in correction latency ($M=120$ ms, SD = 41) (see Online Resource 1 for computation and statistics). Overall, the results of this analysis revealed that between modality differences in target shift detection could not fully explain the differences in correction latency observed between the visual and somatosensory target conditions.

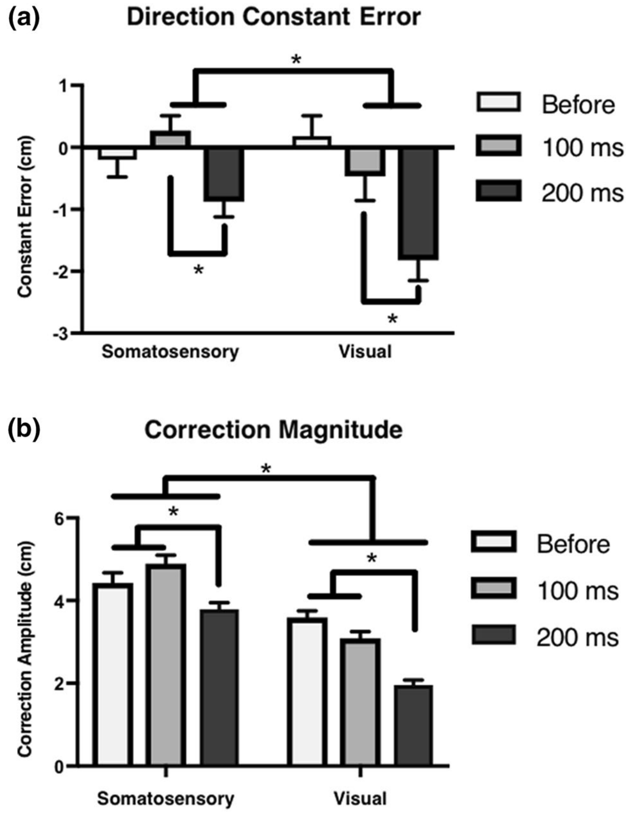

Fig. 5 **a** Direction constant error. Participants were more accurate when performing reaches to somatosensory targets perturbed after movement onset compared to when performing reaches to visual targets. When aiming to visual targets participants exhibited a larger under-correction relative to when making movements to somatosensory targets. **b** Correction magnitude. Participants exhibited larger corrections in response to somatosensory target perturbations than in response to visual target perturbations at all perturbation times. Furthermore, for both modalities, participants exhibited smaller corrections in response to perturbations at 200 ms than in response to the before and 100 ms perturbation times

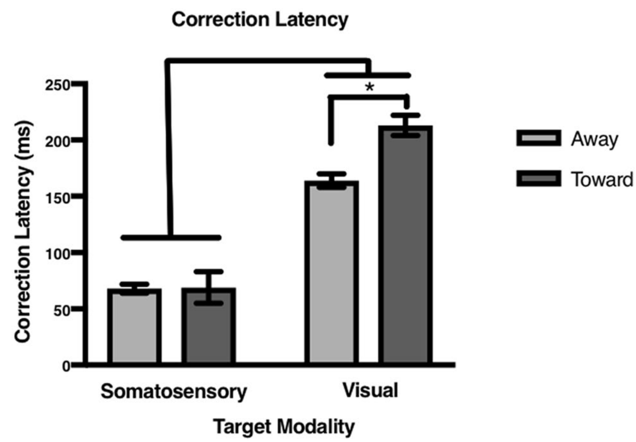

Fig. 6 Correction latencies in response to target perturbations. Overall, participants had shorter correction latencies in response to somatosensory target perturbations than in response to visual target perturbations. Furthermore, for visual targets, correction latencies were longer in response to targets perturbed toward the body

Discussion

The goal of the present study was to investigate whether the online sensorimotor transformations for movements to somatosensory targets, performed without vision of the limb, occurred in a visual or non-visual reference frame. Participants performed reaches to both somatosensory and visual targets that were either stationary or perturbed either before (~450 ms) or after (~100 ms or ~200 ms) movement onset. If sensorimotor transformations for the online control of movements to perturbed somatosensory targets employed a visual reference frame, then higher endpoint errors and longer correction latencies were expected in response to such perturbations. In contrast to this hypothesis, participants produced larger corrections and were more accurate when reaching to perturbed somatosensory targets compared to when reaching to perturbed visual targets. Also, correction latencies were shorter in response to somatosensory target perturbations than in response to visual target perturbations for perturbations that occurred after movement onset. Taken together, these results provide evidence that non-visual sensorimotor transformations are employed for the online control of movements to somatosensory targets when reaching with an unseen limb.

Participants were able to implement adjustments in response to somatosensory target perturbations (average correction latency = 68 ms) more rapidly than in response to visual target perturbations (average correction latency = 188 ms). These differences in latency were observed even though the amplitude, the speed and timing of target displacements were the same for both conditions. Correction latencies in response to the shift of visual target position (e.g. 120–300 ms) were in the range of what is typically found in other studies that examined reaching movements performed without vision of the reaching limb (Day and Lyon 2000; Komilis et al. 1993; Prablanc and Martin 1992; Reichenbach et al. 2009; Saunders and Knill 2003). Furthermore, the noted correction latencies were longer than the online visual feedback processing times observed when vision of the reaching limb is available (e.g. ~100 ms: Carlton 1992; Oostwoud Wijdenes et al. 2013; Zelaznik et al. 1983). These findings suggest that, similar to previous studies, corrections in response to perturbed visual targets likely involved the online remapping of the unseen reaching hand position to a visual reference frame.

In contrast, correction latencies in response to somatosensory target perturbations were much shorter than those commonly found when examining movements to visual targets. As mentioned above (see, above section: *Latency of Online Corrections*), technical differences between the current study and previous work could account for some of these discrepancies. However, the much shorter latencies in response to somatosensory target perturbations as compared to visual target perturbations do provide evidence against the hypothesis that the online control of reaching movements occur in a common visual reference frame. For upper-limb reaches to perturbed somatosensory targets, both the unseen target location and the unseen limb position would have to be remapped onto an extrinsic coordinate system prior to the initiation of online trajectory amendments. These transformations would likely require more time (Reichenbach et al. 2009) and result in greater errors (Sarlegna et al. 2009) than transformations required when reaching to a visual target with the unseen hand position, where only the latter must be remapped in visual coordinates. Thus, in the present study, it is likely that online sensorimotor transformations occurred in a non-visual reference frame for planning and correcting reaches to somatosensory targets.

The use of non-visual sensorimotor transformations for reaches to somatosensory targets with the unseen hand would support the more rapid and more accurate corrections found in the present study. For this type of sensorimotor transformation, corrections would be computed in somatosensory coordinates based on inputs from both the target and the reaching limb (Battaglia-Mayer et al. 2003; Burnod et al. 1999; Sarlegna and Sainburg 2007). Previous studies investigating connections of the posterior parietal cortex in macaque monkeys have revealed that neural networks capable of performing computations in somatosensory coordinates (Prevosto et al. 2011). Specifically, the medial intraparietal area of the posterior parietal cortex, which is implicated in sensorimotor transformations during the planning and control of arm movements (Buneo and Andersen 2006; Desmurget et al. 1998; Reichenbach et al. 2014), was shown to receive direct projections from both the somatosensory cortex (area 3a) and the dorsal column nuclei (Prevosto et al. 2010, 2011). It is thus possible that when reaching to a somatosensory target, updates to target location and reaching limb positions are processed directly through these network connections. Some support for this hypothesis could be drawn from previous studies which showed that disrupting processing in medial intraparietal area through transcranial magnetic stimulation impaired somatosensory-based corrections during the control of goal-directed actions (Reichenbach et al. 2014).

The short correction latencies noted when participants reached to somatosensory targets may also suggest the use of predictive mechanisms for correcting the movements. The fact that the target finger was always displaced by 3 cm may have contributed to the speed of movement corrections. That is, a priori knowledge of the final finger target position might have facilitated processes responsible for the trajectory corrections and thus reducing the correction latency. Although the visual target was always similarly displaced by 3 cm, the latencies for correcting the movements were much longer in the visual target condition. Together, these observations might suggest that predictive mechanisms are facilitated for controlling goal-directed arm movements on-line when both the target and the reaching hand can be encoded in a common sensory modality.

Similar to previous studies (e.g., Saunders and Knill 2003; Reichenbach et al. 2009), there was no effect of perturbation time on correction latency for movements to both visual and somatosensory targets. This finding supports those of previous studies that showed that online corrections occurred at roughly the same time relative to the onset of visual target perturbations (i.e., 163 ms after) in response to both early (25% of movement distance) and mid (50% of movement distance) perturbation conditions (Saunders and Knill 2003). This result was taken as evidence for the pseudo-continuous use of visual feedback throughout the reaching trajectory (see also Elliott et al. 1991). In the present study, our observation that correction latencies were not significantly altered by perturbation time when reaching to both visual and somatosensory targets may indicate that somatosensory information can be used in a pseudo-continuous manner at least in the first 200 ms of a movement lasting at least 500 ms (see also Tremblay et al. 2017).

It is also important to note that the aforesaid differences in correction latencies between movements to visual and somatosensory targets were not attributable to differences in the detection of the target displacement. Although participants detected perturbations to somatosensory targets faster than they detected perturbations to visual targets, the between modality differences in detection time was much lower than the between modality differences in correction latencies (see Online Resource 1).

The response times in both detection tasks (i.e., visual and somatosensory) may appear longer (i.e. >440 ms) compared to previous studies. However, it is important to note that, in the present study, participants had to respond only if the visual or somatosensory targets moved toward or away from them and had to refrain from responding when the targets moved to their left. Therefore, the detection tasks used here can be considered as the go/no-go tasks which are known to increase the latency of the go response compared to the response latency obtained through simple reaction tasks (Miller and Low 2001). Moreover, the longer detection times in the visual target condition could also be explained by the fact that it takes less time to detect motion onset than to detect motion direction (Sarlegna and Blouin 2010).

In agreement with the correction latency results, the analyses of direction constant errors revealed that participants were more effective at implementing corrections in response to perturbed somatosensory targets compared to perturbed visual targets. Participants exhibited larger corrections when reaching to perturbed somatosensory targets compared to perturbed visual targets for all perturbation times. Moreover, the constant error analyses revealed that participants were more accurate when correcting for somatosensory target perturbations as compared to visual target perturbations after movement onset (i.e. 100 ms and 200 ms conditions). No differences in accuracy were noted with respect to target modality for target perturbations that occurred before movement onset.

Similar to previous studies (Goodale et al. 1986; Komilis et al. 1993), the current results showed that, if the target was perturbed during movement planning, participants were able to fully correct for changes in target location. In the present study, the time available to implement trajectory amendments in response to perturbations that occurred before movement onset (> 900 ms) could explain the absence of differences in movement accuracy between target modalities.

In contrast, when target perturbations occurred after movement onset, movement endpoints were more accurate for reaches to somatosensory targets compared to visual targets. This finding could have two possible explanations. First, because corrections latencies were ~ 120 ms shorter in the somatosensory target condition, participants had more time to implement corrections when reaching to somatosensory targets than to visual targets. Second, when both the target and the hand are mapped in the same sensory coordinate system, sensorimotor transformations leading to the movements would be more accurate compared to when a reference frame conversion is necessary (Blouin et al. 2014; Sarlegna et al. 2009; Sober and Sabes 2005). To investigate whether target information obtained from somatosensory sources provides a better estimate of new target position, future studies should examine how disruptions in the accuracy of somatosensory information from the target limb (e.g., via tendon vibration) affects endpoint accuracy. If more accurate reference frame transformations are responsible for endpoint accuracy, then disrupting somatosensory target information should decrease movement accuracy. This decrease in accuracy would also be independent of the time required to implement corrections.

In the present study, differences were found when targets were perturbed away vs. towards the body, and that was the case for both the detection and control processes. Participants were quicker at detecting perturbed somatosensory targets compared to perturbed visual targets, but the difference between the two detection times was smaller when the targets were perturbed toward the body. This result could be explained by the physical attributes of the experimental setup. In the somatosensory target condition, the limb was already in slight extension. Thus, further extension may be more easily sensed than flexion due to the increased loading of muscle spindles (Hulliger 1984). A further extension also shifts the limb further away from the body's center of gravity likely invoking a greater postural response that could have been more salient due to greater activation of vestibular and cutaneous receptors (Lacquaniti and Soechting 1986). For the visual target, the physical setup of the experiment could have also played a role. Because of the position of the eyes and the fixation LED, the angular displacement of the target resulting from the 3-cm perturbations was greater when the target moved towards than away from the body. Even though all perturbations took place in the lower visual field, it is possible that this wider change in angle could have facilitated perturbation detection.

For somatosensory targets, the shorter detection times appeared to have a positive impact on performance as movements to somatosensory targets perturbed away from the body were significantly more precise than movements to somatosensory targets perturbed towards the body. In contrast, the pattern of results in detection times was not consistent with the results obtained for correction latency for visual targets. For example, it was found that correction latency was significantly longer for movements to visual targets perturbed towards the body compared to visual targets perturbed away from the body. These findings are, therefore, consistent with the hypothesis that detection processes have very little influence on correction processes during ongoing reaching movements (Smeets et al. 2016).

Conclusions

The results of the present study suggest that corrections to perturbed somatosensory targets are faster and more accurate than corrections to perturbed visual targets when reaching with an unseen limb. Thus, in contrast to movements to external visual targets, movements to somatosensory targets can be controlled using non-visual transformation processes based on somatosensory information about the reaching limb and target positions. These findings lend support to the idea that different sensorimotor transformations and perhaps different cortical networks are responsible for the online control of movements to somatosensory and visual targets performed without vision of the limb.

Acknowledgements The authors gratefully acknowledge Intishar Kazi for his help during data collection and Stephen Bested for the design of Fig. 1. The authors also acknowledge Damian Manzone and Sadiya Abdulrabba for providing helpful comments on the manuscript. This work was funded by the Natural Sciences and Engineering Research Council of Canada, the Canadian Foundation for Innovation, the Ontario Research Fund, and Campus France.

References

Ambrosini E, Ciavarro M, Pelle G et al (2012) Behavioral investigation on the frames of reference involved in visuomotor transformations during peripheral arm reaching. PLoS One 7:e51856. https://doi.org/10.1371/journal.pone.0051856

Bard C, Turrell Y, Fleury M et al (1999) Deafferentation and pointing with visual double-step perturbations. Exp Brain Res 125:410–416. https://doi.org/10.1007/s002210050697

Battaglia-Mayer A, Caminiti R, Lacquaniti F, Zago M (2003) Multiple levels of representation of reaching in the parieto-frontal network. Cereb Cortex 13:1009–1022. https://doi.org/10.1093/cercor/13.10.1009

Bernier P-M, Gauthier GM, Blouin J (2007) Evidence for distinct, differentially adaptable sensorimotor transformations for reaches to visual and proprioceptive targets. J Neurophysiol 98:1815–1819. https://doi.org/10.1152/jn.00570.2007

Bernier P-M, Burle B, Vidal F et al (2009) Direct evidence for cortical suppression of somatosensory afferents during visuomotor adaptation. Cereb Cortex 19:2106–2113. https://doi.org/10.1093/cercor/bhn233

Blangero A, Rossetti Y, Honoré J, Pisella L (2005) Influence of gaze direction on pointing to unseen proprioceptive targets. Adv Cogn Psychol 1:9–16. https://doi.org/10.2478/v10053-008-0039-7

Blouin J, Saradjian AH, Lebar N et al (2014) Opposed optimal strategies of weighting somatosensory inputs for planning reaching movements toward visual and proprioceptive targets. J Neurophysiol 112:2290–2301. https://doi.org/10.1152/jn.00857.2013

Bock O (1986) Contribution of retinal versus extraretinal signals towards visual localization in goal-directed movements. Exp Brain Res 64:476–482. https://doi.org/10.1007/BF00340484

Buneo CA, Andersen RA (2006) The posterior parietal cortex: sensorimotor interface for the planning and online control of visually guided movements. Neuropsychologia 44:2594–2606. https://doi.org/10.1016/j.neuropsychologia.2005.10.011

Burnod Y, Baraduc P, Battaglia-Mayer A et al (1999) Parieto-frontal coding of reaching: an integrated framework. Exp Brain Res 129:325–346. https://doi.org/10.1007/s002210050902

Carlton LG (1992) Visual processing time and the control of movement. In: Proteau L, Elliott D (eds) Advances in psychology. North-Holland, Oxford, pp 3–31

Dadarlat MC, O'Doherty JE, Sabes PN (2015) A learning-based approach to artificial sensory feedback leads to optimal integration. Nat Neurosci 18:138–144. https://doi.org/10.1038/nn.3883

Day BL, Lyon IN (2000) Voluntary modification of automatic arm movements evoked by motion of a visual target. Exp Brain Res 130:159–168. https://doi.org/10.1007/s002219900218

Desmurget M, Pélisson D, Rossetti Y, Prablanc C (1998) From eye to hand: planning goal-directed movements. Neurosci Biobehav Rev 22:761–788. https://doi.org/10.1016/S0149-7634(98)00004-9

Elliott D, Carson RG, Goodman D, Chua R (1991) Discrete vs. continuous visual control of manual aiming. Hum Mov Sci 10:393–418. https://doi.org/10.1016/0167-9457(91)90013-N

Goodale MA, Pelisson D, Prablanc C (1986) Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. Nature 320:748–750. https://doi.org/10.1038/320748a0

Goodman R, Crainic VA, Bested SR et al (2018) Amending ongoing upper-limb Reaches: Visual and proprioceptive contributions? Multisensory Res 31:455–480. https://doi.org/10.1163/22134808-00002615

Heath M (2005) Role of limb and target vision in the online control of memory-guided reaches. Mot Control 9:281–311

Henriques DY, Klier EM, Smith MA et al (1998) Gaze-centered remapping of remembered visual space in an open-loop pointing task. J Neurosci 18:1583–1594. https://doi.org/10.1523/JNEUROSCI.18-04-01583.1998

Hulliger M (1984) The mammalian muscle spindle and its central control. In: Reviews of physiology, biochemistry and pharmacology, vol 101. Springer Berlin Heidelberg, Berlin, pp 1–110

Johnson H, Van Beers RJ, Haggard P (2002) Action and awareness in pointing tasks. Exp Brain Res 146:451–459. https://doi.org/10.1007/s00221-002-1200-z

Jones SAH, Henriques DYP (2010) Memory for proprioceptive and multisensory targets is partially coded relative to gaze. Neuropsychologia 48:3782–3792. https://doi.org/10.1016/j.neuropsychologia.2010.10.001

Kennedy A, Bhattacharjee A, Hansen S et al (2015) Online vision as a function of real-time limb velocity: another case for optimal windows. J Mot Behav 47:465–475. https://doi.org/10.1080/00222895.2015.1012579

Komilis E, Pélisson D, Prablanc C (1993) Error processing in pointing at randomly feedback-induced double-step stimuli. J Mot Behav 25:299–308. https://doi.org/10.1080/00222895.1993.9941651

Lacquaniti F, Soechting JF (1986) EMG responses to load perturbations of the upper limb: effect of dynamic coupling between shoulder and elbow motion. Exp Brain Res 61:482–496. https://doi.org/10.1007/BF00237573

Manson GA, Alekhina M, Srubiski SL et al (2014) Effects of robotic guidance on sensorimotor control: Planning vs. online control? Neuro Rehabilitation 35:689–700. https://doi.org/10.3233/NRE-141168

McGuire LMM, Sabes PN (2009) Sensory transformations and the use of multiple reference frames for reach planning. Nat Neurosci 12:1056–1061. https://doi.org/10.1038/nn.2357

Miller JO, Low K (2001) Motor processes in simple, go/no-go, and choice reaction time tasks: a psychophysiological analysis. J Exp Psychol Hum Percept Perform 27:266–289

Mueller S, Fiehler K (2014) Effector movement triggers gaze-dependent spatial coding of tactile and proprioceptive-tactile reach targets. Neuropsychologia 62:184–193. https://doi.org/10.1016/j.neuropsychologia.2014.07.025

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9:97–113

Oostwoud Wijdenes L, Brenner E, Smeets JBJ (2011) Fast and fine-tuned corrections when the target of a hand movement is displaced. Exp Brain Res 214:453–462. https://doi.org/10.1007/s00221-011-2843-4

Oostwoud Wijdenes L, Brenner E, Smeets JBJ (2013) Comparing online adjustments to distance and direction in fast pointing movements. J Mot Behav 45:395–404. https://doi.org/10.1080/00222895.2013.815150

Oostwoud Wijdenes L, Brenner E, Smeets JBJ (2014) Analysis of methods to determine the latency of online movement adjustments. Behav Res Methods 46:131–139. https://doi.org/10.3758/s13428-013-0349-7

Pélisson D, Prablanc C, Goodale MA, Jeannerod M (1986) Visual control of reaching movements without vision of the limb. II. Evidence of fast unconscious processes correcting the trajectory of the hand to the final position of a double-step stimulus. Exp Brain Res 62:303–311. https://doi.org/10.1007/BF00238849

Pouget A, Ducom JC, Torri J, Bavelier D (2002) Multisensory spatial representations in eye-centered coordinates for reaching. Cognition 83:B1–B11

Prablanc C, Martin O (1992) Automatic control during hand reaching at undetected two-dimensional target displacements. J Neurophysiol 67:455–469. https://doi.org/10.1152/jn.1992.67.2.455

Prevosto V, Graf W, Ugolini G (2010) Cerebellar inputs to intraparietal cortex areas LIP and MIP: functional frameworks for adaptive control of eye movements, reaching, and arm/eye/head movement coordination. Cereb Cortex 20:214–228. https://doi.org/10.1093/cercor/bhp091

Prevosto V, Graf W, Ugolini G (2011) Proprioceptive pathways to posterior parietal areas MIP and LIPv from the dorsal column nuclei and the postcentral somatosensory cortex. Eur J Neurosci 33:444–460. https://doi.org/10.1111/j.1460-9568.2010.07541.x

Redon C, Hay L, Velay JL (1991) Proprioceptive control of goal-directed movements in man, studied by means of vibratory muscle tendon stimulation. J Mot Behav 23:101–108. https://doi.org/10.1080/00222895.1991.9942027

Reichenbach A, Thielscher A, Peer A et al (2009) Seeing the hand while reaching speeds up on-line responses to a sudden change in target position. J Physiol 587:4605–4616. https://doi.org/10.1113/jphysiol.2009.176362

Reichenbach A, Thielscher A, Peer A et al (2014) A key region in the human parietal cortex for processing proprioceptive hand feedback during reaching movements. Neuroimage 84:615–625. https://doi.org/10.1016/j.neuroimage.2013.09.024

Sarlegna FR, Mutha PK (2015) The influence of visual target information on the online control of movements. Vision Res 110:144–154. https://doi.org/10.1016/j.visres.2014.07.001

Sarlegna FR, Sainburg RL (2007) The effect of target modality on visual and proprioceptive contributions to the control of movement distance. Exp Brain Res 176:267–280. https://doi.org/10.1007/s00221-006-0613-5

Sarlegna FR, Blouin J (2010) Visual guidance of arm reaching: online adjustments of movement direction are impaired by amplitude control. J Vis 10:24. https://doi.org/10.1167/10.5.24

Sarlegna FR, Przybyla A, Sainburg RL (2009) The influence of target sensory modality on motor planning may reflect errors in sensori-motor transformations. J Neurosci 164:597–610. https://doi.org/10.1016/j.biotechadv.2011.08.021.Secreted

Sober SJ, Sabes PN (2005) Flexible strategies for sensory integration during motor planning. Nat Neurosci 8:490–497. https://doi.org/10.1038/nn1427

Saunders JA, Knill DC (2003) Humans use continuous visual feedback from the hand to control fast reaching movements. Exp Brain Res 152:341–352. https://doi.org/10.1007/s00221-003-1525-2

Saunders JA, Knill DC (2004) Visual feedback control of hand movements. J Neurosci 24:3223–3234. https://doi.org/10.1523/JNEUROSCI.4319-03.2004

Smeets JB, Erkelens CJ, Denier van der Gon JJ (1990) Adjustments of fast goal-directed movements in response to an unexpected inertial load. Exp Brain Res 81:303–312. https://doi.org/10.1007/BF00228120

Smeets JB, Oostwoud Wijdenes L, Brenner E (2016) Movement adjustments have short latencies because there is no need to detect anything. Mot Control 20:137–148. https://doi.org/10.1123/mc.2014-0064

Thompson AA, Glover CV, Henriques DYP (2012) Allocentrically implied target locations are updated in an eye-centred reference frame. Neurosci Lett 514:214–218. https://doi.org/10.1016/j.neulet.2012.03.004

Thompson AA, Byrne PA, Henriques DYP (2014) Visual targets aren't irreversibly converted to motor coordinates: eye-centered updating of visuospatial memory in online reach control. PLoS One 9:e92455. https://doi.org/10.1371/journal.pone.0092455

Tremblay L, Crainic VA, de Grosbois J et al (2017) An optimal velocity for online limb-target regulation processes? Exp Brain Res 235:29–40. https://doi.org/10.1007/s00221-016-4770-x

Veerman MM, Brenner E, Smeets JBJ (2008) The latency for correcting a movement depends on the visual attribute that defines the target. Exp Brain Res 187:219–228. https://doi.org/10.1007/s00221-008-1296-x

Zelaznik HZ, Hawkins B, Kisselburgh L (1983) Rapid visual feedback processing in single-aiming movements. J Mot Behav 15:217–236. https://doi.org/10.1080/00222895.1983.10735298