Somatosensory target information is used for reaching but not for saccadic eye movements

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Running Head: Somatosensory information for goal-directed movements

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Abstract
For any type of goal-directed hand and eye movement, it is important to determine the position of the target. Though many of these movements are directed toward visual targets, humans also perform movements to targets derived by somatosensory information only, such as proprioceptive (sensory signals about static limb position), kinaesthetic (sensory signals about limb movement), and tactile signals (sensory signals about touch on skin). In this study we investigated how each of these types of somatosensory information influences goal-directed hand and eye movements. Further, we examined whether somatosensory target information has a differential influence on isolated and combined eye-hand movements. Participants performed right-hand reaching, eye, or coordinated eye-hand movements to their left index or middle fingers in the absence of any visual information. We varied somatosensory target information by allowing proprioceptive, proprioceptive-kinaesthetic, proprioceptive-tactile, or proprioceptive-kinaesthetic-tactile information. Reach endpoint precision was poorest when the target was derived by proprioceptive information only, but improved when two different types of input were available. In addition, reach endpoints in conditions with kinaesthetic target information were systematically shifted toward the direction of movement, while static somatosensory information decayed over time and led to systematic undershoots of the reach target location. In contrast to the effect on reaches, somatosensory information did not influence gaze endpoint accuracy or precision. When performing coordinated eye-hand movements reach accuracy and gaze endpoint precision improved, suggesting a bidirectional use of efferent information. We
conclude that somatosensory target information influence endpoint control differently for goal-directed hand and eye movements to unseen targets.

**New & Noteworthy**

A systematic investigation of contributions of different somatosensory modalities (proprioception, kinaesthesia, tactile) for goal-directed movements is missing. Here we demonstrate that while eye movements are not affected by different types of somatosensory information, reach precision improves when two different types of information are available. Moreover, reach accuracy and gaze precision to unseen somatosensory targets improve when performing coordinated eye-hand movements, suggesting bidirectional contributions of efferent information in reach and eye movement control.

**Keywords**

Proprioception; tactile; kinaesthesia; eye-hand coordination; reaching; saccades
Introduction

Goal-directed movements are an integral part of everyday life. Due to the foveal organization of the visual system and the fact that many movements are primarily based on vision, humans deploy eye movements to acquire task-relevant visual input (Prablanç & Martin, 1992; Voudouris et al., 2018; Mann et al., 2019). This input is then used to plan and guide associated goal-directed body movements (Spering et al., 2011; Grant, 2015). Although humans typically have access to visual information about both the target and their moving body part, they can also plan and guide movements to targets that are derived on the basis of other sensory input, such as audition (Kolarik et al., 2017) or somatosensation (van Beers et al., 2002; Ren et al., 2006; Monaco et al., 2010; Voudouris et al., 2016). When both visual and somatosensory information is available, humans combine these signals to form a coherent estimate about the position of their body (van Beers et al., 2002; Reuschel et al., 2010; 2011). Obviously, when visual input is not available, somatosensory information is the sole source to derive body position.

Somatosensory information can be classified into three different types. First, static proprioceptive signals provide information about body position and arise primarily from muscle spindles, Golgi tendons and joint receptors (Purves et al., 2001). Static proprioception is thought to decay over time (Jones et al., 2012; Cameron et al., 2015), though this is not always the case (Rincon-Gonzalez et al., 2011; Kuling et al., 2019). Second, dynamic proprioception, hereby referred to as kinaesthesia, provides information input about both body position and movement (Colins et al., 2005). Although information from cutaneous receptors is involved (Edin & Johansson, 1995), the main kinaesthetic signals arise from changes in muscle length, such as afferents from dynamically activated muscle spindles during movement (Dimitriou & Edin, 2008). If changes in muscle length arise from actively performed movements, additional efferent information is generated by the associated motor command (Wolpert & Miall, 1996; Proske & Gandevia, 2009), possibly already available in muscle spindles that act as forward models (Dimitriou & Edin, 2010). Combining efferent and afferent signals contributes to estimations about the position of a limb (Debats et al., 2010). If neither of these signals is more reliable than the other, combining such information may lead to improvements of both precision (van Beers et al., 1999) and accuracy with which one can derive the position of that limb (van Beers et al., 2011). Another type of somatosensory information is tactile input, which mainly arises from mechanical activations of cutaneous receptors in the skin reacting to touch and vibration, independently of whether the limb moves or remains static. Tactile input can be helpful for movement control, as it contributes to the
accuracy of goal-directed hand movements (Rao & Gordon, 2001). The processing of tactile input on a limb largely depends on the postural configuration of that limb (Azanon & Soto-Faraco, 2008; Azanon et al., 2015; Longo, 2017), suggesting a close relationship between the proprioceptive and tactile sense.

Different types of somatosensory information can improve goal-directed hand movements. Indeed, reaching accuracy relies on proprioceptive input from the moving (Ghez et al., 1995) and the target limb (Rao & Gordon, 2001), while vibrotactile input from the unseen target hand can further improve reaching to that hand (Mikula et al., 2018). In contrast, contributions of somatosensory input on eye movements are limited. Saccades to an unseen proprioceptive target do not benefit from additional tactile (Blanke & Gruesser, 2001) or kinaesthetic signals (Voudouris et al., 2016) from that target. However, saccades are initiated faster when kinaesthetic input from the target hand is available (Voudouris et al., 2016). The finding that somatosensory target information improves hand movements but has limited contributions on eye movements may be due to the fact that for eye movements the body-centered somatosensory input needs to be transformed and expressed in a gaze-centered reference system, in which eye movements are primarily controlled (Nanayakkara & Shadmehr, 2003), and such conversion requires several reference frame transformations (Buneo et al., 2002). In contrast, transformations of body targets for reaching movements are less complex because body targets for reaching are represented in mixed body- and gaze-centered, or even only in body-centered coordinates (Mueller & Fiehler, 2016). Because sensorimotor transformations introduce noise (Abedi Khoozani & Blohm, 2018; Abedi Khoozani et al., 2020) and delays (Manson, Blouin et al., 2019), more elaborate transformations may lead to greater uncertainty in the transformed signal about body target position, possibly explaining why somatosensory input contributes less to goal-directed eye than hand movements.

Although previous studies examined how different types of somatosensory input influence hand and eye movements, a systematic investigation of how each of these three types of somatosensory signals contributes to goal-directed movements is still missing. More specifically, combining different types of somatosensory information about a body target may lead to improved representation of that target, enhancing movement planning and control. Such benefits may be more pronounced for hand than for eye movements because the more elaborate transformations required for eye movements to body targets introduce noise and may hinder possible benefits of the richer somatosensory input. However, the use of different somatosensory input signals may differ when coordinated eye-hand movements are performed.
to the same body target. Coordinated eye-hand movements are coupled to each other, at least when directed to visual targets (Neggers & Bekkering, 2000; Armstrong et al., 2013). In addition, although the saccadic and reaching systems may operate independently, these systems may constantly interact when simultaneously activated (Lazzariet al., 1997), for instance through sharing efference copies (Prablanc & Martin, 1992; Chen et al., 2016), or they may even be controlled on the basis of a single, common control signal (Bock, 1987). Therefore, during coordinated eye-hand movements to unseen somatosensory targets, the eye movement may benefit from the available somatosensory input that is used to facilitate the concurrently performed reaching movement.

To investigate the role of different types of somatosensory information separately on isolated and coordinated goal-directed hand and eye movements in the absence of any visual information, we asked participants to perform either isolated hand, or isolated eye, or coordinated eye-hand movements toward unseen fingers of their other hand. In different blocks of trials, we varied somatosensory information from the target finger by providing proprioceptive, proprioceptive-kinaesthetic, proprioceptive-tactile, or proprioceptive-kinaesthetic-tactile information and examined how the available input influences reach and gaze endpoint accuracy and precision during isolated and coordinated movements.

**Methods**

**Participants and apparatus.** Twelve healthy volunteers (5 females; mean age ± SD: 26 ± 4 years, age range: 20-35) with normal or corrected-to-normal vision participated in this study. Two of them were authors; the others were naïve to the purpose of this study. Participants were right-handed according to the Edinburgh Handedness inventory (Oldfield, 1971; mean ± SD: 89 ± 17). All participants gave their signed informed consent, and all but the authors received either financial compensation (8€/hour) or course credits for their participation. The study was approved by the local ethics committee of the Justus Liebig University Giessen and was in accordance with the Declaration of Helsinki (2013).

A top-view of the setup is shown in Figure 1. Participants sat in front of a table in a dark room. They held their mouth in an individually fitted bite-board that was fixed to a pole attached to the table. In front of the participant and 20 cm away from them, a custom-made frame (46 x 38 x 15 cm) was placed with its upper part covered with a touchscreen (MagicTouch 2.0, KeyTec Inc., Texas, USA) and a transparent foil below the touchscreen. The foil prevented participants from seeing anything below it, except when a small halogen lamp, below the frame, was switched on, in which case participants could see anything below
the foil. The bite-board and frame were inclined at 65° and 150°, respectively, relative to the table so that gaze direction was approximately orthogonal to the centre of the touchscreen. The eyes were at a distance of 30cm from the centre of the touchscreen.

A light-emitting diode (LED) was fixed below the touchscreen and was centrally placed at the part of the frame that was closest to the participant. The start position of the right hand was located on the touchscreen, 1 cm to the right of the LED. The participant’s body midline was aligned to the touchscreen and start position. Two rings were fixed on a slider that was attached to a rail below the frame. The slider could only move along this rail and only along the sagittal plane with respect to the participant. Two solenoids, 5 cm apart from each other laterally, were attached below the foil at the target positions, 20 cm away from the start position in the sagittal direction. Each of these solenoids could present tactile stimuli (mechanical taps) to the participants’ fingertips through a pin (diameter: 3 mm; length: 10mm) that touched the participant’s finger with a force of 0.1 N. The participants’ index and middle fingers were fit into the rings throughout the experiment. The two fingers did not contact with any other surface, except for when being stimulated by the respective solenoid at the target position.

Eye movements of the right eye were recorded at 500 Hz using an Eyelink II eye-tracker (SR Research Ltd.). The recording of the eye movements was calibrated with the standard nine-point calibration procedure of the Eyelink II, which was projected through an LCD projector on the touchscreen. The touchscreen recorded the coordinates of the positions that were touched during the trial.

Procedure. Participants performed isolated hand, isolated eye or coordinated eye-hand movements toward the unseen index or middle finger of their left hand. In the absence of any visual information, the position of the target digit could be derived by proprioceptive (P), proprioceptive-kinaesthetic (PK), proprioceptive-tactile (PT) or proprioceptive-kinaesthetic-tactile (PKT) information. Each of the three different effector movements was examined separately for each of the four different sources of somatosensory information, resulting in a total of 12 blocks of trials per participant, presented in counterbalanced order.

When performing isolated hand movements, the LED turned on and participants had to fixate it. They then pressed the touchscreen at the start position with their right index finger, which prompted a standard drift correction of the Eyelink eye-tracker, by aligning the current gaze position at that moment with the predefined start position. This also indicated the start of the trial. In the proprioceptive-kinaesthetic block, a sound 50 ms after drift correction prompted
participants to move their left hand from the start to the target position while maintaining fixation at the LED. A barrier at the target position would stop the slider from moving further in the sagittal direction. A high or a low pitch tone 50 ms after the left hand arrived at the target position cued a right-hand reaching movement to the unseen index or middle finger of the left target hand, respectively. Participants were asked to immediately perform the reaching movement (mean ± SD latency across all conditions: 387 ± 120 ms) by lifting their right index finger off the touchscreen and touching the touchscreen right above the target digit. Then, they moved their left hand back to the start position, which determined the end of the trial and stopped data collection. The procedure in the proprioceptive-kinaesthetic-tactile block was similar with the only difference being that there was no auditory cueing of the target digit. Rather, a tactile stimulus was applied to one of the two digits 50 ms after the left hand arrived at the target position. The procedure in the proprioceptive and in the tactile blocks was almost similar to the above-mentioned blocks but with the difference that the left hand was stationary at the target position throughout the whole block, and that the cue (auditory or tactile, respectively) was presented 50 ms after drift correction. In these two conditions, the trial ended immediately after the reaching movement was completed, as this was determined by the contact of the right index finger with the touchscreen. For these four blocks, gaze was always kept fixed at the LED throughout the trial.

When performing isolated eye movements the procedure was similar to that described for isolated hand movements. The main difference was that once the target digit was cued, the LED turned off and participants had to perform immediately an eye movement to the unseen target digit (mean ± SD of gaze latency: 223 ± 69 ms). Trials with kinaesthetic information were completed when the left hand returned to the start position. Trials without kinaesthetic information were completed 650 ms after the onset of the (auditory or tactile) cue. For these four blocks, the right index finger was kept at the start position throughout the trial.

When performing coordinated eye-hand movements, the procedure was similar to the above-mentioned ones, but participants had to initiate a combined eye-hand movement toward the target digit. Due to the differences in latency (gaze: 262 ± 104 ms; reach: 397 ± 87 ms) this typically led to an initial saccade followed by a hand movement toward the target. In these conditions, each trial ended immediately after the right index finger finished the reaching movement.

In each of the above-mentioned 12 experimental blocks, participants performed 40 trials toward each digit, resulting in a total of 80 trials per block. Blocks with and without kinaesthetic information lasted around 7 and 4 minutes, respectively. Participants took short
self-paced breaks between blocks. The experiment was performed on three days, with participants performing four blocks of trials on each day. The order of blocks was randomized across participants. The total duration of the experiment was ~2 hours.

After the end of the last experimental block on the last day of measurement, participants performed a calibration block, throughout which they kept their left hand at the target position. While having their gaze and right index finger at the start position, the light below the touchscreen turned on and the position of their digits became visible. An auditory cue was then presented and participants performed a combined eye-hand movement toward the visible target digit. Once they did so, the light turned off and participants moved their right hand and gaze back to the start position in anticipation of the next calibration trial. We decided to present the calibration after the experimental blocks to prevent participants using any memorized visual cues about the target position when performing the experimental blocks. In the calibration block, participants performed 15 trials for each of the two target digits for a total of 30 calibration trials. The calibration block lasted approximately 3 minutes.

**Data analysis.** We were interested in examining how the different sources of somatosensory information and the coordinated execution of eye-hand movements influence reach and gaze endpoint accuracy and precision. For this, we determined the endpoint errors of the reach and eye movements in each trial.

We first calculated the calibrated reach and gaze endpoint for each target digit based on the measurements in the calibration block. For each of the calibration trials, we first determined the reach endpoint as the position where participants touched the touchscreen after reach onset (right index finger lift off) and the gaze endpoint as the median 2D gaze position in the last 100 ms before the moment of the reach endpoint. We then calculated each participant’s calibrated reach and gaze endpoint separately for each digit by averaging across the 15 endpoints that we determined for that digit. These represent the calibrated target positions.

We then calculated the endpoints during the experimental trials. We determined the reach endpoint as the position where participants touched the touchscreen after reach onset. Subsequently, we calculated the reach endpoint error in each trial separately for each digit. This error was calculated as the two-dimensional Euclidean distance between each participant’s calibrated reach target position and their reach endpoint. Because there was no visual target to anchor gaze, participants could perform several eye movements to localize the unseen target within each trial. Therefore, we were especially interested in gaze position just
before the end of the reach and determined gaze endpoint as the median gaze position during
the last 100 ms before the end of the reaching movement, which was also the end of the trial
(as in the calibration block). In the isolated eye conditions, where no reaching movements
were performed, we determined gaze endpoint as the median gaze position during 550 and
650 ms after cue onset. By using this criterion, we reassured that we keep our analyses
approach consistent between conditions with and without kinaesthetic information, as we
examine gaze always at the last 100 ms of the trial. Doing so allowed for robust and
comparable calculations of gaze endpoints in both the isolated and coordinated eye
conditions, while reassuring that there was enough time to bring gaze to the felt target
position and to perform any additional corrective eye movements. Gaze endpoint error was
then calculated in each trial, separately for each digit, as the two-dimensional distance
between each participant’s calibrated gaze target position and their gaze endpoint.

Endpoint errors were averaged across the 40 trials performed toward each digit,
separately for each condition and participant. We consider the average endpoint error to
represent endpoint accuracy. For each participant we fit a 95% confidence interval ellipse to
each digit’s reach and gaze endpoints in each condition. We consider the area of this ellipse to
represent endpoint precision. Endpoint accuracy and precision were computed for each digit
separately and then averaged across the two target digits since there was no effect of target
digit on any of the relevant measures (for details see Results). Effects of the different sources
of somatosensory information (proprioceptive, proprioceptive-kinaesthetic, proprioceptive-
tactile, proprioceptive-kinaesthetic-tactile) and movement type (isolated vs. coordinated
movement) on endpoint accuracy and precision for hand or eye movements were analyzed
with separate 4 (somatosensory information) x 2 (movement type) x 2 (target digit) repeated-
measures ANOVAs. When required, significant differences between conditions were further
examined with post-hoc t-tests (Bonferroni-corrected for multiple comparisons, corrected
alpha: alpha/n, with n being the number of comparisons). To test for covariance of reach and
eye endpoint accuracy in the coordinated condition, bivariate correlations were computed
within subjects on the trial-by-trial level and across participants. All statistical analyses were
performed in MATLAB, and effect sizes were calculated with JASP.

To evaluate a possible temporal component to the representation of target position, we
also looked at the change of reach and gaze endpoint errors across trials in each block. Since a
different amount of trials per participants were excluded (see below for exclusion criteria) and
the order of target digits was randomized across trials we could not simply average the
endpoint error in each trial across participants. For this reason, we obtained the sorted vector
containing the endpoint error values in all valid trials for each participant and each condition and then normalized the length of this vector to 21 steps (representing 0 to 100% block duration in 5% steps) using the interp1 function in MATLAB. As a result of this normalization procedure we could average the values across digits and participants to investigate the fluctuation of endpoint error over the time-course of each block.

**Exclusion of trials.** Reach and gaze endpoints were excluded respectively (1) if the calculated reach or gaze endpoint error was larger than 15 cm (95 reach trials, 281 gaze trials), or (2) when an endpoint was more than 2.5 standard deviations away from the median endpoint of the same participant in the same condition (198 reach trials, 271 gaze trials). Additionally, we excluded trials from the gaze analysis if there was a blink in the time interval when we determined gaze endpoint (56 trials). For the isolated reach condition, we checked for gaze movements toward the target location (defined by more than 5cm distance from the initial fixation), but did not observe any of these trials. Based on these criteria we analyzed 7387 of 7680 reaching trials (exclusion between 2 and 10% of the total number of trials per participant) and 7072 of 7680 gaze trials (exclusion between 4 and 19% of the total number of trials per participant) across the three movement conditions.

**Results**

The goal of the present study was to investigate the contribution of different types of somatosensory information on goal-directed reaching and eye movements. In addition, we examined whether the type of somatosensory input influences differently isolated or coordinated hand and eye movements. We designed an experiment where participants had to reach and/or look to the index or middle fingertip of their unseen left hand and varied the available somatosensory information from the target digit, importantly always in the absence of vision. In the following, we will report results separately for endpoint accuracy and precision.

**Endpoint accuracy.** To analyze reach and gaze endpoint accuracy we computed the respective endpoint errors for each of the different levels of somatosensory information and for isolated and coordinated movements (Figure 2). We used two separate repeated measures ANOVAs, each for reach and eye movements, with the factors *somatosensory information* (proprioceptive, proprioceptive-kinaesthetic, proprioceptive-tactile, proprioceptive-kinaesthetic-tactile), *movement type* (isolated, coordinated) and *target digit* (index finger, middle finger) to assess the influence of these factors on reach and gaze endpoint accuracy.
Because the target digit had no influence on reach \((F(1,11) = 0.16, p = .698, \eta^2 = .001)\) or gaze \((F(1,11) = .003, p = .958, \eta^2 < .001)\) accuracy, we report the following results after averaging reach and gaze endpoints across the two target digits.

For reach endpoint accuracy, there was no systematic influence of somatosensory information \((F(3,33) = 2.23, p = .103, \eta^2 = .058; \text{ Figure 3A})\). However, reach endpoint accuracy improved in the coordinated \((3.27 \pm 1.27 \text{ cm})\) compared to the isolated condition \((4.15 \pm 0.99 \text{ cm}; F(1,11) = 8.75, p = .013, \eta^2 = .116)\). This is remarkable, as it indicates that shifting gaze toward an invisible target improves reach accuracy, even though this gaze shift provides no visual information about the target or the moving hand. While the accuracy in the isolated and coordinated conditions was correlated \((r(10) = .61, p = .036)\), there was a consistent benefit for the coordinated movement across participants (Figure 3B). No interaction between somatosensory information and movement type was found \((F(3,33) = 0.84, p = .484, \eta^2 = .018)\).

For gaze endpoint accuracy there was also no effect of the type of somatosensory information \((F(3,33) = 2.01, p = .132, \eta^2 = .058)\). In addition, and in contrast to reaching behavior, there was no significant effect of movement type \((F(1,11) = 2.31, p = .157, \eta^2 = .045)\), and no systematic interaction between the factors \((F(3,33) = 2.61, p = .068, \eta^2 = .024)\).

Gaze endpoint errors were greater than reach endpoint errors in the coordinated condition \((4.71 \pm 1.75 \text{ cm} \text{ vs. } 3.27 \pm 1.27 \text{ cm}; t(11) = 3.59, p = .004, \text{ Figure 3C})\) and the extent of these errors was correlated across participants \((r(10) = .62, p = .032)\). That the amount of reach endpoint error was closely related to the amount of gaze endpoint error in the coordinated conditions was further confirmed by significant within-participants correlations (9/12 participants). Interestingly, the improvement of each participant’s reach accuracy in coordinated compared to isolated reaches also correlated with gaze endpoint accuracy \((r(10) = .63, p = .027)\). Taken together, these results suggest that efferent information associated with the eye movement is used for reach control.

To further analyze the influence of the concurrent eye movement on reach accuracy, we examined reach endpoint errors along the frontal and sagittal plane, separately. For convenience, these endpoint errors will be hereafter referred to as lateral and distal endpoint errors. This approach allowed us to detect potential shifts in reaching endpoints along each movement direction (c.f., Mueller & Fiehler, 2014, 2016). For the lateral reach endpoint error (Figure 4A), we did not find any influence of somatosensory information \((F(3,33) = 2.51, p = .076, \eta^2 = .038)\) or movement type \((F(1,11) = 0.67, p = .430, \eta^2 = .014)\), nor a significant interaction \((F(3,33) = 1.34, p = .286, \eta^2 = .008)\). Interestingly, there was a systematic effect of
the type of somatosensory information on distal endpoint errors (F(3,33) = 44.32, p < .001, η² = .459; Figure 4B). More specifically, reach endpoints were shifted further along the sagittal direction when kinaesthetic information was available (average error without K: -2.42 ± 2.15 cm; average error with K: 0.52 ± 2.78 cm). Note here that despite the average distal error being close to zero in the kinaesthetic conditions, the variability across participants was large as individuals who had small distal errors in non-kinaesthetic conditions (P and PT) had larger distal errors in kinaesthetic conditions (PK and PKT). Thus, kinaesthetic information did not always improve reach endpoint accuracy, but it systematically led to a shift of the reach endpoint in the direction of the movement. There was no influence of movement type (F(1,11) = 0.15, p = .703, η²= .003) and no significant interaction (F(3,33) = 1.40, p = .260, η²= .021) on distal errors.

One potential explanation for the effects of the kinaesthetic information on the distal reach endpoint errors could be an increased drift of the proprioceptive information from the target hand when kinaesthetic target information was not available (c.f., Jones et al., 2012; Cameron et al., 2015). To explore this, we normalized the distribution of trials within each block and computed the distal reach endpoint error in steps of 5% of the block, separately for each type of somatosensory information and movement type (see Methods for details). We observed an increase in the distal error over the time-course of the block for conditions without kinaesthetic information (see Figure 5A), while the distal error remained nearly constant when kinaesthetic information from the target hand was available. To quantify this effect, we computed the average distal error during the first 25% and during the last 25% of each block for each participant and took the difference between these two values, with negative differences reflecting larger undershoots in the late than early trials. We expected that position drift would increase in conditions without kinaesthetic information (e.g., Cameron et al., 2015), but would remain low in kinaesthetic conditions, when the combination of afferent and efferent input in each trial may facilitate target representation (Debats et al., 2010). To examine this, we computed a 4 (somatosensory input) x 2 (movement type) repeated measures ANOVA. There was a main effect of somatosensory information (F(3,33) = 26.00, p <.001, η²= .401), driven by a substantial drift in the conditions without kinaesthetic information (P: t(11) = 5.96, p <.001; PT: t(11) = 4.51, p < .001; Figure 5B), but not in those with kinaesthetic information (PK: t(11) = 1.04, p =.319; PKT: t(11) = 2.13, p =.057), suggesting increased drift when kinaesthetic information was not available. Though there was a trend for less drift of reach endpoints in the coordinated condition, this was not systematic (F(1,11) = 4.53, p =.057, η²= .072; Figure 5B), and there was no interaction between the two factors (F(3,33) =
0.58, p = .635, \eta^2 = .009). Together, these results suggest that the difference in distal error depending on the somatosensory information could be explained by an increased drift in the conditions without kinaesthetic information.

**Endpoint precision.** To quantify the precision of the reach and eye movement endpoints we again performed two separate ANOVAs, each for reach and gaze endpoints, with the factors *somatosensory information* (proprioceptive, proprioceptive-kinaesthetic, proprioceptive-tactile, proprioceptive-kinaesthetic-tactile), *movement type* (isolated, coordinated) and *target digit* (index finger, middle finger). There was again no influence of target digit on reach (F(1,11) = 3.93, p = .073, \eta^2 = .005) or gaze endpoints (F(1,11) = 0.59, p = .458, \eta^2 = .010); thus, we averaged the data across digits.

In contrast to reach endpoint accuracy, somatosensory information this time influenced reach endpoint precision (F(3,33) = 6.31, p = .002, \eta^2 = .174; Figure 6A). Precision was poorest when only proprioceptive information was available, and increased when two types of somatosensory information were available (P vs. PK: t(11) = 3.37, p = .006; P vs. PT: t(11) = 3.37, p = .006). Improvements were also observed when all three types of somatosensory information were available (P vs. PKT: t(11) = 2.61, p = .024, corrected alpha: 0.083), however this comparison did not survive the multiple comparisons. No other comparison reached significance (PT vs. PK: t(11) = 2.13, p = .056; PK vs. PKT: t(11) = 1.47, p = .170; PT vs. PKT: t(11) = 0.30, p = .773). To visualize the effect of somatosensory information on reach endpoint precision, we subtracted the precision in the proprioceptive condition (P) from the precision in each of the other three conditions (Figure 6B). Together these results suggest that reach precision is improved when two different sources of somatosensory information are available (reduction of variance: 1.51 ± 1.55cm² for PK; 0.94 ± 0.97cm² for PT; 1.05 ± 1.40cm² for PKT). There was no effect of movement type (F(1,11) = 2.49, p = .143, \eta^2 = .023), nor an interaction between somatosensory information and movement type (F(3,33) = 0.80, p = .502, \eta^2 = .016) on reach endpoint precision.

The improvement of reach endpoint precision with two sources of somatosensory information suggests an integration of different somatosensory inputs for reach control. The statistically optimal integration of information suggests that the integrated signals are redundant and thus can compensate for uncertainties in the single senses resulting in increased precision. To examine this in more detail, we tested whether this integration is statistically optimal on the individual level. The independently measured precisions in the proprioceptive-kinaesthetic and proprioceptive-tactile conditions were used to estimate the optimal precision
when both sources were integrated in a Bayesian framework (Ernst & Banks, 2002; Optimal = \sqrt{(PK^2*PT^2/(PK^2+PT^2))}. We computed the optimal precision for each individual participant and compared it to the actually measured precision in the condition with all three somatosensory inputs (PKT). The observed and predicted precision were different from each other (t(11) = 2.70, p = .02) with the observed precision in the PKT condition (2.11 ± 0.35 cm²) being worse than the one predicted by a Bayesian framework (1.29 ± 0.17 cm²). This result indicates that despite the fact that different types of somatosensory information increase reach precision, the integration of these different sources is not statistically optimal.

In contrast to reaching behavior, gaze endpoint precision was not influenced by somatosensory information (F(3,33) = 2.24, p = .102, \eta^2 = .045). However, there was a significant influence of the type of movement (F(1,11) = 4.901, p = .049, \eta^2 = .026; Figure 6D), with improved gaze precision in the coordinated (11.67 ± 6.83 cm²) than isolated condition (14.03 ± 7.04 cm²). There was no interaction between somatosensory information and movement type (F(3,33) = 1.40, p = .259, \eta^2 = .020).

Discussion

We examined how different types of somatosensory information about the target position contribute to reaching and eye movements in the absence of visual information. To this end, participants performed isolated hand, isolated eye, or coordinated eye-hand movements to the felt position of their unseen index and middle fingers. Different types of somatosensory information were presented on these target digits: proprioceptive, proprioceptive-kinaesthetic, proprioceptive-tactile or proprioceptive-kinaesthetic-tactile. We observed a systematic influence of the available somatosensory information on reach performance, while gaze endpoints were unaffected. Reach endpoint precision was poorest when target position was derived solely from proprioceptive input and it improved when two types of somatosensory information were available. In addition, kinaesthetic information from the target digits affected reach endpoints by limiting proprioceptive drift and shifting reach endpoints in the direction of movement. Performing a coordinated eye-hand movement led to improved reach accuracy and gaze precision, suggesting differential use of the available somatosensory afferent and coordinated efferent information for gaze and reach movements.

Somatosensory input for reaching performance

The type of somatosensory information from the target hand did not influence reach endpoint accuracy but it did affect endpoint precision. More specifically, reach endpoint precision was
poorest when only proprioceptive target information was available, but improved with two different somatosensory signals. Our results suggest that different kinds of somatosensory information may be integrated to improve target localization for reaching. Previous studies have shown close to optimal integration of proprioceptive and visual information (van Beers et al., 1999; Reuschel et al., 2010), while others did not observe such effects (Reuschel et al., 2011; Jones et al., 2012). Despite evidence for some integration of different somatosensory signals, reach endpoint precision did not systematically improve when all somatosensory signals were available (Figure 6A), and were not integrated in a statistically optimal manner within participants (see Figure 6C). This might originate from possible dependencies between the available types of somatosensory information: For instance, although proprioceptive and tactile information is processed in different sensory organs, these signals also interact with each other, as the processing of tactile signals on a static limb depends on the postural configuration of that limb (Azanon & Soto-Faraco, 2008; Azanon et al., 2015). Therefore, possible dependencies between the different types of somatosensory information may prevent their optimal integration.

Despite the partial integration of somatosensory information, the imprecision of the reach endpoints in proprioceptive conditions may arise due to drifts of the proprioceptive estimates of the target hand (Brown et al., 2003; Cameron et al., 2015; but see also Rincon-Gonzalez et al., 2011; Kuling et al., 2019). We show that distal reach endpoint errors increase over the time-course of the reaching blocks toward non-kinaesthetic target positions (P and PT; Figure 5A), leading to increased endpoint imprecision along the sagittal direction. Nevertheless, the overall 2D precision in the proprioceptive-tactile condition was higher compared to the only proprioceptive condition (Figure 6A), suggesting that additional tactile information contribute to some extent to endpoint control (e.g., Mikula et al., 2018).

Drift was substantially diminished in conditions with additional kinaesthetic information. In these conditions, the target hand was moved from the start to the target position in each trial, and thus somatosensory information from the target was frequently updated reducing the time for the somatosensory estimate of the target hand to drift. The drift in the proprioceptive conditions (P and PT) was particularly evident along the sagittal direction, as endpoints gradually undershot the unseen target. This was not evident in the kinaesthetic conditions, in which not only the endpoints did not drift, but they also overshoot the target. This increased drift in P and PT could not be explained by differences in overall block duration, since blocks with kinaesthetic information even took roughly 3 minutes longer than the blocks without. Thus, kinaesthetic input from the target hand led to a shift in the
representation of the target’s position in the sagittal direction, likely in the direction of the reaching movement and not of the movement of the target hand (c.f., Mueller & Fiehler, 2014; 2017). The combination of afferent and efferent information from the target limb, both associated with kinaesthesia, might have significantly contributed to both precision (Figure 5A) and accuracy (Figure 5B) with which the position of the unseen body target was derived (van Beers et al., 2011). Yet, with our current design we cannot distinguish the relative contributions of both signals associated with the movement of the target hand. By integrating a condition where the target hand would be passively moved to the target location, afferent and efferent information could be dissociated.

The somatosensory target was cued by either a tactile (PT and PKT) or an auditory input (P and PK). These two cues may have introduced different limitations to the reaching system, as auditory cueing of somatosensory targets requires additional sensorimotor transformations (Manson, Tremblay et al., 2019). In this case, performance in the non-tactile conditions (P and PK) may have been compromised, as additional transformations take time (Manson, Blouin et al., 2019) and introduce uncertainty (Abedi Khoozani & Blohm, 2018). One might argue that the increased precision in PT compared to P arose from less demanding sensorimotor transformations. However, when comparing the P and PK conditions, which both only had auditory cues, we found improved precision in PK, which rather speaks for an integration of different sources of somatosensory information. If the auditory cue in the P and PK conditions indeed caused higher uncertainty about the target’s position, the integration of the additional kinaesthetic information could compensate for this uncertainty, as the precision between PK and PT was similar (see Figure 6).

Somatosensory input for gaze performance

In contrast to reaching, the type of somatosensory information did not systematically influence gaze endpoint control, confirming previous findings (Blanke & Gruesser, 2001; Voudouris et al., 2016). This might be due to the requirement of representing both the target and the effector in the same reference frame (Blouin et al., 2004). When performing an eye movement to a somatosensory target, the body-centered somatosensory target representation needs to be converted into a gaze-centered representation by passing through several steps of reference frame transformations (Buneo et al., 2002; McGuire & Sabes, 2009), while reaching to somatosensory targets requires less complex transformations (Pouget et al., 2002; Mueller & Fiehler, 2016). Sensorimotor transformations introduce noise and may eventually increase the uncertainty about the resultant estimate of the target’s position (Abedi Khoozani &
Blohm, 2018; Abedi Khoozani et al., 2020). If this uncertainty is greater than the possible benefit of the additional somatosensory input, gaze endpoint control to somatosensory targets may not improve.

The endpoint accuracy of eye and reaching movements substantially differed in our study. The gaze endpoint error was on average ~5 cm across the four somatosensory conditions, while the associated reach endpoint error was ~1-2 cm smaller in comparison to the gaze error (see Figure 3C). This increased gaze endpoint error might arise from increased noise in the measurement of gaze position, though it is more likely that it arises from the lack of visual input where participants could anchor their gaze to (c.f., Flanagan et al., 2008).

One possible factor influencing the calculation of gaze and reach accuracy might be that endpoint errors were calculated on the basis of the actual endpoint and the calibrated position. During calibration, participants could see the veridical position of their target digits through the setup. Because in this case both visual and somatosensory information about the target position was available, participants may have relied more on the visual than the proprioceptive estimate (Ernst & Banks, 2002; although this is not always the case: van Beers et al., 2002). If participants relied primarily on vision to guide their reaching movements during calibration, this could have influenced the calculation of the endpoint errors, however, this would only affect the absolute strength of the error, but not the differences between the conditions.

Influences of isolated and coordinated movements on reach and gaze performance

Performing isolated or coordinated movements differently influenced reach and gaze endpoints. First, reach endpoint accuracy improved when an eye movement was concurrently performed toward the unseen target. This reduced the overall reach endpoint error, but it influenced neither its individual components along the frontal and sagittal planes, nor the drift of the endpoints. Second, gaze endpoint precision improved when a concurrent reaching movement was performed to the same somatosensory target.

Two main mechanisms have been proposed for the control of coordinated eye-hand movements: one single signal may govern both movements (Bock, 1987), or two independent signals may be responsible for each movement but these signals may constantly interact (Lazzari et al., 1997; see also Chen et al., 2016 for a discussion of the two possibilities). Recent neurophysiological evidence supports the latter idea, as inactivation of the lateral intraparietal area (LIP), which plays a crucial role in eye-hand coordination (Dean et al., 2012; Yttri et al., 2013), does not affect isolated hand movements, but impairs reaches when
performed in coordination with an eye movement (Yttri et al., 2013). However, this difference may arise because LIP is part of a network responsible mainly for oculomotor behavior and less for reach control (Christopoulos et al., 2018). Our results could be interpreted in line with the idea of independent signals controlling coordinated eye-hand movements, as if there was a single control signal, reach accuracy should have been affected similarly between isolated and coordinated movements.

There are multiple possible mechanisms that could explain how a coordinated eye movement enhances reach accuracy. First, gaze is typically shifted to the target before the hand, and therefore retinal input can be used to guide the reaching movement. Second, sensory processing at the target position is enhanced for visual (Hanning et al., 2018; Nissens & Fiehler, 2018) and tactile targets (Rorden et al., 2002) already before the execution of the eye movement to that target. This selection of a task-relevant region before movement onset (which is often referred to as an attentional shift) can be an efficient way to choose the relevant features for the upcoming action. However, as retinal input did not change in our paradigm, we believe that these two mechanisms are rather unlikely.

An alternative explanation is based on an improvement of reach endpoint errors by efferent eye signals. For instance, ocular-proprioceptive signals about gaze orientation and the corresponding efference copy signals may have been used to guide the upcoming reaching movement (Prablanc & Martin, 1992; Vaziri et al., 2006; Wilmut et al., 2006). In support of this, we did observe a systematic correlation between gaze and reach endpoint errors (Figure 3C), as well as gaze accuracy and the improvement in reach accuracy in coordinated movements. These corroborate the idea that the improvement in reach accuracy during coordinated eye-hand movements most likely arises from efferent eye signals being shared with the reaching system.

We also observed improved gaze endpoint precision when a coordinated reaching movement was performed toward the same somatosensory target. This suggests that efferent signals from the reaching movement are shared with the eye movement system. A question that arises is whether these efferent signals are used in a similar manner in both systems. Our results show that efferent eye movement information enhanced reach accuracy, while efferent reach information improved gaze precision, suggesting that the reaching movement contributed to reducing inherent noise in the saccadic system, which is associated with variable endpoint errors. This effect suggests a differential use of efferent signals within the eye movement and reaching systems.
One possible explanation for this different use might be the temporal order of the eye and hand movements. Eye movements generally have lower latencies than hand movements, which allows them to guide the hand toward the target resulting in increased reach accuracy (Neggers & Bekkering, 2002). However, efference copies of both the reaching and the eye movement were likely available before the initiation of the coordinated eye-hand movement: This is likely due to the lower inertia of the eye that allows faster movement initiations. When the onset of muscular activity of both movements is measured, their latencies are comparable, and might be even shorter for reaches (Gribble et al., 2002). Even though the execution of the reaching movement takes more time than the gaze shift, the contribution of the efference copy does not require the respective movement to be executed, thus efferent reaching information should be available for the eye movement system as well. Having both efferent signals available before the onset of the coordinated eye-hand movement may allow differential use of these signals: While efferent eye movement signals may be used to adjust the position of the upcoming reach, efferent reach signals may reduce the variability of the eye movement system.

It still remains open why efference copies associated with the reaching movement lead to improvements in gaze endpoint precision. Because gaze is typically shifted to the target before the hand arrives, the final gaze orientation may be critical to guide the reach (Prablanc & Martin, 1992). In addition, when performing sequential eye-hand movements, saccades to the second target may only be initiated once the reach to the first target is completed (Neggers & Bekkering, 2002), while gaze shifts away from the target before the hand arrives lead to pronounced reach endpoint errors (Coats et al., 2016). The lack of visual information in our study has likely led to pronounced gaze endpoint errors, as gaze could not anchor to a visual stimulus (cf., Flanagan et al., 2008). Consequently, such errors may jeopardize reaching performance. This can be especially so if ocular-proprioceptive signals are used by the reaching system, in which case variability in these extra-retinal signals may lead to pronounced reach endpoints. Therefore, it might be functionally advantageous if efferent reach information would be combined within the eye movement system in such a way that this integration will reduce the variability of gaze endpoints.

An alternative explanation for the improved gaze precision during coordinated actions might be that the concurrent reaching movement transforms the body target from a body-centered into a gaze-centered reference frame (Mueller & Fiehler, 2014; 2017). For eye movements, the body-centered somatosensory input needs to be transformed and expressed in a gaze-centered reference system, in which eye movements are primarily controlled...
(Nanayakkara & Shadmehr, 2003), and such conversion requires several reference frame transformations (Buneo et al., 2002). The performance of a hand movement to a body target updates the target position to a gaze-centered reference frame (Mueller & Fiehler, 2014), and this may facilitate eye movement control by limiting noise associated with sensorimotor transformations (Abedi Khoozani & Blohm, 2018; Manson, Blouin et al., 2019). However, on the basis of previous work (Mueller & Fiehler, 2014), we would expect such transformations taking place also when a movement of the target hand was performed (kinaesthetic conditions) during isolated eye movements. However, we did not find evidence for an improved gaze precision there. Rather, only hand movements that are performed in coordination with a saccade seem to facilitate the execution of an eye movement (Bekkering et al., 1994), suggesting that the improved gaze precision during coordinated eye-hand movements might indeed arise from the integration of efferent reaching information, and not from reference frame transformations.

Conclusion

We conclude that somatosensory signals are utilized differently to guide goal-directed hand and eye movements to an unseen body target. In contrast to eye movements, different types of somatosensory information (proprioceptive, kinaesthetic, tactile) systematically influenced reaching movements. Coordinated eye-hand movements led to improved reach accuracy and improved gaze precision, suggesting a bidirectional stream of efferent information across the reaching and the gaze systems. Our findings highlight the idea that some underlying mechanisms operate on the basis of extra-retinal input and in the absence of any visual information.
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References


**Figure Legends**

Figure 1. Top-view of the setup. Participants had their left index and middle fingers in the rings attached to the slider below the frame and their right index finger on the start position on the touchscreen. The start position of the hand was slightly to the right of an LED that was placed below the touchscreen; when this LED was illuminated, and thus visible (green circle), participants had to fixate it (dashed lines). A Only in the beginning of trials involving kinaesthetic information (PK and PKT), the left hand was below the start position and participants had to move it to the target position (small circles) after an auditory prompt. B When the left hand was at the target position, an auditory or tactile cue prompted participants to perform either a right hand reaching movement, or an eye movement, or a combined eye-hand movement to the unseen target digit. C Top: Depiction of trial events in conditions without kinaesthetic information (P and PT). Bottom: Depiction of trial events in conditions with kinaesthetic information (PK and PKT).

Figure 2. Example of reach endpoints. Reach endpoints of one example participant in the proprioceptive-tactile condition when gaze was fixed and when a coordinated eye movement to the target digit was performed. Filled red squares at the top indicate the two calibrated reach target positions for that participant. Open red squares at the bottom show the initial start position of each reaching movement, which was slightly to the right of the starting LED (0 cm along the horizontal axis), where gaze was fixed. Triangles pointing to the left and right indicate reach endpoints to the index and middle finger, respectively, with filled and open symbols indicating endpoints when an eye movement was also performed or not, respectively. Ellipses show the 95% CI of the endpoints, the area of which was used as a measurement of each participant’s reach endpoint precision. Endpoint accuracy and precision were evidently improved when performing coordinated eye-hand movements.

Figure 3. Reach endpoint accuracy. A Average reach endpoint errors across participants for the different types of somatosensory information (horizontal axis) and movement type (open vs. filled symbols), averaged across target digits. Lower values indicate higher accuracy. P: proprioceptive; PK: proprioceptive-kinaesthetic; PT: proprioceptive-tactile; PKT: proprioceptive-kinaesthetic-tactile. B Effect of movement type on reach endpoint error. Each open symbol represents the average reach endpoint error for each participant in the coordinated and isolated condition, with the filled symbol showing the average across participants. Data points below the diagonal show that reach endpoint errors are greater when reaches are performed in isolation. C Relationship between reach and gaze endpoint error in the coordinated condition. Notation similar to B. Solid black line depicts a linear regression fitted to the data in B & C.

Figure 4. A Lateral and B distal errors of reach endpoints. Averaged values across conditions and target digits for all available somatosensory information and movement types are shown. Grey lines depict the individual data points across conditions. Stars depict significant differences between the different somatosensory conditions after Bonferroni correction. Details as in Figure 3.
Figure 5. Distal reach endpoint error over the time-course of the blocks. A Average distal error across participants over the normalized length of the blocks for each type of somatosensory information and movement type condition. B Differences between the late and early distal error for the respective conditions. Grey dots show the individual data. Error bars depict the 95% CI. Stars depict significant differences between the somatosensory conditions. Details as in Figure 3.

Figure 6. Reach endpoint precision. A Average reach endpoint variability across participants for the different types of somatosensory information and coordination, averaged across target digits. Lower values indicate higher precision. Error bars show the standard error across the participants’ mean. B Illustration of the main effect of somatosensory information on reach endpoint precision. Data points show the precision in the respective conditions subtracted from the precision in P. Error bars depict the 95% CI. C Comparison of the reach endpoint precision measured in PKT and the predicted optimal precision based on the combination of PK and PT. Open squares depict individual values, the black square shows the average. Error bars depict the standard error of the mean. Details as in Figure 3. D Average gaze endpoint variability. Details as in A.
A trial onset left hand at target

NON-KINAESTHETIC

KINAESTHETIC

left hand at start

 left hand at target

 auditory tactile

 cue

 start hand eye eye-hand

left hand at start

 left hand at target

 auditory tactile

 cue

 start hand eye eye-hand

 auditory tactile

 cue

 start hand eye eye-hand
A

Lateral Reach Error [cm]

right

left

-6
-4
-2
0
2
4
6

P PK PT PKT

calibrated baseline

Somatosensory Information

Isolated

Coordinated

B

Distal Reach Error [cm]

overshoot

undershoot

-10
-5
0
5
10

P PK PT PKT

Somatosensory Information

Isolated

Coordinated

*