



33 conclude that somatosensory target information influence endpoint control differently for goal-  
34 directed hand and eye movements to unseen targets.

### 35 **New & Noteworthy**

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

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### 46 **Keywords**

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

## 48 **Introduction**

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

62 Somatosensory information can be classified into three different types. First, static  
63 *proprioceptive* signals provide information about body position and arise primarily from  
64 muscle spindles, Golgi tendons and joint receptors (Purves et al., 2001). Static proprioception  
65 is thought to decay over time (Jones et al., 2012; Cameron et al., 2015), though this is not  
66 always the case (Rincon-Gonzalez et al., 2011; Kuling et al., 2019). Second, dynamic  
67 proprioception, hereby referred to as *kinaesthesia*, provides information input about both  
68 body position and movement (Colins et al., 2005). Although information from cutaneous  
69 receptors is involved (Edin & Johansson, 1995), the main kinaesthetic signals arise from  
70 changes in muscle length, such as afferents from dynamically activated muscle spindles  
71 during movement (Dimitriou & Edin, 2008). If changes in muscle length arise from actively  
72 performed movements, additional efferent information is generated by the associated motor  
73 command (Wolpert & Miall, 1996; Proske & Gandevia, 2009), possibly already available in  
74 muscle spindles that act as forward models (Dimitriou & Edin, 2010). Combining efferent and  
75 afferent signals contributes to estimations about the position of a limb (Debats et al., 2010). If  
76 neither of these signals is more reliable than the other, combining such information may lead  
77 to improvements of both precision (van Beers et al., 1999) and accuracy with which one can  
78 derive the position of that limb (van Beers et al., 2011). Another type of somatosensory  
79 information is *tactile* input, which mainly arises from mechanical activations of cutaneous  
80 receptors in the skin reacting to touch and vibration, independently of whether the limb moves  
81 or remains static. Tactile input can be helpful for movement control, as it contributes to the

82 accuracy of goal-directed hand movements (Rao & Gordon, 2001). The processing of tactile  
83 input on a limb largely depends on the postural configuration of that limb (Azanon & Soto-  
84 Faraco, 2008; Azanon et al., 2015; Longo, 2017), suggesting a close relationship between the  
85 proprioceptive and tactile sense.

86 Different types of somatosensory information can improve goal-directed hand  
87 movements. Indeed, reaching accuracy relies on proprioceptive input from the moving (Ghez  
88 et al., 1995) and the target limb (Rao & Gordon, 2001), while vibrotactile input from the  
89 unseen target hand can further improve reaching to that hand (Mikula et al., 2018). In  
90 contrast, contributions of somatosensory input on eye movements are limited. Saccades to an  
91 unseen proprioceptive target do not benefit from additional tactile (Blanke & Gruesser, 2001)  
92 or kinaesthetic signals (Voudouris et al., 2016) from that target. However, saccades are  
93 initiated faster when kinaesthetic input from the target hand is available (Voudouris et al.,  
94 2016). The finding that somatosensory target information improves hand movements but has  
95 limited contributions on eye movements may be due to the fact that for eye movements the  
96 body-centered somatosensory input needs to be transformed and expressed in a gaze-centered  
97 reference system, in which eye movements are primarily controlled (Nanayakkara &  
98 Shadmehr, 2003), and such conversion requires several reference frame transformations  
99 (Buneo et al., 2002). In contrast, transformations of body targets for reaching movements are  
100 less complex because body targets for reaching are represented in mixed body- and gaze-  
101 centered, or even only in body-centered coordinates (Mueller & Fiehler, 2016). Because  
102 sensorimotor transformations introduce noise (Abedi Khoozani & Blohm, 2018; Abedi  
103 Khoozani et al., 2020) and delays (Manson, Blouin et al., 2019), more elaborate  
104 transformations may lead to greater uncertainty in the transformed signal about body target  
105 position, possibly explaining why somatosensory input contributes less to goal-directed eye  
106 than hand movements.

107 Although previous studies examined how different types of somatosensory input  
108 influence hand and eye movements, a systematic investigation of how each of these three  
109 types of somatosensory signals contributes to goal-directed movements is still missing. More  
110 specifically, combining different types of somatosensory information about a body target may  
111 lead to improved representation of that target, enhancing movement planning and control.  
112 Such benefits may be more pronounced for hand than for eye movements because the more  
113 elaborate transformations required for eye movements to body targets introduce noise and  
114 may hinder possible benefits of the richer somatosensory input. However, the use of different  
115 somatosensory input signals may differ when coordinated eye-hand movements are performed

116 to the same body target. Coordinated eye-hand movements are coupled to each other, at least  
117 when directed to visual targets (Neggers & Bekkering, 2000; Armstrong et al., 2013). In  
118 addition, although the saccadic and reaching systems may operate independently, these  
119 systems may constantly interact when simultaneously activated (Lazzari et al., 1997), for  
120 instance through sharing efference copies (Prablanc & Martin, 1992; Chen et al., 2016), or  
121 they may even be controlled on the basis of a single, common control signal (Bock, 1987).  
122 Therefore, during coordinated eye-hand movements to unseen somatosensory targets, the eye  
123 movement may benefit from the available somatosensory input that is used to facilitate the  
124 concurrently performed reaching movement.

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

133

## 134 **Methods**

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

143 A top-view of the setup is shown in Figure 1. Participants sat in front of a table in a  
144 dark room. They held their mouth in an individually fitted bite-board that was fixed to a pole  
145 attached to the table. In front of the participant and 20 cm away from them, a custom-made  
146 frame (46 x 38 x 15 cm) was placed with its upper part covered with a touchscreen  
147 (MagicTouch 2.0, KeyTec Inc., Texas, USA) and a transparent foil below the touchscreen.  
148 The foil prevented participants from seeing anything below it, except when a small halogen  
149 lamp, below the frame, was switched on, in which case participants could see anything below

150 the foil. The bite-board and frame were inclined at 65° and 150°, respectively, relative to the  
151 table so that gaze direction was approximately orthogonal to the centre of the touchscreen.  
152 The eyes were at a distance of 30cm from the centre of the touchscreen.

153 A light-emitting diode (LED) was fixed below the touchscreen and was centrally  
154 placed at the part of the frame that was closest to the participant. The *start position* of the  
155 right hand was located on the touchscreen, 1 cm to the right of the LED. The participant's  
156 body midline was aligned to the LED and start position. Two rings were fixed on a slider that  
157 was attached to a rail below the frame. The slider could only move along this rail and only  
158 along the sagittal plane with respect to the participant. Two solenoids, 5 cm apart from each  
159 other laterally, were attached below the foil at the *target positions*, 20 cm away from the start  
160 position in the sagittal direction. Each of these solenoids could present tactile stimuli  
161 (mechanical taps) to the participants' fingertips through a pin (diameter: 3 mm; length:  
162 10mm) that touched the participant's finger with a force of 0.1 N. The participants' index and  
163 middle fingers were fit into the rings throughout the experiment. The two fingers did not  
164 contact with any other surface, except for when being stimulated by the respective solenoid at  
165 the target position.

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

171

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

179 When performing *isolated hand movements*, the LED turned on and participants had to fixate  
180 it. They then pressed the touchscreen at the start position with their right index finger, which  
181 prompted a standard drift correction of the Eyelink eye-tracker, by aligning the current gaze  
182 position at that moment with the predefined start position. This also indicated the start of the  
183 trial. In the *proprioceptive-kinaesthetic* block, a sound 50 ms after drift correction prompted

184 participants to move their left hand from the start to the target position while maintaining  
185 fixation at the LED. A barrier at the target position would stop the slider from moving further  
186 in the sagittal direction. A high or a low pitch tone 50 ms after the left hand arrived at the  
187 target position cued a right-hand reaching movement to the unseen index or middle finger of  
188 the left target hand, respectively. Participants were asked to immediately perform the reaching  
189 movement (mean  $\pm$  SD latency across all conditions:  $387 \pm 120$  ms) by lifting their right  
190 index finger off the touchscreen and touching the touchscreen right above the target digit.  
191 Then, they moved their left hand back to the start position, which determined the end of the  
192 trial and stopped data collection. The procedure in the *proprioceptive-kinaesthetic-tactile*  
193 block was similar with the only difference being that there was no auditory cueing of the  
194 target digit. Rather, a tactile stimulus was applied to one of the two digits 50 ms after the left  
195 hand arrived at the target position. The procedure in the *proprioceptive* and in the *tactile*  
196 blocks was almost similar to the above-mentioned blocks but with the difference that the left  
197 hand was stationary at the target position throughout the whole block, and that the cue  
198 (auditory or tactile, respectively) was presented 50 ms after drift correction. In these two  
199 conditions, the trial ended immediately after the reaching movement was completed, as this  
200 was determined by the contact of the right index finger with the touchscreen. For these four  
201 blocks, gaze was always kept fixed at the LED throughout the trial.

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

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

215         In each of the above-mentioned 12 experimental blocks, participants performed 40  
216 trials toward each digit, resulting in a total of 80 trials per block. Blocks with and without  
217 kinaesthetic information lasted around 7 and 4 minutes, respectively. Participants took short

218 self-paced breaks between blocks. The experiment was performed on three days, with  
219 participants performing four blocks of trials on each day. The order of blocks was randomized  
220 across participants. The total duration of the experiment was ~2 hours.

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

232

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

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

245 We then calculated the endpoints during the experimental trials. We determined the  
246 reach endpoint as the position where participants touched the touchscreen after reach onset.  
247 Subsequently, we calculated the reach endpoint error in each trial separately for each digit.  
248 This error was calculated as the two-dimensional Euclidean distance between each  
249 participant's calibrated reach target position and their reach endpoint. Because there was no  
250 visual target to anchor gaze, participants could perform several eye movements to localize the  
251 unseen target within each trial. Therefore, we were especially interested in gaze position just

252 before the end of the reach and determined gaze endpoint as the median gaze position during  
253 the last 100 ms before the end of the reaching movement, which was also the end of the trial  
254 (as in the calibration block). In the *isolated eye* conditions, where no reaching movements  
255 were performed, we determined gaze endpoint as the median gaze position during 550 and  
256 650 ms after cue onset. By using this criterion, we reassured that we keep our analyses  
257 approach consistent between conditions with and without kinaesthetic information, as we  
258 examine gaze always at the last 100 ms of the trial. Doing so allowed for robust and  
259 comparable calculations of gaze endpoints in both the isolated and coordinated eye  
260 conditions, while reassuring that there was enough time to bring gaze to the felt target  
261 position and to perform any additional corrective eye movements. Gaze endpoint error was  
262 then calculated in each trial, separately for each digit, as the two-dimensional distance  
263 between each participant's calibrated gaze target position and their gaze endpoint.

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

281 To evaluate a possible temporal component to the representation of target position, we  
282 also looked at the change of reach and gaze endpoint errors across trials in each block. Since a  
283 different amount of trials per participants were excluded (see below for exclusion criteria) and  
284 the order of target digits was randomized across trials we could not simply average the  
285 endpoint error in each trial across participants. For this reason, we obtained the sorted vector

286 containing the endpoint error values in all valid trials for each participant and each condition  
287 and then normalized the length of this vector to 21 steps (representing 0 to 100% block  
288 duration in 5% steps) using the `interp1` function in MATLAB. As a result of this  
289 normalization procedure we could average the values across digits and participants to  
290 investigate the fluctuation of endpoint error over the time-course of each block.

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

## 302 **Results**

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

311

312 **Endpoint accuracy.** To analyze reach and gaze endpoint accuracy we computed the  
313 respective endpoint errors for each of the different levels of somatosensory information and  
314 for isolated and coordinated movements (Figure 2). We used two separate repeated measures  
315 ANOVAs, each for reach and eye movements, with the factors *somatosensory information*  
316 (proprioceptive, proprioceptive-kinaesthetic, proprioceptive-tactile, proprioceptive-  
317 kinaesthetic-tactile), *movement type* (isolated, coordinated) and *target digit* (index finger,  
318 middle finger) to assess the influence of these factors on reach and gaze endpoint accuracy.

319 Because the target digit had no influence on reach ( $F(1,11) = 0.16, p = .698, \eta^2 = .001$ ) or gaze  
320 ( $F(1,11) = .003, p = .958, \eta^2 < .001$ ) accuracy, we report the following results after averaging  
321 reach and gaze endpoints across the two target digits.

322 For reach endpoint accuracy, there was no systematic influence of somatosensory information  
323 ( $F(3,33) = 2.23, p = .103, \eta^2 = .058$ ; Figure 3A). However, reach endpoint accuracy improved  
324 in the coordinated ( $3.27 \pm 1.27$  cm) compared to the isolated condition ( $4.15 \pm 0.99$  cm;  
325  $F(1,11) = 8.75, p = .013, \eta^2 = .116$ ). This is remarkable, as it indicates that shifting gaze  
326 toward an invisible target improves reach accuracy, even though this gaze shift provides no  
327 visual information about the target or the moving hand. While the accuracy in the isolated and  
328 coordinated conditions was correlated ( $r(10) = .61, p = .036$ ), there was a consistent benefit  
329 for the coordinated movement across participants (Figure 3B). No interaction between  
330 somatosensory information and movement type was found ( $F(3,33) = 0.84, p = .484, \eta^2 =$   
331  $.018$ ).

332 For gaze endpoint accuracy there was also no effect of the type of somatosensory  
333 information ( $F(3,33) = 2.01, p = .132, \eta^2 = .058$ ). In addition, and in contrast to reaching  
334 behavior, there was no significant effect of movement type ( $F(1,11) = 2.31, p = .157, \eta^2 =$   
335  $.045$ ), and no systematic interaction between the factors ( $F(3,33) = 2.61, p = .068, \eta^2 = .024$ ).  
336 Gaze endpoint errors were greater than reach endpoint errors in the coordinated condition  
337 ( $4.71 \pm 1.75$  cm vs.  $3.27 \pm 1.27$  cm;  $t(11) = 3.59, p = .004$ , Figure 3C) and the extent of these  
338 errors was correlated across participants ( $r(10) = .62, p = .032$ ). That the amount of reach  
339 endpoint error was closely related to the amount of gaze endpoint error in the coordinated  
340 conditions was further confirmed by significant within-participants correlations (9/12  
341 participants). Interestingly, the improvement of each participant's reach accuracy in  
342 coordinated compared to isolated reaches also correlated with gaze endpoint accuracy ( $r(10) =$   
343  $.63, p = .027$ ). Taken together, these results suggest that efferent information associated with  
344 the eye movement is used for reach control.

345 To further analyze the influence of the concurrent eye movement on reach accuracy,  
346 we examined reach endpoint errors along the frontal and sagittal plane, separately. For  
347 convenience, these endpoint errors will be hereafter referred to as lateral and distal endpoint  
348 errors. This approach allowed us to detect potential shifts in reaching endpoints along each  
349 movement direction (c.f., Mueller & Fiehler, 2014, 2016). For the lateral reach endpoint error  
350 (Figure 4A), we did not find any influence of somatosensory information ( $F(3,33) = 2.51, p =$   
351  $.076, \eta^2 = .038$ ) or movement type ( $F(1,11) = 0.67, p = .430, \eta^2 = .014$ ), nor a significant  
352 interaction ( $F(3,33) = 1.34, p = .286, \eta^2 = .008$ ). Interestingly, there was a systematic effect of

353 the type of somatosensory information on distal endpoint errors ( $F(3,33) = 44.32, p < .001, \eta^2$   
354  $= .459$ ; Figure 4B). More specifically, reach endpoints were shifted further along the sagittal  
355 direction when kinaesthetic information was available (average error without K:  $-2.42 \pm 2.15$   
356 cm; average error with K:  $0.52 \pm 2.78$  cm). Note here that despite the average distal error  
357 being close to zero in the kinaesthetic conditions, the variability across participants was large  
358 as individuals who had small distal errors in non-kinaesthetic conditions (P and PT) had larger  
359 distal errors in kinaesthetic conditions (PK and PKT). Thus, kinaesthetic information did not  
360 always improve reach endpoint accuracy, but it systematically led to a shift of the reach  
361 endpoint in the direction of the movement. There was no influence of movement type ( $F(1,11)$   
362  $= 0.15, p = .703, \eta^2 = .003$ ) and no significant interaction ( $F(3,33) = 1.40, p = .260, \eta^2 = .021$ )  
363 on distal errors.

364 One potential explanation for the effects of the kinaesthetic information on the distal reach  
365 endpoint errors could be an increased drift of the proprioceptive information from the target  
366 hand when kinaesthetic target information was *not* available (c.f., Jones et al., 2012; Cameron  
367 et al., 2015). To explore this, we normalized the distribution of trials within each block and  
368 computed the distal reach endpoint error in steps of 5% of the block, separately for each type  
369 of somatosensory information and movement type (see Methods for details). We observed an  
370 increase in the distal error over the time-course of the block for conditions without  
371 kinaesthetic information (see Figure 5A), while the distal error remained nearly constant  
372 when kinaesthetic information from the target hand was available. To quantify this effect, we  
373 computed the average distal error during the first 25% and during the last 25% of each block  
374 for each participant and took the difference between these two values, with negative  
375 differences reflecting larger undershoots in the late than early trials. We expected that position  
376 drift would increase in conditions without kinaesthetic information (e.g., Cameron et al.,  
377 2015), but would remain low in kinaesthetic conditions, when the combination of afferent and  
378 efferent input in each trial may facilitate target representation (Debats et al., 2010). To  
379 examine this, we computed a 4 (somatosensory input)  $\times$  2 (movement type) repeated measures  
380 ANOVA. There was a main effect of somatosensory information ( $F(3,33) = 26.00, p < .001,$   
381  $\eta^2 = .401$ ), driven by a substantial drift in the conditions without kinaesthetic information (P:  
382  $t(11) = 5.96, p < .001$ ; PT:  $t(11) = 4.51, p < .001$ ; Figure 5B), but not in those with kinaesthetic  
383 information (PK:  $t(11) = 1.04, p = .319$ ; PKT:  $t(11) = 2.13, p = .057$ ), suggesting increased  
384 drift when kinaesthetic information was not available. Though there was a trend for less drift  
385 of reach endpoints in the coordinated condition, this was not systematic ( $F(1,11) = 4.53, p$   
386  $= .057, \eta^2 = .072$ ; Figure 5B), and there was no interaction between the two factors ( $F(3,33) =$

387 0.58,  $p = .635$ ,  $\eta^2 = .009$ ). Together, these results suggest that the difference in distal error  
388 depending on the somatosensory information could be explained by an increased drift in the  
389 conditions without kinaesthetic information.

390

391 **Endpoint precision.** To quantify the precision of the reach and eye movement endpoints we  
392 again performed two separate ANOVAs, each for reach and gaze endpoints, with the factors  
393 *somatosensory information* (proprioceptive, proprioceptive-kinaesthetic, proprioceptive-  
394 tactile, proprioceptive-kinaesthetic-tactile), *movement type* (isolated, coordinated) and *target*  
395 *digit* (index finger, middle finger). There was again no influence of target digit on reach  
396 ( $F(1,11) = 3.93$ ,  $p = .073$ ,  $\eta^2 = .005$ ) or gaze endpoints ( $F(1,11) = 0.59$ ,  $p = .458$ ,  $\eta^2 =$   
397  $.010$ ); thus, we averaged the data across digits.

398 In contrast to reach endpoint accuracy, somatosensory information this time  
399 influenced reach endpoint precision ( $F(3,33) = 6.31$ ,  $p = .002$ ,  $\eta^2 = .174$ ; Figure 6A). Precision  
400 was poorest when only proprioceptive information was available, and increased when two  
401 types of somatosensory information were available (P vs. PK:  $t(11) = 3.37$ ,  $p = .006$ ; P vs. PT:  
402  $t(11) = 3.37$ ,  $p = .006$ ). Improvements were also observed when all three types of  
403 somatosensory information were available (P vs. PKT:  $t(11) = 2.61$ ,  $p = .024$ , corrected alpha:  
404  $0.083$ ), however this comparison did not survive the multiple comparisons. No other  
405 comparison reached significance (PT vs. PK:  $t(11) = 2.13$ ,  $p = .056$ ; PK vs. PKT:  $t(11) = 1.47$ ,  
406  $p = .170$ ; PT vs. PKT:  $t(11) = 0.30$ ,  $p = .773$ ). To visualize the effect of somatosensory  
407 information on reach endpoint precision, we subtracted the precision in the proprioceptive  
408 condition (P) from the precision in each of the other three conditions (Figure 6B). Together  
409 these results suggest that reach precision is improved when two different sources of  
410 somatosensory information are available (reduction of variance:  $1.51 \pm 1.55\text{cm}^2$  for PK;  $0.94$   
411  $\pm 0.97\text{cm}^2$  for PT;  $1.05 \pm 1.40\text{cm}^2$  for PKT). There was no effect of movement type ( $F(1,11) =$   
412  $2.49$ ,  $p = .143$ ,  $\eta^2 = .023$ ), nor an interaction between somatosensory information and  
413 movement type ( $F(3,33) = 0.80$ ,  $p = .502$ ,  $\eta^2 = .016$ ) on reach endpoint precision.

414 The improvement of reach endpoint precision with two sources of somatosensory  
415 information suggests an integration of different somatosensory inputs for reach control. The  
416 statistically optimal integration of information suggests that the integrated signals are  
417 redundant and thus can compensate for uncertainties in the single senses resulting in increased  
418 precision. To examine this in more detail, we tested whether this integration is statistically  
419 optimal on the individual level. The independently measured precisions in the proprioceptive-  
420 kinaesthetic and proprioceptive-tactile conditions were used to estimate the optimal precision

421 when both sources were integrated in a Bayesian framework (Ernst & Banks, 2002; Optimal =  
422  $\sqrt{(PK^2*PT^2)/(PK^2+PT^2)}$ ). We computed the optimal precision for each individual participant  
423 and compared it to the actually measured precision in the condition with all three  
424 somatosensory inputs (PKT). The observed and predicted precision were different from each  
425 other ( $t(11) = 2.70, p = .02$ ) with the observed precision in the PKT condition ( $2.11 \pm 0.35$   
426  $\text{cm}^2$ ) being worse than the one predicted by a Bayesian framework ( $1.29 \pm 0.17 \text{ cm}^2$ ). This  
427 result indicates that despite the fact that different types of somatosensory information increase  
428 reach precision, the integration of these different sources is not statistically optimal.

429 In contrast to reaching behavior, gaze endpoint precision was not influenced by  
430 somatosensory information ( $F(3,33) = 2.24, p = .102, \eta^2 = .045$ ). However, there was a  
431 significant influence of the type of movement ( $F(1,11) = 4.901, p = .049, \eta^2 = .026$ ; Figure  
432 6D), with improved gaze precision in the coordinated ( $11.67 \pm 6.83 \text{ cm}^2$ ) than isolated  
433 condition ( $14.03 \pm 7.04 \text{ cm}^2$ ). There was no interaction between somatosensory information  
434 and movement type ( $F(3,33) = 1.40, p = .259, \eta^2 = .020$ ).

435

## 436 **Discussion**

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

451

### 452 **Somatosensory input for reaching performance**

453 The type of somatosensory information from the target hand did not influence reach endpoint  
454 accuracy but it did affect endpoint precision. More specifically, reach endpoint precision was

455 poorest when only proprioceptive target information was available, but improved with two  
456 different somatosensory signals. Our results suggest that different kinds of somatosensory  
457 information may be integrated to improve target localization for reaching. Previous studies  
458 have shown close to optimal integration of proprioceptive and visual information (van Beers  
459 et al., 1999; Reuschel et al., 2010), while others did not observe such effects (Reuschel et al.,  
460 2011; Jones et al., 2012). Despite evidence for some integration of different somatosensory  
461 signals, reach endpoint precision did not systematically improve when all somatosensory  
462 signals were available (Figure 6A), and were not integrated in a statistically optimal manner  
463 within participants (see Figure 6C). This might originate from possible dependencies between  
464 the available types of somatosensory information: For instance, although proprioceptive and  
465 tactile information is processed in different sensory organs, these signals also interact with  
466 each other, as the processing of tactile signals on a static limb depends on the postural  
467 configuration of that limb (Azanon & Soto-Faraco, 2008; Azanon et al., 2015). Therefore,  
468 possible dependencies between the different types of somatosensory information may prevent  
469 their optimal integration.

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

479 Drift was substantially diminished in conditions with additional kinaesthetic  
480 information. In these conditions, the target hand was moved from the start to the target  
481 position in each trial, and thus somatosensory information from the target was frequently  
482 updated reducing the time for the somatosensory estimate of the target hand to drift. The drift  
483 in the proprioceptive conditions (P and PT) was particularly evident along the sagittal  
484 direction, as endpoints gradually undershot the unseen target. This was not evident in the  
485 kinaesthetic conditions, in which not only the endpoints did not drift, but they also overshoot  
486 the target. This increased drift in P and PT could not be explained by differences in overall  
487 block duration, since blocks with kinaesthetic information even took roughly 3 minutes longer  
488 than the blocks without. Thus, kinaesthetic input from the target hand led to a shift in the

489 representation of the target's position in the sagittal direction, likely in the direction of the  
490 reaching movement and not of the movement of the target hand (c.f., Mueller & Fiehler,  
491 2014; 2017). The combination of afferent and efferent information from the target limb, both  
492 associated with kinaesthesia, might have significantly contributed to both precision (Figure  
493 5A) and accuracy (Figure 5B) with which the position of the unseen body target was derived  
494 (van Beers et al., 2011). Yet, with our current design we cannot distinguish the relative  
495 contributions of both signals associated with the movement of the target hand. By integrating  
496 a condition where the target hand would be passively moved to the target location, afferent  
497 and efferent information could be dissociated.

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

511

### 512 **Somatosensory input for gaze performance**

513 In contrast to reaching, the type of somatosensory information did not systematically  
514 influence gaze endpoint control, confirming previous findings (Blanke & Gruesser, 2001;  
515 Voudouris et al., 2016). This might be due to the requirement of representing both the target  
516 and the effector in the same reference frame (Blouin et al., 2004). When performing an eye  
517 movement to a somatosensory target, the body-centered somatosensory target representation  
518 needs to be converted into a gaze-centered representation by passing through several steps of  
519 reference frame transformations (Buneo et al., 2002; McGuire & Sabes, 2009), while reaching  
520 to somatosensory targets requires less complex transformations (Pouget et al., 2002; Mueller  
521 & Fiehler, 2016). Sensorimotor transformations introduce noise and may eventually increase  
522 the uncertainty about the resultant estimate of the target's position (Abedi Khoozani &

523 Blohm, 2018; Abedi Khoozani et al., 2020). If this uncertainty is greater than the possible  
524 benefit of the additional somatosensory input, gaze endpoint control to somatosensory targets  
525 may not improve.

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

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

542

### 543 **Influences of isolated and coordinated movements on reach and gaze performance**

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

550 Two main mechanisms have been proposed for the control of coordinated eye-hand  
551 movements: one single signal may govern both movements (Bock, 1987), or two independent  
552 signals may be responsible for each movement but these signals may constantly interact  
553 (Lazzari et al., 1997; see also Chen et al., 2016 for a discussion of the two possibilities).  
554 Recent neurophysiological evidence supports the latter idea, as inactivation of the lateral  
555 intraparietal area (LIP), which plays a crucial role in eye-hand coordination (Dean et al.,  
556 2012; Yttri et al., 2013), does not affect isolated hand movements, but impairs reaches when

557 performed in coordination with an eye movement (Yttri et al., 2013). However, this difference  
558 may arise because LIP is part of a network responsible mainly for oculomotor behavior and  
559 less for reach control (Christopoulos et al., 2018). Our results could be interpreted in line with  
560 the idea of independent signals controlling coordinated eye-hand movements, as if there was a  
561 single control signal, reach accuracy should have been affected similarly between isolated and  
562 coordinated movements.

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

572         An alternative explanation is based on an improvement of reach endpoint errors by  
573 efferent eye signals. For instance, ocular-proprioceptive signals about gaze orientation and the  
574 corresponding efference copy signals may have been used to guide the upcoming reaching  
575 movement (Prablanc & Martin, 1992; Vaziri et al., 2006; Wilmot et al., 2006). In support of  
576 this, we did observe a systematic correlation between gaze and reach endpoint errors (Figure  
577 3C), as well as gaze accuracy and the improvement in reach accuracy in coordinated  
578 movements. These corroborate the idea that the improvement in reach accuracy during  
579 coordinated eye-hand movements most likely arises from efferent eye signals being shared  
580 with the reaching system.

581         We also observed improved gaze endpoint precision when a coordinated reaching  
582 movement was performed toward the same somatosensory target. This suggests that efferent  
583 signals from the reaching movement are shared with the eye movement system. A question  
584 that arises is whether these efferent signals are used in a similar manner in both systems. Our  
585 results show that efferent eye movement information enhanced reach accuracy, while efferent  
586 reach information improved gaze precision, suggesting that the reaching movement  
587 contributed to reducing inherent noise in the saccadic system, which is associated with  
588 variable endpoint errors. This effect suggests a differential use of efferent signals within the  
589 eye movement and reaching systems.

590           One possible explanation for this different use might be the temporal order of the eye  
591 and hand movements. Eye movements generally have lower latencies than hand movements,  
592 which allows them to guide the hand toward the target resulting in increased reach accuracy  
593 (Neggers & Bekkering, 2002). However, efference copies of both the reaching and the eye  
594 movement were likely available before the initiation of the coordinated eye-hand movement:  
595 This is likely due to the lower inertia of the eye that allows faster movement initiations. When  
596 the onset of muscular activity of both movements is measured, their latencies are comparable,  
597 and might be even shorter for reaches (Gribble et al., 2002). Even though the execution of the  
598 reaching movement takes more time than the gaze shift, the contribution of the efference copy  
599 does not require the respective movement to be executed, thus efferent reaching information  
600 should be available for the eye movement system as well. Having both efferent signals  
601 available before the onset of the coordinated eye-hand movement may allow differential use  
602 of these signals: While efferent eye movement signals may be used to adjust the position of  
603 the upcoming reach, efferent reach signals may reduce the variability of the eye movement  
604 system.

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

619           An alternative explanation for the improved gaze precision during coordinated actions  
620 might be that the concurrent reaching movement transforms the body target from a body-  
621 centered into a gaze-centered reference frame (Mueller & Fiehler, 2014; 2017). For eye  
622 movements, the body-centered somatosensory input needs to be transformed and expressed in  
623 a gaze-centered reference system, in which eye movements are primarily controlled

624 (Nanayakkara & Shadmehr, 2003), and such conversion requires several reference frame  
625 transformations (Buneo et al., 2002). The performance of a hand movement to a body target  
626 updates the target position to a gaze-centered reference frame (Mueller & Fiehler, 2014), and  
627 this may facilitate eye movement control by limiting noise associated with sensorimotor  
628 transformations (Abedi Khoozani & Blohm, 2018; Manson, Blouin et al., 2019). However, on  
629 the basis of previous work (Mueller & Fiehler, 2014), we would expect such transformations  
630 taking place also when a movement of the target hand was performed (kinaesthetic  
631 conditions) during isolated eye movements. However, we did not find evidence for an  
632 improved gaze precision there. Rather, only hand movements that are performed in  
633 coordination with a saccade seem to facilitate the execution of an eye movement (Bekkering  
634 et al., 1994), suggesting that the improved gaze precision during coordinated eye-hand  
635 movements might indeed arise from the integration of efferent reaching information, and not  
636 from reference frame transformations.

637

### 638 **Conclusion**

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

647

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## 829 **Figure Legends**

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

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

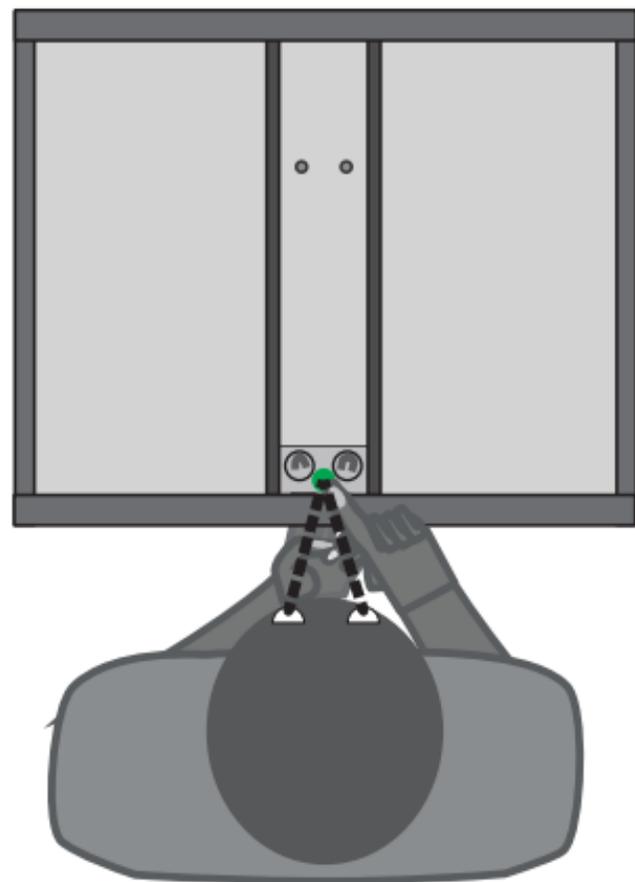
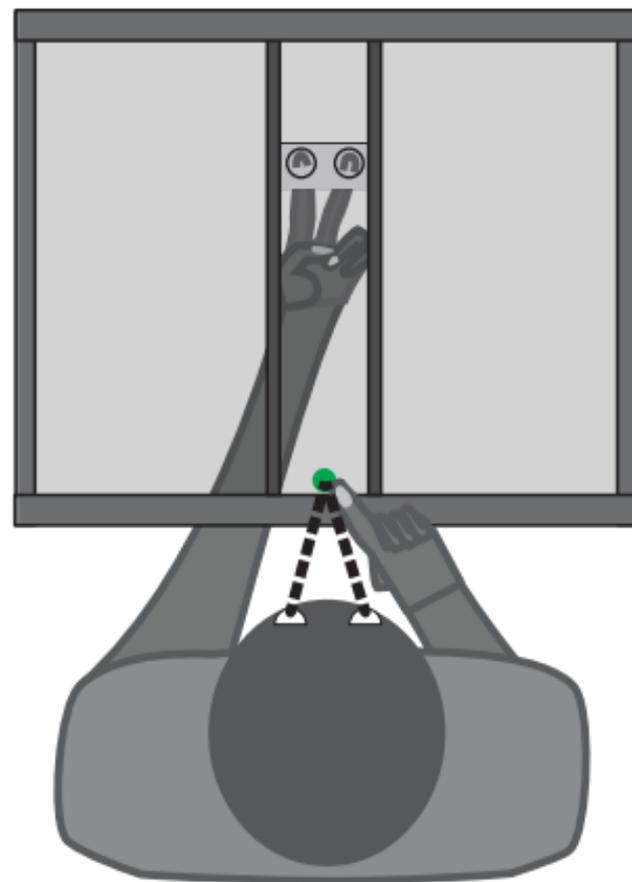
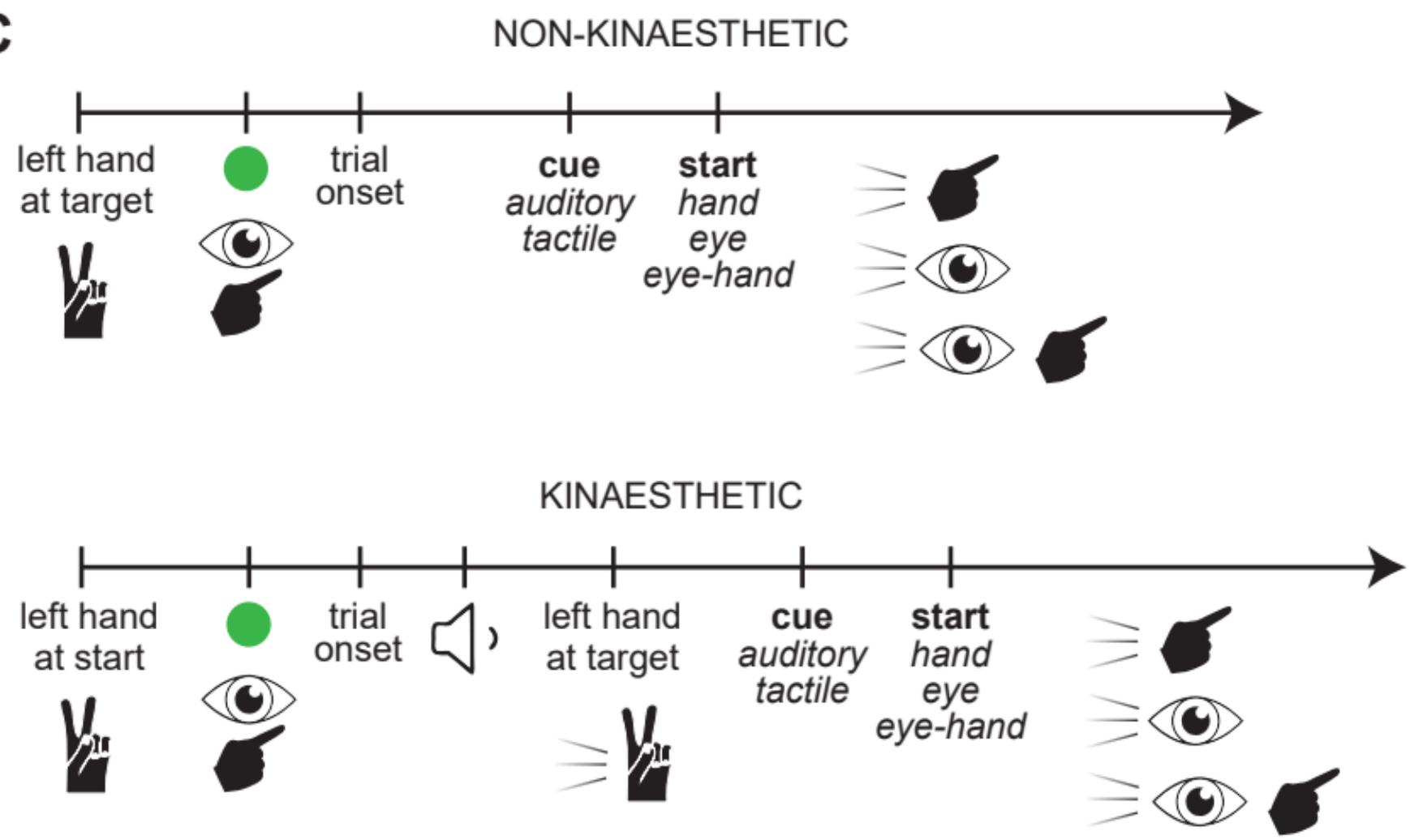
853 **Figure 3. Reach endpoint accuracy.** **A** Average reach endpoint errors across participants for  
854 the different types of somatosensory information (horizontal axis) and movement type (open vs.  
855 filled symbols), averaged across target digits. Lower values indicate higher accuracy. P: 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

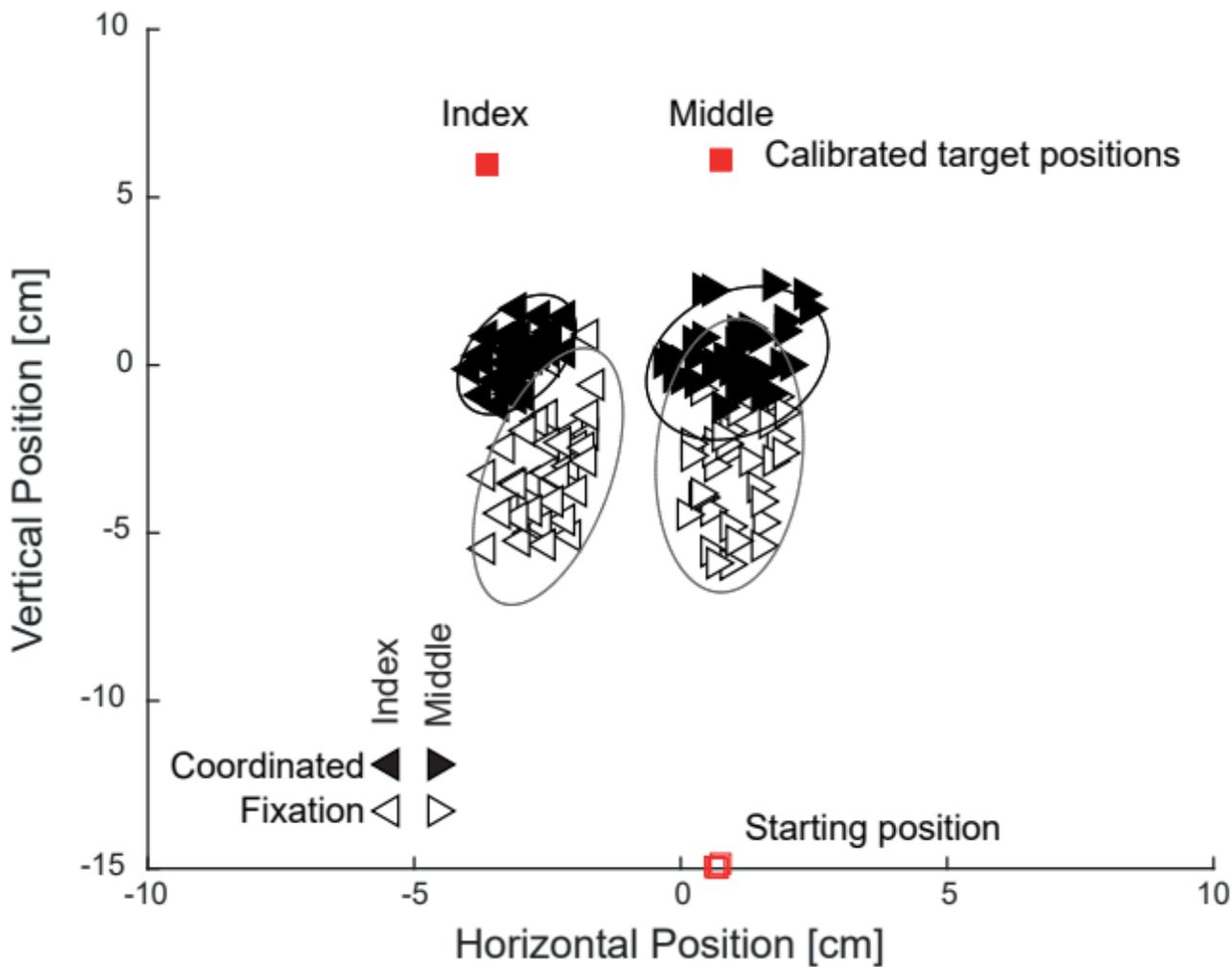
864 **Figure 4. A** Lateral and **B** distal errors of reach endpoints. Averaged values across conditions  
865 and target digits for all available somatosensory information and movement types are shown.  
866 Grey lines depict the individual data points across conditions. Stars depict significant  
867 differences between the different somatosensory conditions after Bonferroni correction. Details  
868 as in Figure 3.

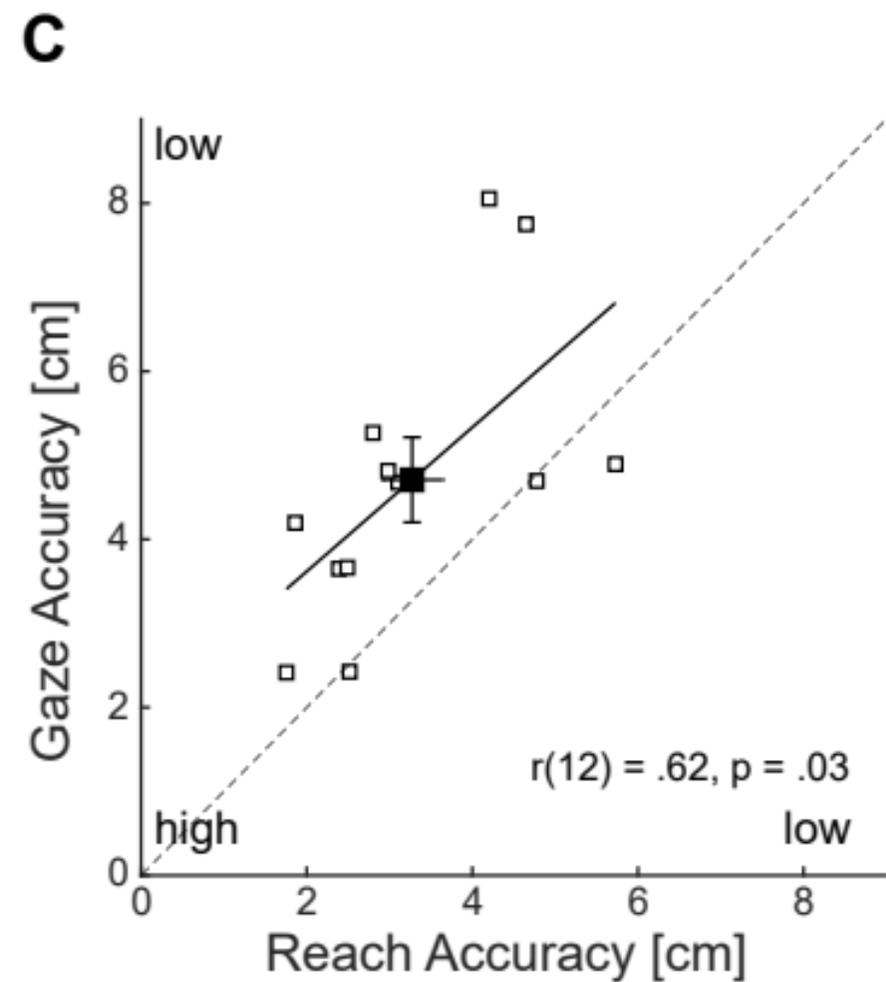
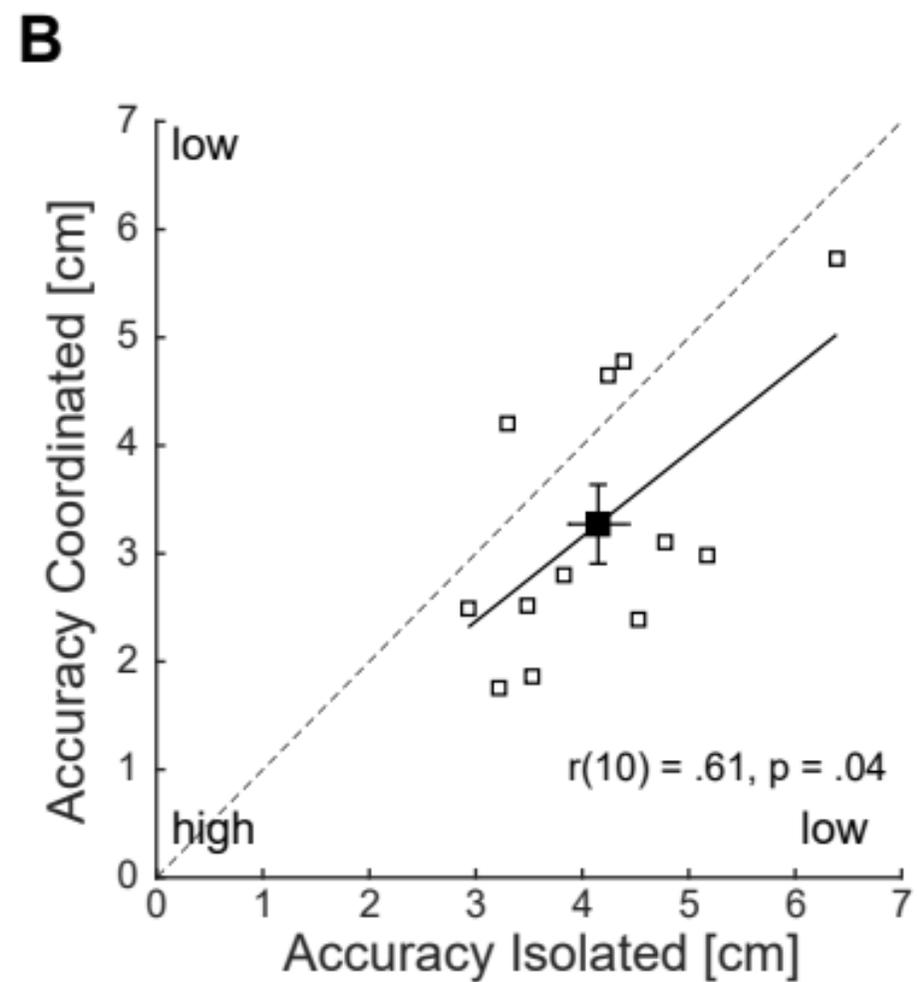
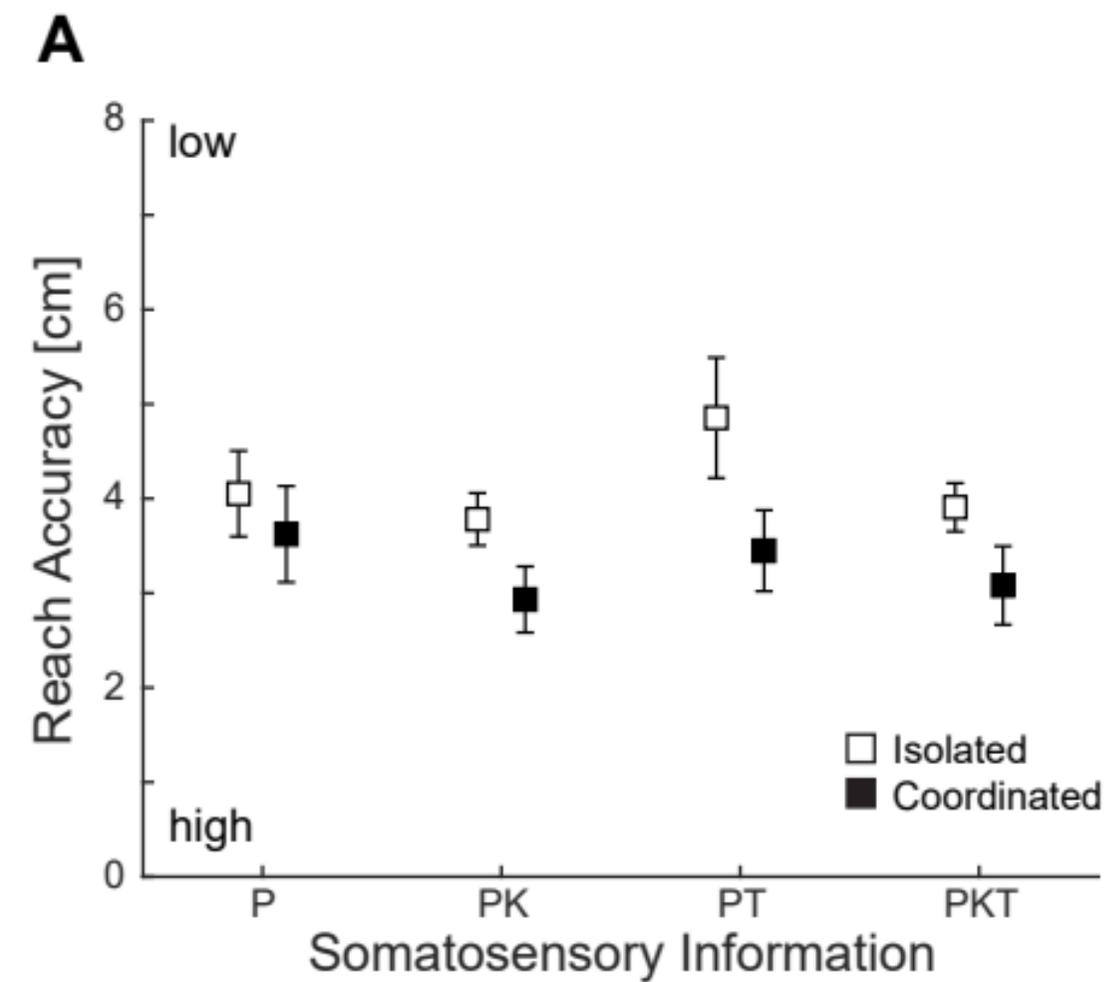
869 **Figure 5. Distal reach endpoint error over the time-course of the blocks.** **A** Average distal  
870 error across participants over the normalized length of the blocks for each type of  
871 somatosensory information and movement type condition. **B** Differences between the late and  
872 early distal error for the respective conditions. Grey dots show the individual data. Error bars  
873 depict the 95% CI. Stars depict significant differences between the somatosensory conditions.  
874 Details as in Figure 3.

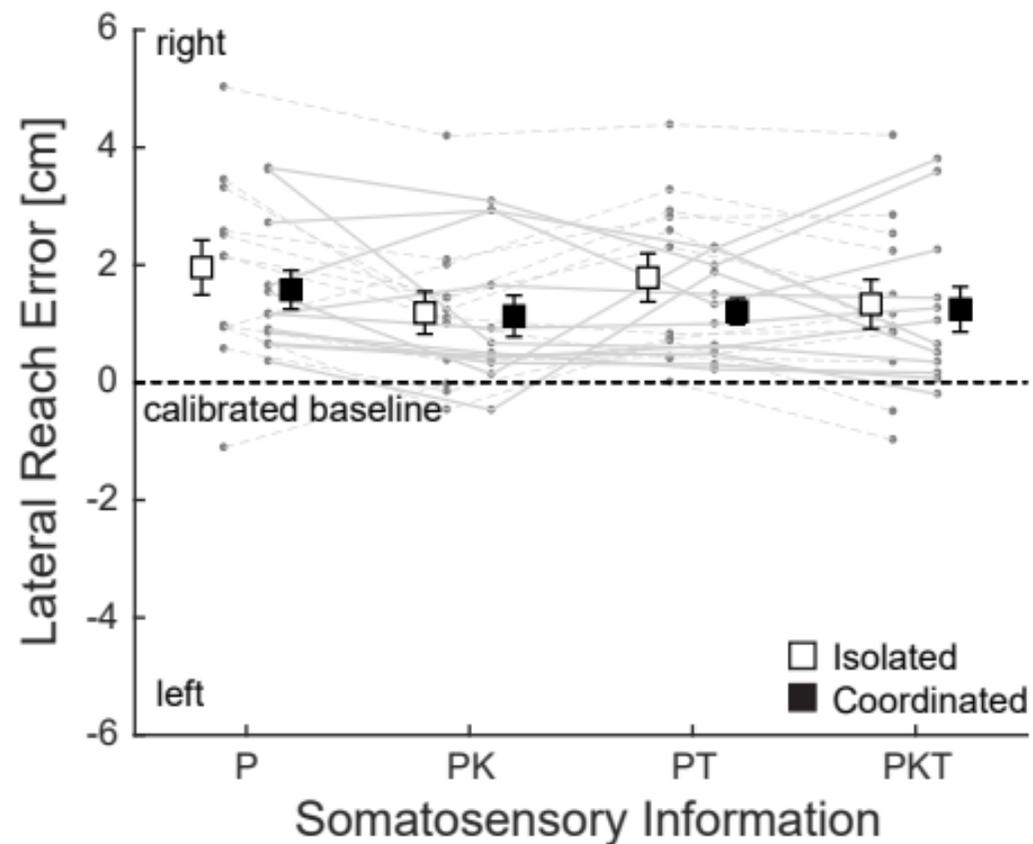
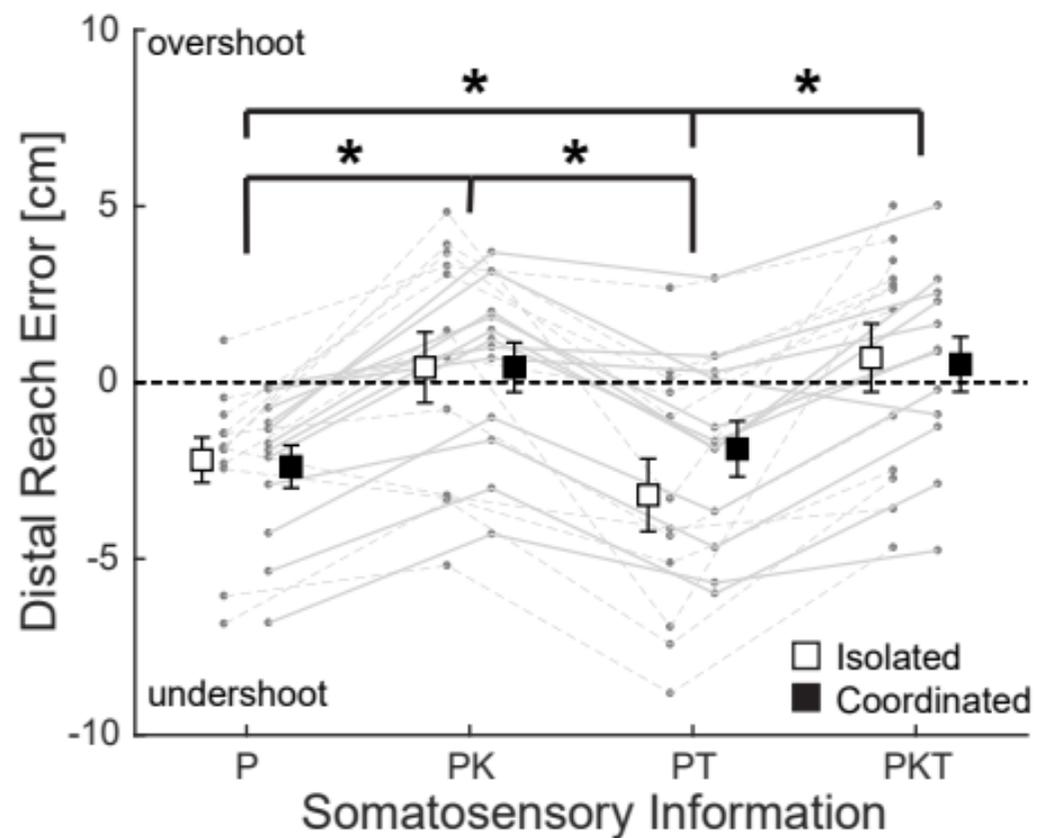
875 **Figure 6. Reach endpoint precision.** **A** Average reach endpoint variability across participants  
876 for the different types of somatosensory information and coordination, averaged across target  
877 digits. Lower values indicate higher precision. Error bars show the standard error across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

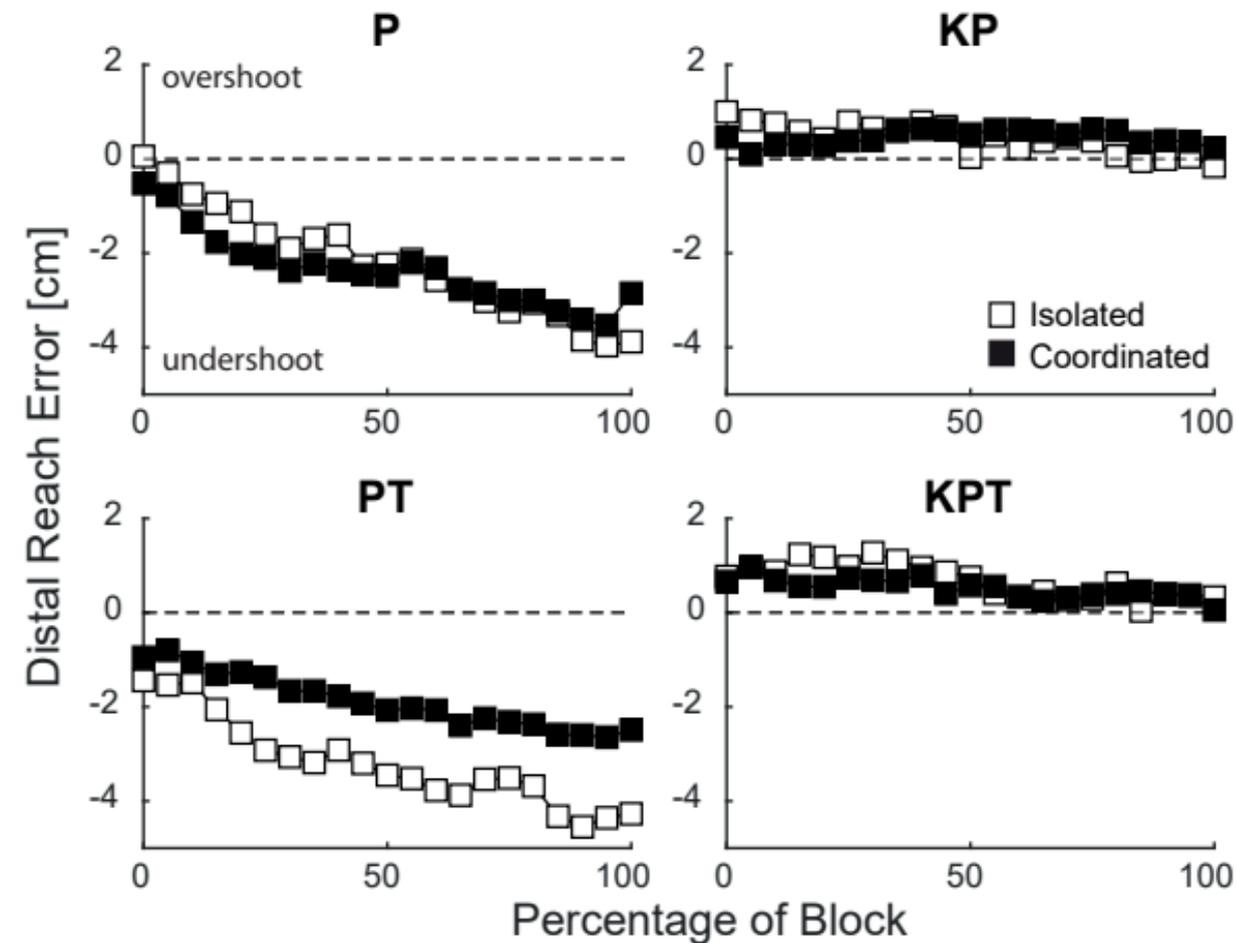
885

**A****B****C**





**A****B**

**A****B**