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1 **Express visuomotor responses reflect knowledge of both target locations**
2 **and contextual rules during reaches of different amplitudes**

3 **Abbreviated title: Express muscle responses reflect reaching metrics**

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28

29

30 ABSTRACT

31 When humans reach to visual targets, extremely rapid (~90 ms) target-directed responses can
32 be observed in task-relevant proximal muscles. Such *express* visuomotor responses are
33 inflexibly locked in time and space to the target and have been proposed to reflect rapid
34 visuomotor transformations conveyed subcortically via the tecto-reticulo-spinal pathway.
35 Previously, we showed that express visuomotor responses are sensitive to explicit cue-driven
36 information about the target, suggesting that the express pathway can be modulated by
37 cortical signals affording contextual pre-stimulus expectations. Here, we show that the
38 express visuomotor system incorporates information about the physical hand-to-target
39 distance and contextual rules during visuospatial tasks requiring different movement
40 amplitudes. In one experiment, we recorded the activity from two shoulder muscles as 14
41 participants (6 females) reached toward targets that appeared at different distances from the
42 reaching hand. Increasing the reaching distance facilitated the generation of frequent and
43 large express visuomotor responses. This suggests that both the direction and amplitude of
44 veridical hand-to-target reaches are encoded along the putative subcortical express pathway.
45 In a second experiment, we modulated the movement amplitude by asking 12 participants (4
46 females) to deliberately undershoot, overshoot, or stop (control) at the target. The overshoot
47 and undershoot tasks impaired the generation of large and frequent express visuomotor
48 responses, consistent with the inability of the express pathway to generate responses directed
49 toward non-veridical targets as in the anti-reach task. Our findings appear to reflect strategic,
50 cortically-driven modulation of the express visuomotor circuit to facilitate rapid and effective
51 response initiation during target-directed actions.

52

53 SIGNIFICANCE STATEMENT

54 *Express* (~90 ms) arm muscle responses that are consistently tuned toward the location of
55 visual stimuli suggest a subcortical contribution to target-directed visuomotor behaviour in
56 humans, potentially via the tecto-reticulo-spinal pathway. Here, we show that express muscle
57 responses are modulated appropriately to reach targets at different distances, but generally
58 suppressed when the task required non-veridical responses to overshoot/undershoot the real
59 target. This suggests that the tecto-reticulo-spinal pathway can be exploited strategically by
60 the cerebral cortex to facilitate rapid initiation of effective responses during a visuospatial
61 task.

62

63 **Keywords:** reaching control; superior colliculus; reticular formation; subcortical
64 sensorimotor control; rapid muscle response; human

65

66

67 INTRODUCTION

68 Target-directed actions require knowledge of both the hand and target positions (Sabes,
69 2011; Proske and Gandevia, 2012). To catch a falling object, for example, the sensed hand-
70 to-target distance must be transformed into accurate motor commands to generate the muscle
71 force and, in turn, accelerate the joints so that the object can be intercepted before it hits the
72 ground. Greater activation of agonists and inhibition of antagonist muscles are, therefore,
73 required to enhance the limb acceleration.

74 Historically, target-directed visuomotor behaviour was thought to be the exclusive
75 domain of the cerebral cortex. This, however, is challenged by mounting evidence showing
76 that human limb muscles start responding to visual targets for reaching at latencies (70-120
77 ms) that leave little time for cortical visuomotor transformation (Goonetilleke et al., 2015; Gu
78 et al., 2019; Selen et al., 2023; Billen 2022). Notably, the onset time of these *express*
79 visuomotor responses is far less variable than the mechanical reaction time (RT; Contemori et
80 al., 2022), which depends mostly on the long-latency (>120ms; plausibly cortically-driven)
81 muscle response components. Express visuomotor responses are also inflexibly tuned to
82 reach the real target even when a non-veridical response is required, such as in the anti-reach
83 task (Gu et al., 2016). Given their temporal and spatial stimulus-locked attributes, express
84 visuomotor responses were proposed to be conveyed subcortically via the tecto-reticulo-
85 spinal pathway (Pruszynski et al., 2010).

86 Delineation of the factors that influence express visuomotor responses should provide
87 clues about their origin and relationships to well-studied (putatively transcortical) visuomotor
88 pathways. Previous work showed that the requirement to avoid rapid target-directed
89 responses impaired the generation of express visuomotor responses (Pruszynski et al., 2010;
90 Wood et al., 2015; Atsma et al., 2018). More recent work showed that express visuomotor
91 responses are modulated by explicit cues about the temporal (Contemori et al., 2021a) and
92 spatial (Contemori et al., 2021b) presentation of visual stimuli, and incorporate advance

93 expectations about the required movement to reach the target (Gu et al., 2018; Contemori et
94 al., 2022). In all, these findings appear to reflect cortically-driven modulation of the putative
95 subcortical express circuit. Here we asked if express visuomotor responses are modulated
96 compatibly with the required movement amplitude to accomplish a visuospatial task. If so, it
97 would suggest that the circuits responsible for express limb activity produce control signals
98 that account for the details of reach metrics, rather than merely the initial reach direction.

99 We conducted two experiments to explore express visuomotor responses to targets that
100 required different movement amplitudes via modulation of: (i) the physical hand-to-target
101 reaching distance; (ii) explicit instruction to overshoot, undershoot, or stop at the target. The
102 first experiment showed that express visuomotor responses were facilitated by increasing the
103 hand-to-target distance, suggesting that the express system encodes both the direction and
104 distance metrics of veridical target-directed reaches. The second experiment showed
105 significantly fewer and smaller express visuomotor responses, and longer RTs, for both
106 overshooting and undershooting tasks compared to veridical target-directed reaching actions.
107 This suggests that express visuomotor behaviour is generally inhibited in circumstances
108 requiring sensory-to-motor transformation for abstract targets; a task that is probably
109 incompatible with the stimulus-locked output of the putative subcortical express circuit (Gu
110 et al., 2016). The findings support the idea that the cerebral cortex strategically exploits the
111 express pathway when its motor output is functional for rapid initiation of veridical target-
112 directed actions, but suppresses the express network when it is incapable of meeting the
113 current task demands.

114

115 MATERIALS AND METHODS

116 **Participants**

117 Fourteen adults completed the first experiment (6 females; mean age: 30.9±9 years), and
118 twelve of them also participated in the second experiment (4 females; mean age:
119 31.8±9.2years). The sample size was selected to be comparable with previous studies
120 investigating express visuomotor responses (Pruszynski et al., 2010; Goonetilleke et al.,
121 2015; Wood et al., 2015; Atsma et al., 2018; Gu et al., 2019; Kozak et al., 2020; Contemori et
122 al. 2021a; Billen 2022; Kearsley et al., 2022; Selen et al., 2023). All participants were right-
123 handed, had normal or corrected-to-normal vision, and reported no current neurological or
124 musculoskeletal disorders. They provided informed consent and were free to withdraw from
125 the experiment at any time. All procedures were approved by the University of Queensland
126 Medical Research Ethics Committee (Brisbane, Australia) and conformed to the Declaration
127 of Helsinki.

128

129 **Experimental set-up and task design**130 *Experimental set-up*

131 For both experiments, the participants performed visually guided target-directed
132 reaches using a two-dimensional planar robotic manipulandum (the vBOT, Figure 1A;
133 Howard and Ingram, 2009). In the vBOT setup, the visual feedback is provided via an LCD
134 computer monitor (120Hz refresh rate) mounted above the robot handle and projected to the
135 participant via a mirror, which occludes direct vision of the arm (Figure 1A). The visual
136 stimuli were created in Microsoft Visual C++ (Version 14.0, Microsoft Visual Studio 2005)
137 using the Graphic toolbox. The hand position was virtually represented by a blue cursor (~1
138 cm in diameter) whose apparent position coincided with actual hand position in the plane of
139 the limb. During the experiments, the upper arm was supported on a custom-built air sled
140 positioned under the right elbow to minimize sliding friction (Figure 1A).

141 In both experiments, the target was a filled black circle of 3 cm in diameter presented
142 against a light grey background (target luminance ~ 0.5 cd/m², background luminance ~ 150
143 cd/m²; Cambridge Research System ColorCAL MKII). This created a high-contrast (Wood et
144 al. 2015) and low spatial-frequency stimulus (Kozak et al., 2019), both features that have
145 proven effective to facilitate express visuomotor responses and rapid correction of ongoing
146 movements (Veerman et al., 2008; Kozak et al., 2019). The target was presented via an
147 *emerging moving* target paradigm (Figure 1B; Kozak et al., 2020; Kearsley et al., 2022;
148 Contemori et al., 2022). To start the trial the participants had to align the cursor and gaze at a
149 ‘home’ position (a blue ring of ~ 2 cm in diameter) located at the centre of the monitor and
150 aligned with the mid-body line. At this point, the ring changed to a ‘+’ sign that defined the
151 gaze fixation spot. Note that for the first experiment the fixation spot position was not always
152 coincident with the starting hand position, but rather changed as a function of the trial
153 condition to ensure equal eccentricity for the left and right targets (for details see Experiment
154 1: task design, and Figure 1C). Simultaneously, a constant rightward load of ~ 5 N was applied
155 to enhance the activity of the shoulder transverse flexor muscles, including the clavicular
156 head of the pectoralis major muscle, which was shown to facilitate the generation of
157 detectable express visuomotor responses (Wood et al., 2015). At the same time, we displayed
158 the target close to the top of the monitor and within a vertical track (Figure 1B). After ~ 1 s of
159 fixation, the target fell at constant velocity (~ 30 cm/s) toward the fixation spot, disappeared
160 behind the barrier and reappeared underneath it by making one single flash of ~ 8 ms of
161 duration at the right or left of participants’ right hand and fixation spot (Figures 1B and C).
162 The participants, therefore, were presented with transient and temporally predictable targets,
163 both attributes that facilitate express visuomotor responses (Contemori et al., 2021a).

164 The participants were instructed to not break fixation until the target emerged from
165 behind the barrier and to start moving the hand toward the target as rapidly as possible. For
166 both experiments, horizontal gaze-on-fixation was checked on-line with bitemporal, direct

167 current electrooculography (EOG). The EOG signal was sampled at 1 kHz, amplified by
168 1,000 and filtered with a 3-3000 Hz bandwidth filter by a Grass P5 AC Series amplifier
169 (Grass Technologies Product Group, Astro-Med Inc; West Warwick, Rhode Island).
170 “Fixation” or “Too fast” errors were shown if the participants did not respect the gaze
171 fixation requirements or moved before the target presentation, respectively, and the trial was
172 reset. The time at which the stimulus was displayed on the monitor was recorded with a
173 photodiode that detected a secondary light appearing at the bottom-left corner of the monitor
174 and simultaneously with the actual target. The photodiode fully occluded the secondary light
175 thus making it invisible for the participants.

176

177 *Experiment 1: task design*

178 In the first experiment, we investigated whether express visuomotor responses are
179 modulated by the physical hand-to-target reaching distance. To this aim, we varied the target
180 distance from participants’ reaching hand to create: (i) a *control-reach* condition, when the
181 hand-to-target distance (~8 cm) was equivalent for both right and left targets; (ii) a *long-*
182 *reach* condition, when the hand-to-target distance was longer (~13 cm) than control; (iii) a
183 *short-reach* condition, when the hand-to-target distance was shorter (~3 cm) than control.
184 The hand-to-target distance was modulated by shifting the target, track, and visual barrier ~5
185 cm rightward, or leftward, relative to the static home position of the hand. Therefore, distinct
186 long and short reaches were required for left and right targets (e.g. leftward shift → left-
187 long/right-short reaches; Figure 1C). Note that the shift of the visual elements happened >1s
188 prior to the target presentation to ensure unambiguous interpretation of the trial context. It is
189 also important to note that the between-target distance (~16 cm) was kept constant, and the
190 fixation point was shifted by ~4 cm such that the target had the same visual eccentricity
191 across conditions.

192 To control the oculomotor behaviour, the EOG was calibrated before the main
193 experiment by asking the participants to look at a target located at the centre of the monitor
194 (consistent with the fixation spot location in control conditions; Figure 1C) for ~10s. Then
195 the target jumped laterally right/left at three different distances (i.e. six direction-x-distance
196 conditions), stayed there for ~2s before returning back to the initial one and made another
197 jump only after another ~5s. For consistency with the main experiment, the target was a filled
198 black circle 3cm in diameter presented against a light grey background and jumped ± 8 , ± 13
199 and ± 3 cm relative to the starting central position. The target jumped laterally five times for
200 every direction and distance condition (i.e. 30 total trials). Importantly, this procedure
201 allowed us to define the within-subject absolute EOG signal values across different eye
202 positions and, thereby control the gaze fixation online.

203 For the main experiment, each participant completed 6 blocks of 48 reaches/block (24
204 for each direction), with each block consisting of 16 control-reach, 16 long-reach and 16
205 short-reach trials, randomly intermingled.

206

207 *Experiment 2: task design*

208 The first experiment showed modulations of express visuomotor response as a function
209 of the reaching distance (see Experiment 1 results for details). This could indicate that the
210 physical hand-to-target distance was encoded along the express sensorimotor circuit.
211 Alternatively, the data might reflect context-based preparation of long, or short, movements
212 irrespective of the real target distance from the reaching hand. Although these alternatives are
213 not mutually exclusive, we ran a second experiment asking the participants to execute
214 movements of different amplitudes as a function of the explicit instruction to: (i) stop at the
215 target (*control*); (ii) *overshoot* the target; (iii) *undershoot* the target (Figure 1D). The control
216 condition replicated that of the first experiment as the participants had to stop at the actual
217 target location within the two vertical black lines underneath the barrier (Figure 1D: control

218 condition). For the overshoot condition, we displayed green vertical lines underneath the
219 barrier and instructed the participants to overshoot the actual target location by ending the
220 movement at least beyond the outermost vertical green line (Figure 1D: overshoot condition).
221 For the undershoot condition, we used red lines beneath the barrier and asked the participants
222 to undershoot the actual target location by ending the movement before the innermost vertical
223 red line (Figure 1D: undershoot condition). On every trial, the target always appeared at ~8
224 cm to the right or left of participants' right hand. Note that the second experiment design did
225 not require distinct movement amplitudes for different target locations (e.g. right-overshoot
226 vs left-undershoot). The motivation for providing advance and equal task instructions for
227 both the right and left targets was to dissociate the executed reach from the target location
228 without adding complexity for the trajectory-endpoint decision at the time of target
229 presentation. To this aim, and consistent with the first experiment, the trial condition (i.e. the
230 colour of the lines underneath the barrier) was made explicit to the participants for >1s before
231 the target presentation.

232 Each participant completed 6 blocks of 48 reaches/block (24 for each direction), with
233 each block consisting of 16 control-reach, 16 overshoot-reach and 16 undershoot-reach trials,
234 randomly intermingled.

235

236 **Data recording and analysis**

237 *Kinematic data recording and analysis*

238 The kinematic data of the vBOT handle were recorded via two optical encoders at a
239 sampling rate of 1 KHz. To define the mechanical RT, we adopted the 'extrapolation'
240 technique (Veerman et al., 2008; Wijdenes et al., 2014; Zhang et al. 2018a, 2018b) as it
241 returns reliable RT measurements even in circumstances requiring short movements evolving
242 at low velocities (Brenner and Smeets 2019). Briefly, we defined the first peak of the radial
243 hand velocity after the time point at which it firstly exceeded the baseline value (i.e. average

244 velocity recorded in the 100 ms preceding the target onset time) by more than five standard
245 deviations. We then fitted a line to the hand velocity data enclosed between 25% and 75% of
246 the peak velocity and indexed the RT as the time at which this line crossed the baseline
247 velocity value. Trials with RT <160 ms (~5%) or >500 ms (<1%) were excluded during
248 offline analysis.

249 To determine the response correctness, we measured the initial reach direction by
250 adopting a procedure previously described by Contemori et al., 2022. Briefly, we compared
251 the initial hand-trajectory direction (i.e. slope of a line connecting the hand position
252 coordinates at the RT and the 75% of the peak velocity) with the actual target location. We
253 then computed the movement endpoint by searching for the point in time at which the total
254 hand velocity fell below 0.5 m/s after having reached its peak value. We reasoned that a trial
255 was correct if the hand initially moved toward the actual target and ended at the location
256 specified by the trial-condition.

257 For correct trials, we computed the movement time (i.e. RT-to-endpoint time), and the
258 time to reach the maximal velocity. We also conducted a trial-by-trial temporal normalization
259 for the whole movement duration to test whether the movement evolved similarly across
260 conditions despite task-dependent differences in movement time. This allowed us to index the
261 point (%) within the movement at which the hand-velocity reached its peak. For both
262 experiments, the kinematic data were averaged across the left and right directions to limit
263 potential biases related to the leftward preloading robot force.

264

265 *EMG data recording*

266 Surface EMG activity was recorded from the clavicular head of the right pectoralis
267 muscle (PMch) and the posterior head of the right deltoid muscle (PD) with double-
268 differential surface electrodes (Delsys Inc. Bagnoli-8 system, Boston, MA, USA). The quality
269 of the EMG signal was checked offline with an oscilloscope by asking the participants to flex

270 (PMch activation-PD inhibition) and extend (PMch inhibition-PD activation) the shoulder in
271 the transverse plane. The sEMG signals were amplified by 1,000, filtered with a 20–450 Hz
272 bandwidth filter by the ‘Delsys Bagnoli-8 Main Amplifier Unit’ and sampled at 2 kHz using
273 a 16-bit analog-digital converter (USB-6343-BNC DAQ device, National Instruments,
274 Austin, TX).

275 Trial-by-trial, the EMG signal was saved on a secondary computer via a custom Matlab
276 script that also generated live plots of the recorded data. This gave us the opportunity to
277 interrupt the experiment in case the EMG signal deteriorated (e.g. loss of electrode-on-skin
278 contact). The sEMG data were then down-sampled to 1 kHz and full-wave rectified offline.

279

280 *Detection of muscle response onset time*

281 To detect the earliest stimulus-driven muscle response, we adopted a single-trial
282 analysis method named the *detrended-integrated* signal method that we recently developed
283 and validated (Contemori et al., 2022). Briefly, we initially computed the integral of the full-
284 wave rectified EMG signal recorded between 100 ms before and 300 ms after the target onset
285 time. We then computed the linear regression function of integrated EMG signal enclosed in
286 the background period (from 100 ms before to 70 ms after the stimulus presentation) and
287 subtracted this function from the entire 400 ms window, thus detrending the integrated EMG
288 trace. We then computed the average and standard deviation values of the detrended-
289 integrated signal in the background epoch. We indexed the ‘candidate’ muscle response onset
290 time as the first time the detrended-integrated signal exceeded the background average value
291 by more (i.e. signature of muscle activation), or less (i.e. signature of muscle inhibition), than
292 five standard deviations.

293 We previously showed that the occurrence of false-positive express muscle response
294 detection (i.e. candidate onset times earlier than 70 ms after the target presentation) is lower
295 than 5% by using a five standard deviations threshold (Contemori et al., 2022). Here, we also

296 tested the occurrence of muscle responses on an earlier time-window at 20-60ms from the
297 target presentation. No muscle response was detected in this ‘pre-express’ time window;
298 neither with a five, four or three standard deviations as threshold for the candidate response
299 onset time. We are, therefore, confident using five standard deviations as the threshold to
300 index the candidate onset time of express visuomotor responses.

301 Critically, the candidate response onset time does not exactly correspond to the earliest
302 deflection-from-background of the signal. To find this time point, we ran a linear regression
303 analysis around the candidate muscle response onset time and indexed the time at which the
304 linear trendline intercepted the zero value of the detrended-integrated signal (see figure 3 in
305 Contemori et al., 2022 for details). A muscle response was classified as ‘express’ if was
306 initiated within 70-110 ms after the target presentation. By contrast, the muscle responses
307 initiated later than 110ms were classified as ‘long-latency’. Note that we used a shorter
308 express time-window relative to previous work (i.e. 70-120 ms; Gu et al., 2016; Contemori et
309 al., 2021a, 2021b, 2022) to prevent contamination of the express epoch by the long-latency
310 (plausibly cortically mediated) EMG activity of faster trials. Further, we found that the delay
311 between the onset time of long-latency muscle response and RT of the corresponding trials
312 was on average 40 ms. Thus, even for the earliest RT trials included in the data analysed (160
313 ms RT cut-off; see the *Kinematic Data Analysis* section), the long-latency EMG response
314 should have started >110 ms from the target presentation. Importantly, this allowed us to
315 minimize the risk that rapid muscle responses from the long-latency phase contaminated the
316 signal enclosed in the express epoch.

317

318 *Identifying participants exhibiting stimulus-locked express visuomotor responses*

319 One of the most distinctive attributes of express visuomotor responses is that their onset
320 time is more locked to the target presentation time than the mechanical RT (Pruszyński et al.,
321 2010; Wood et al., 2015; Kozak et al., 2019, 2020; Kozak and Corneil, 2021; Contemori et

322 al., 2021a, 2021b, 2022). Critically, the broad range of delays for the long-latency motor
323 signal to reach the RT detection threshold is consistent with poly-synaptic nature of cortical
324 sensorimotor networks to transform sensory inputs into deliberate decisions for actions. By
325 contrast, the strikingly short-latency and relative temporal consistency of express visuomotor
326 responses implies a small range of delays in motor signal conduction time, consistent with the
327 few synapses of the tecto-reticulo-spinal pathway. To test the extent to which the express
328 visuomotor response onset times were independent from the RT, we adopted a procedure
329 previously described by Contemori et al., (2022). We first selected the trials showing an
330 express muscle response and then gathered the corresponding RTs. We then divided these
331 trials into “express-fast” and “express-slow” subsets based on whether the associated RT laid
332 above or below the median RT of the full class of express trials. We then computed the
333 average express responses initiation time of the express-fast and express-slow trials as well as
334 the average RT of the corresponding fast and slow trial bins. Finally, we fitted a line to the
335 express-fast and express-slow average data to test if the muscle response onset time did not
336 co-vary with the RT (i.e. line slope >67.5 deg; for details see Contemori et al., 2022; see also
337 Figure 3 in Contemori et al., 2021a and 2021b). Participants with express response onset
338 times that did not co-vary with the RT for both the right and left trials and among all task
339 conditions were classified as an express visuomotor response producer (see results for
340 details). For these subjects, we computed the condition-dependent express response initiation
341 time by averaging this metric across the express visuomotor response trials and then across
342 the right and left target locations. We also computed the condition-dependent express
343 response detection rate by averaging the percentage of express visuomotor response trials
344 within the data set across the two target locations. Further, we quantified the condition-
345 dependent express response magnitude by computing the average EMG activity recorded in
346 the 10ms after the response initiation time for each rightward and leftward trial exhibiting an

347 express visuomotor response. We then averaged this metric across the express response trials
348 and computed the difference between the left and right targets (Contemori et al., 2022).
349

350 *Test whether express visuomotor responses reflect contextual visuomotor behaviour*

351 We and others previously showed that larger express visuomotor responses are
352 associated with earlier RTs (Pruszyński et al., 2010; Gu et al., 2016; Contemori et al., 2021a).
353 Here, we found that express visuomotor responses were facilitated in task conditions that also
354 facilitated the reach onset time (see results for details). Further, modulating the reaching
355 amplitude correlated with task-dependent variation in movement velocity and, thereby the
356 long-latency muscle response magnitude (LLRM; see results for details) that was defined,
357 trial-by-trial, by taking the average EMG signal from 5ms prior to 5ms after the RT.

358 Although we minimized the risk of contamination of the express epoch from the long-
359 latency EMG signal (see ‘Detection of express visuomotor response’ for details), we also
360 verified whether the task-dependent modulation of the express response reflected the
361 contextual visuomotor behaviour. To this aim, we tested express visuomotor responses on
362 data samples with matched RTs across conditions by adopting a trial-matching procedure
363 akin to that used by Dash et al. (2018) and Kozak et al. (2019). Further, we also re-tested
364 express visuomotor responses on data samples with matched LLRM across conditions. We
365 reasoned that if the express visuomotor response reflected task-dependent modulations of the
366 express circuit, then similar between-condition contrasts should be observed in both original,
367 RT-matched, and LLRM-matched data sets. These trial subsets were generated for each
368 participant who exhibited express visuomotor responses across all the three task conditions
369 (see results). We first defined the range of RT and LLRM values by pooling all the correct
370 trials across the three task conditions. We then verified the presence of at least one trial per
371 condition for each $RT \pm 2\text{ms}$ value of the full data sample and repeated this procedure for each
372 $LLRM \pm 5\mu\text{V}$ value. Note that the $\pm 2\text{ms}$ and $\pm 5\mu\text{V}$ tolerances were applied to be conservative
373 on the number of non-matching RT trials to discard, which would otherwise increase by
374 searching for perfect value-match between conditions. Participants were excluded from this
375 analysis if this procedure discarded $>50\%$ of the original trials in one, or more, of the three

376 task conditions. These procedures generated three condition-specific data sets having similar
377 distributions of the variables of interest, but different numbers of trials across conditions. To
378 create compatible data sets, we binned the RT-matched trials every 20ms from the smallest
379 RT value, and then binned the LLRM-matched trials every 20 μ V from the smallest LLRM
380 value. For all task conditions, we then resampled with replacement the binned trials 100 times
381 by using a bootstrapping approach. For each bin of trials, we selected the same number of
382 trials per condition based on the lowest number of trials across conditions for that bin in the
383 original data set. Finally, we re-ran the detrended-integrated signal analysis methods on the
384 RT-matched and then on the LLRM-matched data sets.

385

386 *Statistical analysis*

387 To test the statistical differences across conditions, we ran repeated measures ANOVA
388 (rmANOVA) analyses, unless otherwise stated, as the normality of the distributions was
389 verified by the Shapiro–Wilk test. Specifically, for the kinematics variables we ran the
390 rmANOVA analysis on the mechanical RT, movement time, maximal hand velocity, time to
391 maximal hand velocity, percentage of the movement at which the maximal hand velocity was
392 reached, and variability of the movement endpoint. For the EMG, the rmANOVA analysis
393 was run on the detection rate, onset time, and magnitude of express muscle responses, as well
394 as on the LLRM. The rmANOVA analyses were conducted in SPSS (IBMSPSS Statistics for
395 Windows, version 25, SPSS Inc., Chicago, Ill., USA) with Bonferroni correction and task
396 condition (3 levels: first experiment control long-reach, short-reach; second experiment
397 control, overshoot, undershoot) as within-participant factors. When the ANOVA revealed a
398 significant main effect, we estimated the effect size by computing the Partial eta squared (η_p^2)
399 and ran Bonferroni tests for post-hoc comparisons. Note that the detectable effect size with
400 our smallest sample size ($N=10$; see the EMG results of the second experiment) and
401 statistical power of 0.8 was estimated to be medium-to-large (effect size f 0.44; G*Power,

402 version 3.1.9.4, Heinrich-Heine-Universität Düsseldorf, Düsseldorf, Germany). For all tests,
403 the statistical significance was designated at $p < 0.05$.

404

405 RESULTS

406 Experiment 1

407 *Kinematic results*

408 In the first experiment, the participants reached to visual targets that could appear at
409 different rightward or leftward distances from their dominant hand (for details see
410 Experiment 1 task design). They successfully achieved the task goal in more than 90% of the
411 trials across the three experimental conditions.

412 Figure 2A shows exemplar correct hand-to-target trajectories of a participant who
413 completed the first experiment. For this subject, the targets requiring short reaching distances
414 resulted in longer RT relative to control and long-reach conditions (dashed vertical lines in
415 Figure 2B). After its initiation, the movement evolved at faster and slower velocities than
416 control for the long-reach and short-reach conditions, respectively (dotted vertical lines in
417 Figure 2B). The task-dependent variation in maximal velocity did not fully compensate that
418 in reaching distance thus leading to longer movement times to complete longer than shorter
419 reaches (i.e. RT-to-endpoint time; Figure 2B). The participants, however, were not required
420 to complete the movement within a specific time (see Materials and Methods). Also, the
421 velocity profiles were symmetrically bell-shaped regardless of peak velocity such that the
422 maximum hand velocity was reached at around the movement half across all conditions
423 (Figure 2C).

424 For the entire group, the rmANOVA showed statistically significant task-condition
425 (control vs long-reach vs short-reach) main effects for RT ($F_{2,12}=20$, $p < 0.001$, $\eta_p^2=0.6$),
426 movement time ($F_{2,12}=23.1$, $p < 0.001$, $\eta_p^2=0.54$), maximal hand velocity ($F_{2,12}=366$, $p < 0.001$,
427 $\eta_p^2=0.97$), time to maximal hand velocity ($F_{2,12}=42.5$, $p < 0.001$, $\eta_p^2=0.77$), and endpoint

428 movement variability ($F_{2,12}=4.5$, $p=0.02$, $\eta_p^2=0.26$). The short-reach target condition led to
429 significantly longer RT (Figure 3A), significantly shorter movement time (Figure 3B), and
430 involved significantly lower maximal hand velocities (Figure 3C) that were reached
431 significantly earlier (Figure 3D) than the control conditions. By contrast, the long-reach target
432 condition led to the opposite results, except for the RT that was not statistically different than
433 control. When the peak-velocity event was indexed relative to the whole movement duration,
434 however, we did not find statistically significant differences between conditions ($F_{2,12}=2.9$,
435 $p=0.07$; Figure 3E). The endpoint of the movement trajectory was significantly more variable
436 for the long-reach than the other conditions (Figure 3F), plausibly reflecting a tradeoff
437 between speed and accuracy to accomplish the task.

438 Overall, these results indicate that the participants were biased by the hand-to-target
439 distances such that they took more time to start moving toward targets appearing close to
440 their hand. Once the movement started, the hand velocity was modulated according to the
441 hand-to-target distance but the greater hand speeds for longer reaches were insufficient to
442 complete the task within the same time across conditions. Nevertheless, the hand was always
443 accelerated for approximately half the movement distance before being decelerated to stop at
444 the target, resulting in similar movement profiles for all hand-to-target distances.

445

446 *EMG results*

447 Figure 4 shows EMG data recorded from the PMch of an exemplar participant who met
448 the conditions for positive express visuomotor response detection (see Materials and
449 Methods) across all conditions of the first experiment. In the first two columns of raster plots
450 of Figure 4, express visuomotor responses appear as a vertical band of either muscle
451 activations (left targets) or inhibitions (right targets) at 70-110 ms after the target presentation
452 time. For this subject, the number of trials with an express visuomotor response initiation
453 increased, and that of long-latency responses decreased, by increasing the hand-to-target

454 reaching distance (see the red and magenta scatters and bars in Figures 4A-I). Specifically,
455 the detection rate of express visuomotor response was 55%, 77% and 81% for the short-
456 reach, control, and long-reach conditions respectively. In addition, the average EMG signal
457 enclosed in the express time-window (grey patch in Figure 4J) was smaller for the short-reach
458 condition than the other conditions. The express visuomotor responses onset time, however,
459 was ~90 ms after the target presentation across all conditions (Figure 4J).

460 Ten participants (i.e. 71% of the sample) exhibited express visuomotor responses on the
461 PMch in all three conditions of the first experiment. For these subjects, the rmANOVA
462 showed a statistically significant task-condition (control vs long-reach vs short-reach) main
463 effect for the detection rate of express visuomotor response ($F_{2,8}=39.6$, $p<0.001$, $\eta_p^2=0.81$).
464 The post-hoc analysis revealed that the prevalence of express visuomotor responses was
465 significantly lower for the short reach than the other task conditions (Figure 5A). Although
466 the express response onset time tended to decrease with the hand-to-target-distance (Figure
467 5B), we did not find statistically significant contrast between the three conditions ($F_{2,8}=1.26$,
468 $p=0.3$). The express visuomotor response magnitude was significantly modulated by the
469 hand-to-target distance ($F_{2,8}=11$, $p<0.001$, $\eta_p^2=0.55$) as it was significantly smaller for the
470 short reach than the other conditions (Figure 5C). It is worth noting that these results are
471 unlikely to reflect fixation-dependent differences in target perception, as the left and right
472 targets had equal visual eccentricity among the three task conditions (see Materials and
473 Methods).

474 The short-reach condition led to significantly fewer (Figure 5A) and smaller (Figure
475 5C) express visuomotor responses, but also significantly longer RTs (Figure 3A) and smaller
476 LLRM responses than the other conditions (short-reach $39\pm 15\mu\text{V}$; control $48\pm 19\mu\text{V}$; long-
477 reach $54\pm 21\mu\text{V}$; $F_{2,8}=7.7$, $p=0.004$, $\eta_p^2=0.46$; short-reach vs other conditions $p<0.01$). We
478 sought to differentiate the reaching-distance effects on express visuomotor response from
479 task-dependent underlying variability of responsiveness. To this aim, we tested the express

480 responses on RT-matched and LLRM-matched data samples (see Materials and Methods for
481 details). Notably, the between-condition contrasts in express visuomotor response metrics for
482 the RT-matched and LLRM-matched data sets (Table 1) were consistent with those of the
483 original data samples (Figure 5). This indicates that the express visuomotor response was
484 influenced by the physical distance to reach the target, but not by the time at which the
485 movement was initiated or the long-latency muscle response magnitude. It is also worth
486 noting that these results are unlikely to reflect fixation-dependent differences in target
487 perception, as the retinal location of the target was kept equal across the hemi visual fields for
488 all task conditions (see Materials and Methods).

489 Overall, the first experiment results show that the express visuomotor response was
490 modulated by the metrics of the visuospatial reaching task, such that targets reachable via
491 small (or large) hand displacements inhibited (or facilitated) the generation of frequent and
492 robust muscle responses within similar express time limits.

493

494 **Experiment 2**

495 *Kinematic results*

496 The second experiment tested whether the context-dependent results of the first
497 experiment reflected encoding of the veridical hand-to-target reaching metrics, or preparation
498 of movements of different amplitudes regardless of the real hand-to-target distance.
499 Specifically, the participants were required to overshoot, undershoot, or stop at the target as a
500 function of explicit trial-based instructions (for details see Experiment 2 task design). They
501 successfully achieved the task goal in more than 90% of the trials across the three
502 experimental conditions.

503 For an exemplar subject, the requirement to stop at the actual target location (i.e.
504 control condition) resulted in earlier RTs relative to the other tasks (dashed vertical lines in
505 Figure 6B). Higher velocity and longer movement time were observed for the overshoot than

506 control conditions, whereas the undershoot task led to the opposite results (Figure 6B). Also,
507 the hand was accelerated for longer in conditions with higher peak velocities (Figure 6B).
508 The movement, however, evolved similarly across conditions with a single acceleration phase
509 terminating within the first half of the movement (Figures 6C).

510 For the entire group, the rmANOVA showed statistically significant task-condition
511 (control vs target-overshoot vs target-undershoot) effects for RT ($F_{2,10}=31.9$, $p<0.001$,
512 $\eta_p^2=0.74$), movement time ($F_{2,10}=50.9$, $p<0.001$, $\eta_p^2=0.82$), maximal hand velocity ($F_{2,10}=338$,
513 $p<0.001$, $\eta_p^2=0.97$), time to maximal hand velocity ($F_{2,10}=81.7$, $p<0.001$, $\eta_p^2=0.88$), point of
514 the maximal hand velocity within the movement ($F_{2,10}=6.7$, $p=0.005$, 0.38), and endpoint
515 movement variability ($F_{2,10}=19.8$, $p<0.001$, $\eta_p^2=0.64$). The movement started significantly
516 earlier in the control than other conditions, and significantly earlier in the undershoot than
517 overshoot condition (Figure 7A). The movement endpoint was reached significantly earlier
518 and later than control for the undershoot and overshoot conditions, respectively (Figure 7B).
519 The hand moved significantly slower than control for the undershoot and significantly faster
520 than control for the overshoot conditions (Figure 7C). Peak velocity occurred significantly
521 earlier than control for the undershoot and significantly later than control for the overshoot
522 conditions (Figure 7D). The peak velocity occurred at around half of the movement distance
523 for all conditions, but significantly earlier for the overshoot condition (Figure 7E). The
524 trajectory endpoint variability was not significantly different than control for the undershoot
525 condition (Figure 7F). Notably, this indicates that the undershooting movements were
526 oriented toward an abstract target location that was reached trial-by-trial with a precision
527 error akin to that of the reaches terminating at the veridical target in the control condition.
528 The movement endpoint was significantly more variable for the overshoot than the other
529 conditions (Figure 7F). This result, however, was consistent with the contrast between the
530 long-reach condition and the other task conditions of the first experiment (Figure 3F) and
531 could reflect a speed-accuracy tradeoff.

532 These results show that the requirement to not reach the actual target location increased
533 the time to initiate the response, whereas the online movement evolved similarly across
534 conditions besides expectable task-dependent variations in movement velocity and time.
535 These results are consistent with a delay in the long-latency muscle response arising from the
536 need to compute an abstract movement endpoint, rather than using the hand-to-target metrics
537 directly.

538

539 *EMG results*

540 Figure 8 shows exemplar EMG data recorded from the PMch of a participant who
541 exhibited express visuomotor responses across all the three conditions of the second
542 experiment (same subject as Figure 4). For this subject, the express visuomotor response
543 detection rate was 79% for the control condition, 49% for the overshoot and 52% undershoot
544 conditions (see the red scatters and bars in Figures 8A-I). Consistently, fewer long-latency
545 muscle responses were detected for the control than the other conditions (see the magenta
546 scatters and bars in Figures 8A-I). The EMG signal enclosed in the express time-window
547 started diverging from baseline ~85-90 ms after the target presentation and exhibited a
548 similar incremental rate across the three task conditions up to 100 ms (Figure 8J). For both
549 the overshoot and undershoot conditions, however, the express EMG signal returned close to
550 the background level prior to initiation of the long-latency response (see the red and green
551 arrows in Figure 8J). By contrast, for the control condition the long-latency EMG signal
552 followed the express EMG signal with little or no pause between these two phases (see the
553 black arrow in the inset plot of Figure 8J); this was observed also across all task conditions of
554 the first experiment when participants always executed veridical target-directed reaches
555 (Figure 4J).

556 For the second experiment, ten participants (i.e. 83% of the sample) met the conditions
557 for positive express visuomotor responses detection on the PMch across the three conditions.

558 For these subjects, the rmANOVA showed a statistically significant effect of task-condition
559 on the detection rate of express visuomotor response ($F_{2,8}=9.3, p=0.002, \eta_p^2=0.51$), which was
560 significantly larger in the control than the other task conditions (Figure 9A). The express
561 visuomotor response tended to initiate earlier for the control than the other conditions (Figure
562 9B), but this between-condition contrast was not statistically significant ($F_{2,8}=1, p=0.37$). The
563 express visuomotor response magnitude was significantly modulated by the task conditions
564 ($F_{2,8}=5, p=0.02, \eta_p^2=0.36$) as it was significantly smaller than control for both the overshoot
565 and undershoot task conditions (Figure 9C).

566 As was noted in the first experiment, the task condition that facilitated express
567 visuomotor responses corresponded to that leading to earlier RTs (i.e. control condition;
568 Figure 7A). The LLRM response magnitude, however, correlated with the movement
569 amplitude ($F_{2,8}=17, p<0.001, \eta_p^2=0.65$), as it was significantly higher for the overshoot
570 ($76\pm 30\mu\text{V}$) than both the control ($62\pm 31\mu\text{V}; p=0.02$) and undershoot conditions ($41\pm 21\mu\text{V};$
571 $p<0.001$). Therefore, we tested whether the between-condition contrasts in express
572 visuomotor response metrics held true for RT-matched and LLRM-matched data sets (see
573 Materials and Methods for details). Again, the results of the RT-matched and LLRM-matched
574 subsets of trials (Table 2) were consistent with those obtained from the original data samples
575 (Figure 9). This indicates that the express visuomotor responses were modulated by the
576 contextual task instructions, irrespective of the RT or the long-latency muscle response
577 magnitude.

578 Our results suggest that the reaching amplitude modulates the express visuomotor
579 response differently for veridical target-directed reaches (Experiment 1: Figure 5 and Table
580 1) versus reaches that under or overshoot the location of physical targets (Experiment 2:
581 Figure 9 and Table 2). To test whether the qualitative differences between the two experiments
582 were statistically significant, we ran a two-way rmANOVA with experiment-type (2
583 levels: experiment 1; experiment 2) and task-condition (3 levels: short/undershoot, control,

584 long/overshoot) as within-subject factors. Note that this analysis was conducted only for
585 those subjects (n=8) who completed both experiments and exhibited the express behaviour
586 across all conditions (see Materials and Methods). The two-way rmANOVA showed that the
587 task-condition significantly modulated the detection rate and magnitude of express
588 visuomotor responses (detection rate: $F_{2,6}=10.12$, $p=0.002$, $\eta_p^2=0.59$; magnitude: $F_{2,6}=9.33$,
589 $p=0.003$, $\eta_p^2=0.57$). Notably, however, the effect of task-condition on express response
590 detection rate and magnitude differed for the two experiments as shown by a statistically
591 significant interaction between experiment-type and task-condition (detection rate:
592 $F_{2,6}=13.86$, $p<0.001$, $\eta_p^2=0.66$, Figure 10A; magnitude: $F_{2,6}=4.69$, $p=0.003$, $\eta_p^2=0.4$, Figure
593 10C). No significant main effect or interaction was found for the express response onset time
594 (Figure 10B).

595 Overall, the results of the second experiment indicate that matching the real target with
596 the task-goal endpoint facilitates express transformation of visual inputs into appropriate
597 motor outputs compared to reaches toward non-veridical target locations. When express
598 responses occurred, however, they reflected express sensory-to-motor transformations of the
599 target location within similar times for both veridical and non-veridical target-directed
600 reaches.

601

602 DISCUSSION

603 This study showed that express visuomotor responses reflect both the physical hand-to-
604 target reaching distance and explicit instructions about the required movement amplitude
605 during a visuospatial task. This suggests that the express visuomotor outputs can be
606 strategically exploited by the cerebral cortex to facilitate rapid and appropriate responses to
607 visual targets. A schematic representation of a possible circuit organisation is outlined in
608 Figure 11.

609

610 **Mechanisms for express visuomotor responses during veridical target-directed reaches**

611 The first experiment showed that the hand-to-target reaching distance modulated
612 express visuomotor transformations putatively performed along a tecto-reticulo-spinal circuit.
613 The involvement of the superior colliculus in the generation of express visuomotor responses
614 (Corneil et al., 2004, 2008; Pruszynski et al., 2010) is consistent with its capability to encode
615 the location of either target or distractor stimuli within ~40–70ms (Boehnke and Munoz,
616 2008). Further, the surface layer of this midbrain structure is organized in a retinotopic map,
617 whereas its deeper layers are organized in somatotopic maps (for review see Basso and May,
618 2017; Boehnke and Munoz, 2008). Therefore, the superior colliculus could integrate visual
619 and somatosensory information to compute the direction and distance of a target-directed
620 action. Downstream from the superior colliculus, the reticular formation also receives inputs
621 from somatosensory afferents (Leiras et al., 2010). Thus, a tecto-reticulo-spinal pathway has
622 the required sophistication to compute and generate appropriate express visuomotor
623 responses during veridical target-directed actions of different amplitudes (Figure 11).

624 We recently documented circumstances of express visuomotor response modulation
625 secondary to explicit cues (Contemori et al., 2021a, 2021b, 2022). Pre-stimulus information
626 might facilitate processing of expected stimuli at the superficial superior colliculus (for
627 review see Corneil and Munoz, 2014) and/or initiation of expected responses along the
628 express pathway (Basso and Wurtz, 1998; Cisek and Kalaska, 2005; Contemori et al., 2022).
629 Here, the eccentricity (hence saliency) of opposite targets was constant but local thresholds
630 for responding could be modulated asymmetrically by corticotectal projections (Boehnke and
631 Munoz, 2008). Alternatively, or additionally, the advance information about the required
632 distance for each possible target could bias the tecto-reticular circuit to generate larger
633 express signals for targets requiring larger movements. These signals would be more likely to
634 cross the spike threshold for neurons along the express pathway, consistent with the increased
635 number of large express visuomotor responses associated with increased reaching distance.

636 Such a mechanism would also be expected to result in slightly shorter latencies for the larger
637 responses, but the differences would be difficult to detect from these EMG signals.

638 Previous work suggests that the express responses contribute to the volitional
639 visuomotor behaviour because larger express outputs were associated with earlier RTs
640 (Pruszyński et al., 2010; Gu et al., 2016; Contemori et al., 2021a). Mechanically, RT detection
641 depends on muscle force accelerating the arm to the threshold velocity. Notably, the muscle
642 force will rise more rapidly if the same motor units receive close temporospatial summation
643 of express and long-latency motor signals, which would enhance intramuscular calcium
644 release and diffusion (i.e. the *catch* property of muscle; for review see Tsianos and Loeb,
645 2017). In the first experiment, more frequent and larger express visuomotor responses were
646 associated with the amplitude of the long-latency EMG signal (Figure 4G) that reflected the
647 required reaching length (Figure 2). As expected, summation of larger express and long-
648 latency muscle recruitment generated earlier RTs and higher peak velocities. It is also
649 possible that the weaker express visuomotor responses associated with shorter reaches reflect,
650 at least partially (Wong et al., 2017), the higher complexity (i.e. RT delay) inherent in
651 planning short movements that offer less time for online correction.

652

653 **Mechanisms for express visuomotor responses during reaches to non-veridical targets**

654 In the second experiment, the requirement to overshoot or undershoot the real target led
655 to fewer and smaller express visuomotor responses relative to control. Why should the
656 express response be inhibited in circumstances requiring non-veridical responses?

657 The fact that express visuomotor responses rigidly encode the visual stimulus location
658 (Wood et al., 2015; Gu et al., 2016; Atsma et al., 2018) is consistent with their proposed
659 subcortical origin (Pruszyński et al., 2010). Nevertheless, this also suggests that the express
660 motor output might be counterproductive when the task requires non-veridical responses. For
661 instance, Gu et al., (2016) showed that large pro-target express responses delayed the

662 initiation of correct anti-target reaches, plausibly because of larger time costs to override the
663 express pro-target muscle forces (Gu et al., 2016). The express system, however, appears to
664 be flexible to contextual task rules when these are predictable. For instance, Wood and
665 colleagues (2015) recorded express target-directed muscle responses in delayed-reach task
666 trials that were randomly intermingled with no-delay trials (i.e. task condition
667 unpredictability). By contrast, express visuomotor responses were obliterated when only
668 delayed-reach trials were presented within a block (Pruszynski et al., 2010). Notably, these
669 results are consistent with more recent evidence of cortically-driven modulation of express
670 visuomotor responses (Contemori et al., 2021a, 2021b, 2022). Considering that express
671 visuomotor responses aid rapid movement initiation (Pruszynski et al., 2010; Gu et al., 2016;
672 Contemori et al., 2021a), their inhibition could reflect strategic cortico-subcortical inhibition
673 in contexts requiring longer RTs, such as for reaching toward non-veridical targets (Figure
674 11).

675 The overshoot/undershoot tasks resulted in longer RTs than control, which could reflect
676 increased complexity to plan a non-veridical response trajectory (Wong et al., 2016). Cortical
677 planning of appropriate responses for achieving complex task goals can modulate the
678 networks downstream from the cerebral cortices (Selen et al., 2012; see for review Kurtzer,
679 2015). Critically, these include the reticulo-spinal circuits that are proposed to process the
680 superior colliculus signals to generate express visuomotor responses (Corneil et al., 2004,
681 2008; Pruszynski et al., 2010; Figure 11).

682 The mammalian reticular formation is involved in the control of static posture
683 (Sherrington, 1898; Rhines and Magoun, 1946; Magoun and Rhines, 1946). More recent
684 neurophysiological and behavioural work also suggest that this brainstem structures
685 contributes to volitional upper-limb movements (Alstermark and Isa, 2012; Contemori et al.,
686 2021c) and reflexive responses to mechanical perturbations of static upper-limb postures
687 (Kurtzer, 2015). Notably, the reticular formation receives descending signals from both the

688 superior colliculus (Boehnke and Munoz, 2008) and cortical brain areas (Keizer and Kuypers,
689 1984, 1989; Fregosi et al., 2017; Darling et al., 2018; Fisher et al., 2021). The reticular
690 formation, therefore, appears to be well-placed to integrate descending collicular signals
691 encoding the physical stimulus location (Everling et al., 1999; McPeck and Keller, 2002)
692 with cortical premotor signals affording task-related rules (e.g. to overshoot/undershoot the
693 target). In this circumstance, express stimulus-driven motor signals may be inhibited (or even
694 obliterated) to delay the RT when there is uncertainty about the reach goal, such as for our
695 non-veridical reaching tasks.

696

697 **A common subcortical network for rapid initiation and online control of reaching?**

698 Both the superior colliculus (Werner, 1993) and reticular formation (Buford and
699 Davidson, 2004; Schepens and Drew, 2004) are active before and during upper limb reaching
700 movements. The tecto-reticulo circuit, therefore, might contribute to both the reach initiation
701 (Pruszyński et al., 2010; Gu et al., 2016; Contemori et al., 2021a) and rapid kinematic (Day
702 and Lyon, 2000; Day and Brown, 2001; Veerman et al., 2008; Smeets et al., 2016; Brenner et
703 al., 2022) and postural (Fautrelle et al., 2010; Zhang et al., 2018a, 2018b) adjustments during
704 ongoing reaching actions. Notably, this is consistent with recent evidence of express
705 visuomotor responses to correct the online movement trajectory in a jump-target task (Kozak
706 et al., 2019). Furthermore, the size of muscle responses starting ~90-120 ms after visual
707 perturbation of virtual hand position showed a non-linear scaling for perturbation amplitudes
708 >2 cm (Cross et al., 2019). Although we did not characterise a function that defines express
709 response modulation according to movement distance, our observation that the express
710 response to the farthest target was not greater than that to the middle target is consistent with
711 observations of response saturation in the dynamic tasks of Cross and colleagues (2019).

712 Initiation and online control of real-world visuospatial actions rely on visuomotor
713 circuits that must integrate multisensory information about the body and target positions,

714 which is inherently variable and noisy. The current data are consistent with previous evidence
715 suggesting that the putative subcortical express circuits can be primed to generate flexible
716 context-dependent motor outputs that support the accomplishment of visuospatial tasks from
717 both static (Kurtzer, 2015; Weiler et al., 2019; Contemori et al., 2022) and dynamic postures
718 (Cross et al., 2019; Kozak et al., 2019; Weiler et al., 2021).

719

720 **Conclusions**

721 This study shows that express visuomotor responses can be flexibly modulated to
722 achieve visuospatial task-goals. The data are consistent with the idea of a subcortical
723 visuomotor pathway whose motor output is strategically exploited by the cerebral cortex to
724 facilitate rapid initiation of veridical target-directed reaches. It remains to be determined
725 whether the longer latency, presumably cortically-driven, motor responses rely on some or all
726 of the same subcortical circuits to convert reaching targets in extra-personal space
727 coordinates into patterns of muscle activity that will achieve the desired limb movements.
728 Overall, our findings emphasise the need for consideration of subcortical sensorimotor
729 circuits in theories of human motor control and behaviour.

730

731 REFERENCES

- 732 • Alstermark B, Isa T (2012) Circuits for skilled reaching and grasping. *Annu Rev*
733 *Neurosci* 35:559-578.
- 734 • Atsma J, Majij F, Gu C, Medendorp WP, Corneil BD (2018) Active braking of whole-
735 arm reaching movements provides single-trial neuromuscular measures of movement
736 cancellation. *J Neurosci* 38:4367-4382.
- 737 • Basso MA, May PJ (2017) Circuits for action and cognition: A view from the superior
738 colliculus. *Annu Rev Vis Sci* 3:197-226.
- 739 • Basso MA, Wurtz RH (1998) Modulation of neuronal activity in superior colliculus
740 by changes in target probability. *J Neurosci* 7519–7534.
- 741 • Billen LS, Corneil BD, Weerdesteijn V (2022) Evidence for an intricate relationship
742 between express visuomotor responses, postural control and rapid step initiation in the
743 lower limbs. *bioRxiv*10.21.513067.
- 744 • Boehnke SE, Munoz DP (2008) On the importance of the transient visual response in
745 the superior colliculus. *Curr Opin Neurobiol*18:544-551.
- 746 • Brenner E, de la Malla C, Smeets JBJ (2022) Tapping on a target: dealing with
747 uncertainty about its position and motion. *Exp Brain Res* 241:81-104.
- 748 • Brenner E, Smeets JBJ (2019) How Can You Best Measure Reaction Times? *J Mot*
749 *Behav* 51:486-495.
- 750 • Buford JA, Davidson AG (2004) Movement-related and preparatory activity in the
751 reticulospinal system of the monkey. *Exp Brain Res* 159:284– 300.
- 752 • Cisek P, Kalaska JF (2005) Neural correlates of reaching decisions in dorsal premotor
753 cortex: Specification of multiple direction choices and final selection of action.
754 *Neuron* 3: 801–814.

- 755 • Contemori S, Loeb GE, Corneil BD, Wallis G, Carroll TJ (2021a) The influence of
756 temporal predictability on express visuomotor responses. *J Neurophysiol* 125:731–
757 747.
- 758 • Contemori S, Loeb GE, Corneil BD, Wallis G, Carroll TJ (2021b) Trial-by-trial
759 modulation of express visuomotor responses induced by symbolic or barely detectable
760 cues. *J Neurophysiol* 126(5):1507-1523.
- 761 • Contemori S, Panichi R, Biscarini A (2021c) Mechanisms of modulation of automatic
762 scapulothoracic muscle contraction timings. *J Mot Behav* 53: 669-679.
- 763 • Contemori S, Loeb GE, Corneil BD, Wallis G, Carroll TJ (2022) Symbolic cues
764 enhance express visuomotor responses in human arm muscles at the motor planning
765 rather than the visuospatial processing stage. *J Neurophysiol* 128(3):494-510.
- 766 • Corneil BD and Munoz DP (2014) Overt responses during covert orienting. *Neuron*
767 82: 1230–1243.
- 768 • Corneil BD, Munoz DP, Chapman BB, Admans T, Cushing SL (2008)
769 Neuromuscular consequences of reflexive covert orienting. *Nat Neurosci* 11:13-15.
- 770 • Corneil BD, Olivier E, Munoz DP (2004) Visual responses on neck muscles reveal
771 selective gating that prevents express saccades. *Neuron* 42:831-841.
- 772 • Cross KP, Cluff T, Takei T, Scott SH (2019) Visual feedback processing of the limb
773 involves two distinct phases. *J Neurosci* 39:6751-6765.
- 774 • Darling WG, Ge J, Stilwell-Morecraft KS, Rotella DL, Pizzimenti MA, Morecraft RJ
775 (2018) Hand motor recovery following extensive frontoparietal cortical injury is
776 accompanied by upregulated corticoreticular projections in monkey. *J Neurosci*
777 38:6323–6339.
- 778 • Dash S, Peel TR, Lomber SG, Corneil BD (2018) Frontal eye field inactivation
779 reduces saccade preparation in the superior colliculus but does not alter how

- 780 preparatory activity relates to saccades of a given latency. *eNeuro* 5: ENEURO.0024-
781 18.2018.
- 782 • Day BL, Brown P (2001) Evidence for subcortical involvement in the visual control
783 of human reaching. *Brain* 124:1832–1840.
 - 784 • Day BL, Lyon IN (2000) Voluntary modification of automatic arm movements
785 evoked by motion of a visual target. *Exp Brain Res* 130:159-168.
 - 786 • Everling S, Dorris MC, Klein RM, Munoz DP (1999) Role of primate superior
787 colliculus in preparation and execution of anti-saccades and prosaccades. *J Neurosci*
788 19:2740 –2754.
 - 789 • Fautrelle L, Prablanc C, Berret B, Ballay Y, Bonnetblanc F (2010) Pointing to double-
790 step visual stimuli from a standing position: very short latency (express) corrections
791 are observed in upper and lower limbs and may not require cortical involvement.
792 *Neuroscience* 169:697–705.
 - 793 • Fisher KM, Zaaimi B, Edgley SA, Baker SN (2021) Extensive cortical convergence to
794 primate reticulospinal pathways. *J Neurosci* 41:1005–1018.
 - 795 • Fregosi M, Contestabile A, Hamadjida A, Rouiller EM (2017) Corticobulbar
796 projections from distinct motor cortical areas to the reticular formation in macaque
797 monkeys. *Eur J Neurosci* 45:1379–1395.
 - 798 • Glover IS, Baker SN (2019) Modulation of rapid visual responses during reaching by
799 multimodal stimuli. *J Neurophysiol* 122: 1894–1908.
 - 800 • Goonetilleke SC, Katz L, Wood DK, Gu C, Huk AC, Corneil BD (2015) Cross-
801 species comparison of anticipatory and stimulus-driven neck muscle activity well
802 before saccadic gaze shifts in humans and non-human primates. *J Neurophysiol*
803 114:902-913.

- 804 • Gu C, Pruszynski JA, Gribble PL, Corneil BD (2018) Done in 100 ms: Path-
805 dependent visuomotor transformation in the human upper limb. *J Neurophysiol*
806 119:1319-1328.
- 807 • Gu C, Pruszynski JA, Gribble PL, Corneil BD (2019) A rapid visuomotor response on
808 the human upper limb is selectively influenced by implicit motor learning. *J*
809 *Neurophysiol* 121:85-95.
- 810 • Gu C, Wood DK, Gribble PL, Corneil BD (2016) A trial-by-trial window into
811 sensorimotor transformations in the human motor periphery. *J Neurosci* 36:8273-82.
- 812 • Howard S, Ingram JN, Wolpert DM (2009) A modular planar robotic manipulandum
813 with endpoint torque control. *J Neurosci Methods* 181(2):199-211.
- 814 • Kearsley SL, Cecala AL, Kozak RA, Corneil BD (2022) Express Arm Responses
815 Appear Bilaterally on Upper-limb Muscles in an Arm Choice Reaching Task. *J*
816 *Neurophysiol* 127: 969-983.
- 817 • Keizer K, Kuypers HGJM (1984) Distribution of corticospinal neurons with
818 collaterals to lower brain stem reticular formation in cat. *Exp Brain Res* 54:107–120.
- 819 • Keizer K, Kuypers HGJM (1989) Distribution of corticospinal neurons with
820 collaterals to the lower brain stem reticular formation in monkey (*Macaca*
821 *fascicularis*). *Exp Brain Res* 74:311–318.
- 822 • Kozak AR, Cecala AL, Corneil BD (2020) An emerging target paradigm evokes fast
823 visuomotor responses on human upper limb muscles. *J Vis Exp* e61428.
- 824 • Kozak AR, Corneil BD (2021) High contrast, moving targets in an emerging target
825 paradigm promote fast visuomotor responses during visually guided reaching. *J*
826 *Neurophysiol* 126(1):68-81.
- 827 • Kozak RA, Kreyenmeier P, Gu C, Johnston K, Corneil BD (2019) Stimulus-locked
828 responses on human upper limb muscles and corrective reaches are preferentially
829 evoked by low spatial frequencies. *eNeuro* 6(5):ENEURO.0301-19.

- 830 • Kurtzer IL (2015) Long-latency reflexes account for limb biomechanics through
831 several supraspinal pathways. *Front Integr Neurosci* 8:99.
- 832 • Leiras R, Velo P, Martín-Cora F, Canedo A (2010) Processing afferent proprioceptive
833 information at the main cuneate nucleus of anesthetized cats. *J Neurosci* 30:15383-
834 15399.
- 835 • Magoun H, Rhines R (1946) An inhibitory mechanism in the bulbar reticular
836 formation. *J Neurophysiol* 9:165-171.
- 837 • McPeck RM, Keller EL (2002) Saccade target selection in the superior colliculus
838 during a visual search task. *J Neurophysiol* 88:2019-2034.
- 839 • Proske U, Gandevia SC (2012) The proprioceptive senses: their roles in signalling
840 body shape, body position and movement, and muscle force. *Physiol Rev* 92:1651-
841 1697.
- 842 • Pruszynski AJ, King GL, Boisse L, Scott SH, Flanagan RJ, Munoz DP (2010)
843 Stimulus-locked responses on human arm muscles reveal a rapid neural pathway
844 linking visual input to arm motor output. *Eur J Neurosci* 32:1049-1057.
- 845 • Rhines R, Magoun H (1946) Brain stem facilitation of cortical motor response. *J*
846 *Neurophysiol* 9:219–229.
- 847 • Sabes PN (2011) Sensory integration for reaching: models of optimality in the context
848 of behavior and the underlying neural circuits. *Prog Brain Res* 191:195–209.
- 849 • Schepens B, Drew T (2004) Independent and convergent signals from the
850 pontomedullary reticular formation contribute to the control of posture and movement
851 during reaching in the cat. *J Neurophysiol* 92, 2217–2238.
- 852 • Selen LP, Shadlen MN, Wolpert DM (2012) Deliberation in the motor system: reflex
853 gains track evolving evidence leading to a decision. *J Neurosci* 32:2276 –2286

- 854 • Selen LPJ, Corneil BD, Medendorp WP (2023). Single-trial dynamics of competing
855 reach plans in the human motor periphery. *J Neurosci*. 10.1523/JNEUROSCI.1640-
856 22.2023.
- 857 • Sherrington CS (1898) Decerebrate rigidity and reflex coordination of movements. *J*
858 *Physiol* 22:319-332.
- 859 • Smeets JBJ, Wijdenes OL, Brenner E (2016) Movement adjustments have short
860 latencies because there is no need to detect anything. *Mot Control* 20:137–148.
- 861 • Tsianos GA, Loeb GE (2017) Muscle and limb mechanics. *Comprehensive Physiol*
862 7:429–462.
- 863 • Veerman MM, Brenner E, Smeets JBJ (2008) The latency for correcting a movement
864 depends on the visual attribute that defines the target. *Exp Brain Res* 187:219–228.
- 865 • Weiler J, Gribble PL, Pruszynski JA (2019) Spinal stretch reflexes support efficient
866 hand control. *Nat Neurosci* 22:529–533.
- 867 • Weiler J, Gribble PL, Pruszynski JA (2021) Spinal stretch reflexes support efficient
868 control of reaching. *J Neurophysiol* 125:1339-1347.
- 869 • Werner W (1993) Neurons in the primate superior colliculus are active before and
870 during arm movements to visual targets. *Eur J Neurosci* 5:335-340.
- 871 • Wijdenes OL, Brenner E, Smeets JBJ (2014) Analysis of methods to determine the
872 latency of online movement adjustments. *Behav Res Methods* 46(1):131–139.
- 873 • Wong AL, Goldsmith J, Forrence AD, Haith AM, Krakauer JW (2017) Reaction
874 times can reflect habits rather than computations. *eLife* 6e28075
- 875 • Wong AL, Goldsmith J, Krakauer JW (2016) A motor planning stage represents the
876 shape of upcoming movement trajectories. *J Neurophysiol* 116:296–305.
- 877 • Wood DK, Gu C, Corneil BD, Gribble PL, Goodale MA (2015) Transient visual
878 responses reset the phase of low-frequency oscillations in the skeletomotor periphery.
879 *Eur J Neurosci* 42:1919-1932.

- 880 • Zhang Y, Brenner E, Duysens J, Verschueren S, Smeets JBJ (2018a) Effects of aging
881 on postural responses to visual perturbations during fast pointing. *Front Aging*
882 *Neurosci* 10:401.
- 883 • Zhang Y, Brenner E, Duysens J, Verschueren S, Smeets JBJ (2018b) Postural
884 responses to target jumps and background motion in a fast pointing task. *Exp Brain*
885 *Res* 236:1573–1581.
- 886

887 **Figure 1:** A: experimental setup. Participants' hand positions were virtually represented via a cursor (blue dot in
888 panels B-D) displayed on the monitor and projected into the (horizontal) plane of hand motion via a mirror. The
889 head position was stabilized by a forehead rest (not shown here). B: schematic diagram of the timeline of events
890 in the *emerging target* paradigm. Once the cursor was at the home position, the '+' sign for fixation was
891 presented underneath the barrier. After one second of fixation, the target started dropping from the stem of the
892 track at constant velocity of ~30 cm/s until it passed behind the barrier (i.e., occlusion epoch) for ~480 ms, and
893 reappeared underneath it at ~640 ms from its movement onset time. C: task conditions in experiment one. In the
894 control condition, the right and left potential target locations (unfilled grey circles underneath the barrier) had
895 equal distance from the reaching hand. In the long-reach condition the target required a longer reach relative to
896 control condition, whereas in the short-reach condition the target appeared closer to the reaching hand relative to
897 control conditions. For all conditions, the target moved initially toward the fixation spot. In these examples,
898 shifting the visual elements toward the left required long and short reaching distances to address the location of
899 left and right targets, respectively. By contrast, rightward shifts of the visual element generated the opposite
900 direction-x-distance conditions of reaching. D: task conditions in experiment two. Here, the right and left target
901 potential target locations (unfilled grey circles underneath the barrier) had equal distance from the reaching hand
902 across all conditions. In the control condition, the vertical lines underneath the barrier were coloured black and
903 the hand had to stop at the actual target location. By contrast, the hand had to overshoot or undershoot the actual
904 target location when the vertical lines underneath the barrier were green (i.e. overshooting condition) or red (i.e.
905 undershooting condition), respectively.

906

907 **Figure 2:** Kinematic data of an exemplar participants for the first experiment. A, hand trajectories in the control
908 (black traces), long-reach (green traces) and short-reach (red traces) conditions. B, condition-dependent hand
909 velocity traces. The time is relative to the target presentation. Vertical dashed and dotted lines are used to
910 display the mechanical reaction times and maximal velocities across conditions, respectively. C, time-
911 normalization of the hand velocity traces for the entire movement duration and point of the movement at which
912 the peak velocity was reached. The data are plotted as mean (solid lines) and standard deviation (shaded area
913 around the mean lines).

914

915 **Figure 3:** First experiment condition-dependent variations of the reaction time (A), maximal velocity (B),
916 movement time (C), time to the maximal velocity (D), index of the maximal velocity within the movement (E),
917 and variability of the trajectory endpoint (F). On each plot, the thin light-grey lines represent the 14 subjects

918 who completed the first experiment, whereas the thick black dotted line represents the average across subjects.
919 The horizontal thick dark-grey lines on top of the subjects represent the between-condition statistically
920 significant differences: (A) reaction time, short-reach vs control and long-reach $p<0.001$, control vs long-reach
921 $p=0.1$; (B) movement time, short-reach vs control $p=0.016$, long-reach vs short-reach and control $p<0.001$; (C)
922 maximal velocity, $p<0.001$ for all between-condition contracts; (D) time to maximal velocity, $p<0.001$ for all
923 between-condition contracts; (F) endpoint trajectory variability, short-reach vs control $p=0.96$, short-reach vs
924 long-reach $p=0.045$, control vs long-reach $p=0.008$.

925

926 **Figure 4:** Surface EMG activity of the PMch muscle during the leftward and rightward movements executed
927 toward the target requiring short (~3 cm; panels A and B), control (~8cm; panels D and E) and long (~13 cm;
928 panels G and H) reaching distances of an exemplar participant who completed the first experiment and exhibited
929 an express response in each of the three different hand-to-target distance conditions (see Materials and
930 Methods). Each raster plot shows the rectified EMG activity from individual trials sorted by reaction time
931 (brighter white colours indicate greater EMG activity). The white vertical line at 0ms indicates the target
932 presentation time, and the blue scatters indicate the reaction time. The express and long latency muscle response
933 initiation times are represented with red and magenta scatters, respectively. Panels C, F and I show the
934 distribution of express (red histograms) and long-latency (magenta histograms) muscle response onset times as
935 is that of reaction time (blue histograms) across the left and right target conditions. Panel J shows the average
936 EMG activity across all trials (thick lines = left target reaches; thin lines =right target reaches) and the grey
937 patch at 70-110 ms highlights the average muscle activity enclosed in the express time window. In this panel,
938 the vertical dashed lines represent the onset time (averaged across right and left target-directed express trials;
939 see Materials and Methods) of express visuomotor response in the three task conditions.

940

941 **Figure 5:** Condition-dependent variations of the express visuomotor response detection rate (A), onset time (B)
942 and magnitude (C). On each plot, each light-grey line represents one of the ten subjects who exhibited the
943 express response behaviour across all the three conditions of the first experiment, whereas the black dots
944 represent the average across subjects. The horizontal dark-grey lines on top of the subjects represent the
945 between-condition statistically significant differences: (A) express response detection rate, short-reach vs
946 control and long-reach $p<0.001$, control vs long-reach $p=0.13$; (C) express response magnitude, short-reach vs
947 control $p<0.001$, short-reach vs long-reach $p=0.01$, control vs long-reach $p=0.78$.

948

949 **Figure 6:** Task-dependend hand trajectories (A), velocity traces (B) and time-normalized hand velocity traces
950 showing the point at which the hand reached the peak velocity within the entire movement (C) of an exemplar
951 participant for the second experiment (same format as Figure 2).

952

953 **Figure 7:** Second experiment task-dependent variations of the reaction time (A), maximal velocity (B),
954 movement time (C), time to the maximal velocity (D), index of the maximal velocity within the movement (E),
955 and variability of the trajectory endpoint (F; same format as figure 3). Statistically significant differences: (A)
956 reaction time, undershoot vs control and overshoot $p<0.001$, control vs overshoot $p=0.002$; (B) movement time,
957 $p<0.001$ for all between-condition contrasts; (C) maximal velocity, $p<0.001$ for all between-condition contrasts;
958 (D) time to maximal velocity, $p<0.001$ for all between-condition contrasts; (E) index of the maximal velocity
959 within the movement, undershoot vs control $p=0.89$, undershoot vs overshoot $p=0.02$, control vs overshoot
960 $p<0.001$; (F) endpoint trajectory variability, overshoot vs undershoot and control <0.001 .

961

962 **Figure 8:** Surface EMG activity of the PMch muscle and distributions of express response onset time, long-
963 latency response onset time, and reaction time during the undershooting (panels A-C), control (i.e. stop at the
964 target; panels D-F) and overshooting (panels G-I) visuospatial tasks of an exemplar participant who completed
965 the second experiment. Panels A-I have the same format as figure 4. The task-dependent average EMG activity
966 computed across all trials is shown in panel J. In this panel, the arrows highlight the transition of the EMG
967 signal across the express (grey patch at 70-110ms from the target presentation time) and long-latency epochs
968 (>110 ms from the target presentation; see Materials and Methods for details).

969

970 **Figure 9:** Second experiment task-dependent variations of express visuomotor response detection rate (A), onset
971 time (B) and magnitude (C; same format as figure 5). (A) express response detection rate, undershoot vs control
972 $p=0.03$, undershoot vs overshoot $p=0.15$, control vs overshoot $p=0.003$; (C) express response magnitude,
973 undershoot vs control $p=0.003$, undershoot vs overshoot $p=0.67$, control vs overshoot $p=0.04$.

974

975 **Figure 10:** Between-experiments contrasts in express visuomotor response detection rate (A), onset time (B)
976 and magnitude (C). Every thin line represents one of the eight subjects that completed either the first (black
977 lines) or second (dark-red lines) experiment and exhibited express visuomotor responses across all conditions
978 (experiment 1: short, control and long reaches; experiment 2: undershoot, control and overshoot tasks; see

979 Materials and Methods), whereas the thick lines represent the average across subjects. For each subject, the data
980 are normalized to the control condition.

981

982 **Figure 11:** Proposed cortico-subcortical coordination for visuomotor response generation in which cerebral
983 cortex areas inhibit or facilitate the express tecto-reticulo-spinal system according to whether the task involves
984 veridical or non-veridical targets to reach. The reach-goal location resulting from integration of physical target
985 location and cued instructions is converted into the extent of the reach based on multisensory signalling of the
986 current arm position (kinematics), the required joint torques (kinetics) and muscle activation via spinal
987 interneurons and motoneurons. Dashed black lines with '?' mark denote uncertainty about whether the
988 kinematic-kinetic metrics for the later (voluntary) reach component are computed by a transcortical or
989 subcortical network.

990

991 **Table 1:** First experiment task-dependent variation of express visuomotor response metrics for data samples
 992 with matched reaction time and matched long-latency muscle response magnitude between conditions.

Matched variable	Express visuomotor response metric	Task condition			mANOVA	Statistics		
		Short reach (SR)	Control (C)	Long reach (LR)		Post-hoc comparisons		
					SR vs C	SR vs LR	C vs LR	
Reaction time	Detection rate (%)	53±23	58±24	63±16	$F_{2,6} = 8.4$ $p = 0.004^*$ $\eta_p^2 = 0.54$	$p = 0.016^*$	$p = 0.009^*$	$p = 0.11$
	Onset time (ms)	95±2	96±3	96±1	$F_{2,6} = 0.75$ $p = 0.49$	\	\	\
	Magnitude (µV)	25±15	33±16	32±15	$F_{2,6} = 12$ $p < 0.001^*$ $\eta_p^2 = 0.63$	$p = 0.005^*$	$p = 0.009^*$	$p = 0.17$
Long-latency muscle response	Detection rate (%)	53±22	68±18	70±21	$F_{2,8} = 9.15$ $p = 0.002^*$ $\eta_p^2 = 0.5$	$p = 0.001^*$	$p = 0.007^*$	$p = 0.67$
	Onset time (ms)	96±2	94±3	95±3	$F_{2,8} = 0.73$ $p = 0.49$	\	\	\
	Magnitude (µV)	24±12	33±13	32±12	$F_{2,8} = 12.8$ $p < 0.001^*$ $\eta_p^2 = 0.59$	$p < 0.001^*$	$p = 0.005^*$	$p = 0.53$

993 Data reported as mean ± standard deviation. *, statistically significant results.

994

995 **Table 2:** Second experiment task-dependent variation of express visuomotor response metrics for data samples
 996 with matched reaction time and matched long-latency muscle response magnitude between conditions.

Matched variable	Express visuomotor response metric	Task condition			rmANOVA	Statistics		
		Undershoot (US)	Control (C)	Overshoot (OS)		Post-hoc comparisons		
					US vs C	US vs OS	C vs OS	
	Detection rate (%)	52±23	61±16	56±20	$F_{2,6} = 4.3$ $p = 0.03^*$ $\eta_p^2 = 0.35$	$p = 0.032^*$	$p = 0.1$	$p = 0.17$
Reaction time	Onset time (ms)	96±3	94±3	95±3	$F_{2,6} = 1.79$ $p = 0.2$	\	\	\
	Magnitude (μV)	32±11	37±11	30±9	$F_{2,6} = 4.3$ $p = 0.03^*$ $\eta_p^2 = 0.36$	$p = 0.035^*$	$p = 0.52$	$p = 0.015^*$
	Detection rate (%)	53±22	65±15	51±15	$F_{2,8} = 8.7$ $p = 0.002^*$ $\eta_p^2 = 0.49$	$p = 0.02^*$	$p = 0.4$	$p = 0.03^*$
Long-latency muscle response	Onset time (ms)	95±4	94±3	94±3	$F_{2,8} = 0.37$ $p = 0.69$	\	\	\
	Magnitude (μV)	29±12	39±13	30±10	$F_{2,8} = 7.2$ $p = 0.005^*$ $\eta_p^2 = 0.46$	$p = 0.016^*$	$p = 0.4$	$p = 0.015^*$

997 Data reported as mean ± standard deviation. *, statistically significant results.

998

Table 1: First experiment task-dependent variation of express visuomotor response metrics for data samples with matched reaction time and matched long-latency muscle response magnitude between conditions.

Matched variable	Express visuomotor response metric	Task condition			rmANOVA	Statistics <i>Post-hoc comparisons</i>		
		Short reach (SR)	Control (C)	Long reach (LR)		SR vs C	SR vs LR	C vs LR
Reaction time	Detection rate (%)	53±23	58±24	63±16	$F_{2,6} = 8.4$ $p = 0.004^*$ $\eta_p^2 = 0.54$	$p = 0.016^*$	$p = 0.009^*$	$p = 0.11$
	Onset time (ms)	95±2	96±3	96±1	$F_{2,6} = 0.75$ $p = 0.49$	\	\	\
	Magnitude (μV)	25±15	33±16	32±15	$F_{2,6} = 12$ $p < 0.001^*$ $\eta_p^2 = 0.63$	$p = 0.005^*$	$p = 0.009^*$	$p = 0.17$
Long-latency muscle response	Detection rate (%)	53±22	68±18	70±21	$F_{2,8} = 9.15$ $p = 0.002^*$ $\eta_p^2 = 0.5$	$p = 0.001^*$	$p = 0.007^*$	$p = 0.67$
	Onset time (ms)	96±2	94±3	95±3	$F_{2,8} = 0.73$ $p = 0.49$	\	\	\
	Magnitude (μV)	24±12	33±13	32±12	$F_{2,8} = 12.8$ $p < 0.001^*$ $\eta_p^2 = 0.59$	$p < 0.001^*$	$p = 0.005^*$	$p = 0.53$

Data reported as mean ± standard deviation. *, statistically significant results.

Table 2: Second experiment task-dependent variation of express visuomotor response metrics for data samples with matched reaction time and matched long-latency muscle response magnitude between conditions.

Matched variable	Express visuomotor response metric	Task condition			rmANOVA	Statistics		
		Undershoot (US)	Control (C)	Overshoot (OS)		<i>Post-hoc comparisons</i>		
					US vs C	US vs OS	C vs OS	
Reaction time	Detection rate (%)	52±23	61±16	56±20	$F_{2,6} = 4.3$ $p = 0.03^*$ $\eta_p^2 = 0.35$	$p = 0.032^*$	$p = 0.1$	$p = 0.17$
	Onset time (ms)	96±3	94±3	95±3	$F_{2,6} = 1.79$ $p = 0.2$	\	\	\
	Magnitude (μV)	32±11	37±11	30±9	$F_{2,6} = 4.3$ $p = 0.03^*$ $\eta_p^2 = 0.36$	$p = 0.035^*$	$p = 0.52$	$p = 0.015^*$
Long-latency muscle response	Detection rate (%)	53±22	65±15	51±15	$F_{2,8} = 8.7$ $p = 0.002^*$ $\eta_p^2 = 0.49$	$p = 0.02^*$	$p = 0.4$	$p = 0.03^*$
	Onset time (ms)	95±4	94±3	94±3	$F_{2,8} = 0.37$ $p = 0.69$	\	\	\
	Magnitude (μV)	29±12	39±13	30±10	$F_{2,8} = 7.2$ $p = 0.005^*$ $\eta_p^2 = 0.46$	$p = 0.016^*$	$p = 0.4$	$p = 0.015^*$

Data reported as mean ± standard deviation. *, statistically significant results.





















