

The Sensorimotor System Modulates Muscular Co-Contraction Relative to Visuomotor Feedback Responses to Regulate Movement Variability.

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1 **ABSTRACT**

2 The naturally occurring variability in our movements often poses a significant challenge
3 when attempting to produce precise and accurate actions, which is readily evident
4 when playing a game of darts. Two differing, yet potentially complementary, control
5 strategies that the sensorimotor system may use to regulate movement variability are
6 impedance control and feedback control. Greater muscular co-contraction leads to
7 greater impedance that acts to stabilize the hand, while visuomotor feedback responses
8 can be used to rapidly correct for unexpected deviations when reaching towards a tar-
9 get. Here we examined the independent roles and potential interplay of impedance
10 control and visuomotor feedback control when regulating movement variability. Partic-
11 ipants were instructed to perform a precise reaching task by moving a cursor through
12 a narrow visual channel. We manipulated cursor feedback by visually amplifying move-
13 ment variability and or delaying the visual feedback of the cursor. We found that partic-
14 ipants decreased movement variability by increasing muscular co-contraction, aligned
15 with an impedance control strategy. Participants displayed visuomotor feedback re-
16 sponses during the task but, unexpectedly, there was no modulation between condi-
17 tions. However we did find a relationship between muscular co-contraction and visuo-
18 motor feedback responses, suggesting that participants modulated impedance control
19 relative to feedback control. Taken together, our results highlight that the sensorimotor
20 system modulates muscular co-contraction, relative to visuomotor feedback responses,
21 to regulate movement variability and produce accurate actions.

22 **NEW AND NOTEWORTHY**

23 The sensorimotor system has the constant challenge of dealing with the naturally occur-
24 ring variability in our movements. Here we investigated the potential roles of muscular
25 co-contraction and visuomotor feedback responses to regulate movement variability.
26 When we visually amplified movements, we found that the sensorimotor system pri-
27 marily uses muscular co-contraction to regulate movement variability. Interestingly, we
28 found that muscular co-contraction was modulated relative to inherent visuomotor feed-
29 back responses, suggesting an interplay between impedance and feedback control.

30 INTRODUCTION

31 Humans have a remarkable ability to perform precise and accurate motor actions, such
32 as when threading a needle or throwing a fastball. Naturally occurring movement vari-
33 ability poses a significant challenge to the sensorimotor system when attempting to per-
34 form precise actions.¹ Movement variability can arise from noisy sensory information or
35 stochastic neuromuscular processes, which are often jointly referred to as sensorimotor
36 noise.^{2,3} Further, time delays in the sensorimotor system may allow movement variability
37 to accumulate prior to corrective actions. Past work has shown that humans modulate
38 movement variability at the end of the movement when reaching towards targets of dif-
39 ferent sizes^{4,5,6} and shapes.⁷ While it has long been recognized that the sensorimotor
40 system aims to reduce movement variability to improve accuracy and task success,^{8,2,3}
41 different theories have been proposed to explain the underlying control strategy that
42 regulates movement variability.

43 One potential strategy for regulating movement variability is through impedance
44 control, where an increase in joint stiffness acts to stabilize the limb and hand. Joint stiff-
45 ness can be increased by the co-contraction of agonist and antagonist muscles.^{9,10,11,12,13,14}
46 Joint stiffness about the shoulder and elbow leads to effective hand stiffness.¹⁵ Impor-
47 tantly, greater effective hand stiffness may reduce hand movement variability by resist-
48 ing internally generated deviations caused by sensorimotor noise.^{10,16,17} A study by Grib-
49 ble and colleagues (2003) examined movement accuracy when participants made reach-
50 ing movements to different sized targets.⁴ They found that muscular co-contraction was
51 correlated with endpoint accuracy, which was defined as the difference between final
52 hand position and the target. Another study by Wong and colleagues (2009) assessed
53 movement accuracy and effective hand stiffness during the reach.¹⁸ Participants were
54 instructed to reach towards a target while maintaining their hand within a narrow or
55 wide visual channel. On probe trials, effective hand stiffness was estimated by mea-
56 suring the restoring force applied by the hand, after the hand was perturbed a fixed

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57 positional distance during the reach (i.e. $k = \frac{F}{x}$). They defined movement accuracy as
58 the average distance away from the centerline of the visual channel during the reach.
59 Participants displayed greater effective hand stiffness and greater movement accuracy
60 when attempting to keep their hand within the narrow channel. These works collectively
61 suggest that impedance control, via muscular co-contraction, is a potential strategy to
62 reduce movement variability. However, this may not be the only strategy used by the
63 sensorimotor system to regulate movement variability during the reach.

64 Another potential strategy for regulating movement variability is through feedback
65 control. Optimal feedback control has been a useful theoretical framework to explain a
66 broad range of human behaviour.^{19,20,21,22} Central to this theory is that the sensorimo-
67 tor system modulates feedback gains as a function of task demands (e.g., large versus
68 small target) and plant dynamics (e.g., sensorimotor time delays and noise). Feedback
69 gains transform state-related feedback (e.g., distance of the hand from a desired target)
70 into motor commands. Feedback gains that display task-relevant properties are probed
71 behaviourally by examining either movement speed,²³ long-latency muscular responses
72 (50 - 100 ms) following a mechanical perturbation,^{24,25,26,27,28,29} or visuomotor feedback
73 response (180 - 230 ms) following a visual perturbation.^{30,31,32,33,34} It has been shown
74 that feedback responses scale with sensory noise²³ and target size.²⁶ Further, optimal
75 feedback control models predict bell-shaped hand velocity profiles, which arises from
76 accounting for signal-dependent motor noise.^{21,35} Signal-dependent motor noise has a
77 variance that scales proportionally with the control signal,^{2,36} which theoretically influ-
78 ences feedback gain magnitudes.^{21,35} However, whether feedback gains physiologically
79 modulate as a function of movement variability has not been tested empirically.

80 Inherent time delays in the sensorimotor system may also influence movement vari-
81 ability. These sensorimotor time delays arise from physiological limits in nerve conduc-
82 tion velocity, synaptic diffusion and binding rates, and the lag between muscle activity
83 and muscle force production.³ Sensorimotor time delays may allow movement variability

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84 to both propagate and accumulate before any possible correction.^{23,37} Experimentally,
85 it has been shown that greater visual delays result in less accurate movements.^{38,39} How-
86 ever, it is unknown whether the sensorimotor system would use impedance control and
87 or feedback control to reduce movement variability that may arise from time delays.

88 Two differing, yet potentially complementary, control strategies to respond to
89 movement variability are impedance control (muscular co-contraction) and feedback
90 control (visuomotor feedback responses). To what extent or whether the sensorimotor
91 system uses muscular co-contraction, visuomotor feedback responses, or both to regu-
92 late movement variability during a reach (i.e., trajectory variability) remains unknown. In
93 this study, we investigated the independent roles and potential interplay of muscular co-
94 contraction and visuomotor feedback responses when regulating trajectory variability.
95 Participants performed a reaching task where they moved a cursor through a narrow,
96 visually displayed channel. Experimentally, we visually amplified lateral movement vari-
97 ability and or delayed lateral cursor position feedback. To visually amplify movement
98 variability we used 'error augmentation'.^{40,41,42} Specifically we amplified lateral move-
99 ments by doubling the cursor's distance, relative to hand position, from the centerline
100 of the visually displayed channel. Thus, we visually amplified any trajectory variability
101 that caused the hand to laterally deviate as participants attempted to reach straight
102 through the narrow, visually displayed channel. Visual feedback of the cursor was de-
103 layed by either 200 ms or 0 ms in the lateral direction.

104 The goal of this work was to test how the sensorimotor system regulates trajec-
105 tory variability. We hypothesized that the sensorimotor system uses both impedance
106 control and feedback control to regulate trajectory variability. We predicted that am-
107 plified movement variability and greater time delays would lead to greater muscular
108 co-contraction and altered visuomotor feedback responses. We also explored the pos-
109 sibility that there is an interplay between muscular co-contraction and visuomotor feed-
110 back responses.

111 **METHODS**

112 **Participants**

113 Sixteen individuals (23.6 ± 2.8 years old) participated in **Experiment 1**, and twelve in-
114 dividuals (23.9 ± 2.5 years old) participated in the control experiment. Participants re-
115 ported they were right-handed and free of musculoskeletal or neuromuscular disorders.
116 All participants provided informed consent to participate in the experiment and the
117 procedures were approved by the University of Delaware's institutional review board.
118 Participants were provided \$10 USD compensation.

119 **Apparatus**

120 In both experiments, participants had their right arm supported by a robotic exoskeleton
121 (**Fig. 1A**; KINARM, BKIN Technologies, Kingston, ON, Canada). The exoskeleton per-
122 mitted elbow and shoulder movement along the horizontal plane that intersected the
123 shoulder joint. The exoskeleton can generate effective hand-based loads by applying
124 torques independently about the elbow and shoulder joints.^{43,44} A semi-silvered mirror
125 blocked vision of both the participant's upper-limb and the exoskeleton arm. Images
126 (start position, target) were projected from an LCD screen onto the horizontal plane of
127 motion.

128 To assess muscular co-contraction we recorded electromyography (EMG) signals
129 from the following six muscles of the upper limb with bipolar surface electrodes (Single
130 Differential Electrode, Trigno system, Delsys, Natick, MA, USA): brachioradialis, lateral
131 head of the triceps, pectoralis major, posterior deltoid, short head of the biceps, and
132 long head of the triceps. Kinematic and EMG data were recorded at 1000 Hz and stored
133 offline for data analysis.

134 **Protocol**

135 EMG Normalization Posture Task:

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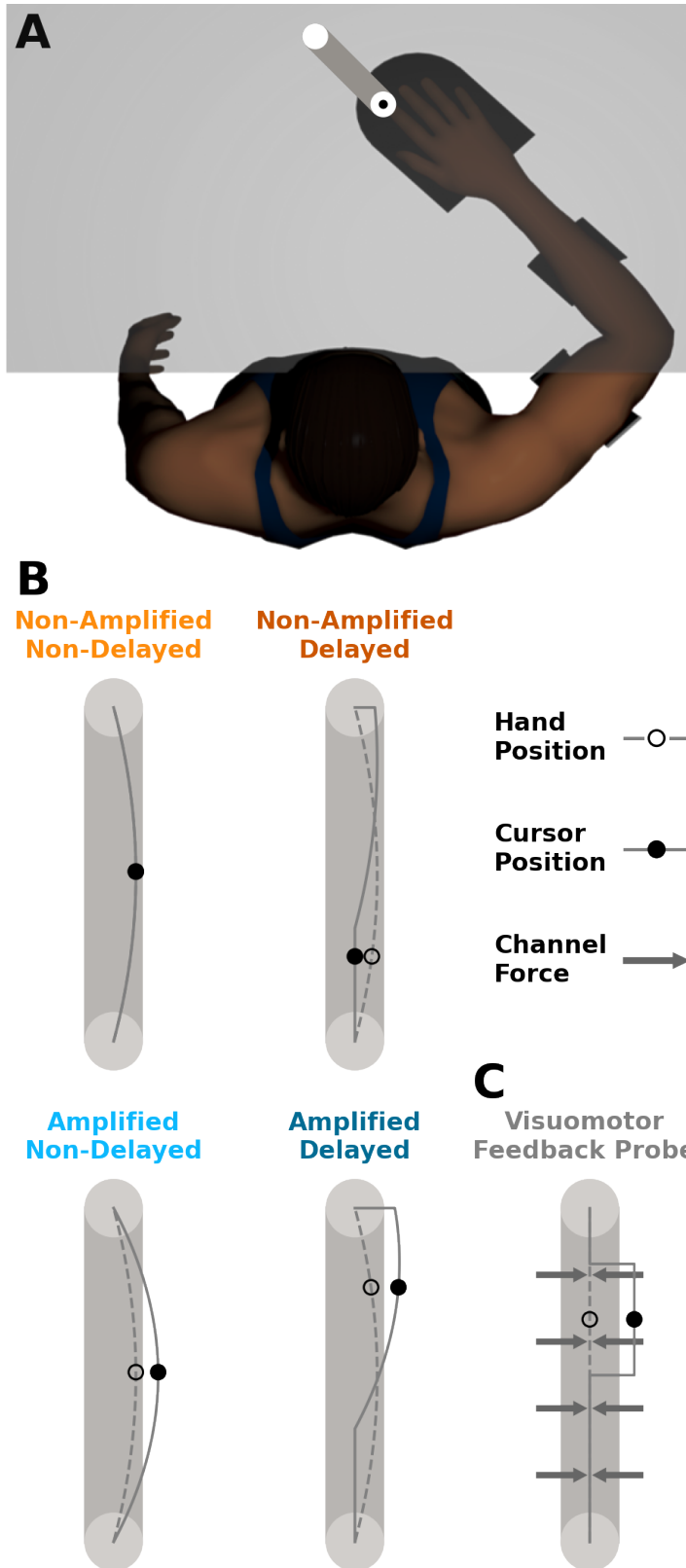


Figure 1: Experimental Design. **A)** Participants had their right arm supported by an exoskeleton (Kinarm). A semi-silvered mirror projected images from an LCD screen and occluded vision of the hand. Participants were told that the visually displayed cursor was aligned with their hand position. Participants were instructed to reach forward from a start position (white circle) to an end target (white circle) while keeping the cursor inside a visually displayed channel (grey). The forward and lateral axes were parallel and perpendicular to the visually displayed channel. We recorded electromyography of six upper limb muscles. **B)** We amplified and or delayed the lateral position of the cursor relative to the hand. Participants performed four experimental conditions in separate blocks of trials. In one condition, the cursor (solid black circle) and hand position (open black circle) were aligned during the reach (non-amplified, non-delayed; light orange). In a second condition, we imposed a 200 ms delay on the lateral cursor position relative to the participant's hand position (non-amplified, delay; dark orange). In a third condition, we amplified the cursor position relative to the hand by doubling its lateral distance from the straight line connecting the start position and target (amplified, non-delayed; light blue). In a fourth condition, we amplified and delayed the lateral cursor position relative to the participant's hand position (amplified, delayed; dark blue). **C)** We interleaved visuomotor feedback probe trials to measure visuomotor feedback responses. Probe trials consisted of participants reaching within a force channel that prevented lateral hand movement. During probe trials, the hand and cursor were aligned for the initial portion of the reach. Halfway through the reach, the cursor was displaced 25 mm to the left or right of the force channel. After 250 ms, the cursor realigned with the hand. We measured the visuomotor feedback response as the force (N) participants applied to the wall of the stiff force channel.

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137

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138 Prior to **Experiment 1** or the control experiment, participants performed a postural task
139 to normalize their muscle activity to known joint moments (see Pruzynski et al., 2008 or
140 Maeda et al., 2018 for further details).^{45,46} Participants were asked to hold their hand
141 within the start position while resisting 2 Nm loads applied to the shoulder and elbow
142 joint. Participants also performed a rest condition where they were told to completely
143 relax while staying within the start position. Summarily, participants experienced the
144 following loads: 2 Nm elbow flexion, 2 Nm elbow extension, 2 Nm shoulder flexion,
145 2 Nm shoulder extension, and a 0 Nm rest condition. These 5 loads were repeated 5
146 times in a random order.

147 General Task Protocol for Experiment 1 and the Control Experiment:

148 For each trial, participants were visually presented with a white start position (14 mm
149 diameter). Participants were told that the yellow cursor (4.0 mm diameter) provided
150 real-time feedback of the index fingertip position. The participants were instructed to
151 move the cursor into the start position. The start position was calibrated such that the
152 elbow joint angle was at 90 deg (forearm relative to the upper arm, where 0 deg is full
153 extension) and the shoulder joint angle was at 30 deg relative to the frontal plane (see
154 **Fig. 1A**). Once the participant entered the start position, a target (14mm diameter) and
155 a visual channel appeared after a randomized period of time (500 - 1500 ms; uniformly
156 distributed). There were no imposed constraints on when participants had to leave the
157 start position. The single target used in the experiment was located at a distance of
158 13 cm from the start position along the long axis of the forearm. Additionally, a grey
159 visual channel (14 mm wide) was displayed between the start position and the target.
160 We instructed the participants to maintain the cursor within the grey visually displayed
161 channel as they reached towards the target. When the cursor went outside the bounds
162 of the visual channel it would turn from grey to red. Here, we define the forward axis
163 as being parallel to the long axis of the visual channel, and the lateral axis as being per-
164 pendicular to the long axis of the visual channel. As a safety precaution for the control

165 experiment, the robot would cease applying loads if the cursor deviated more than 7
166 cm from the centerline of the visual channel and the participant would repeat the trial
167 (0.57% of all trials).

168 Participants were instructed to reach from the start position to the target within
169 550 - 650 ms. Across conditions, this time constraint ensured similar hand velocities
170 that were not modulated according to the speed-accuracy tradeoff.⁸ Participants were
171 informed that the target would turn blue or red if they moved too slow or too fast, re-
172 spectively. Participants were also required to stay within the target for 500 ms. After
173 waiting in the target, the cursor disappeared and the robot moved them back to the
174 start position with a minimum jerk trajectory. The cursor then reappeared upon the
175 hand being returned to the start position.

176 Experiment 1:

177 The goal of **Experiment 1** was to determine how the sensorimotor system responds to
178 movement variability. We also considered that sensorimotor delays may allow move-
179 ment variability to propagate and remain uncorrected for a period of time. Experi-
180 mentally, we visually amplified lateral movement variability and or delayed lateral cur-
181 sor position feedback. We used error augmentation as a way to amplify lateral move-
182 ments.^{40,41,42} Specifically, we amplified lateral movements by doubling the cursor's dis-
183 tance from the centerline of the visually displayed channel. Thus, by using error augmen-
184 tation, we magnified movement variability that caused the hand to laterally deviate as
185 participants reached through the narrow, visually displayed channel. During conditions
186 with delay, the visual feedback of the cursor was delayed by 200 ms in the lateral di-
187 rection. Participants performed four conditions in a two-way repeated measures experi-
188 mental design: (i) non-amplified, non-delayed; (ii) non-amplified, delayed; (iii) amplified,
189 non-delayed; (iv) amplified, delayed (**Fig. 1B**). Cursor amplification and or delays were
190 applied as soon as the robot finished moving the participant back to the start position.
191 Each condition was performed in an experimental block that contained 180 trials.

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192 Experiment 1 consisted of 845 total trials. First, participants performed 50 base-
193 line trials. For baseline trials, participants reached towards the target without a visually
194 displayed channel. Participants then performed the 4 conditions in separate blocks of
195 180 experimental trials. The 180 experimental trials were split into 15 separate sets that
196 each contained 12 trials. Of those 12 trials, there were 9 visual manipulation trials, one
197 left probe trial, one right probe trial, and one null probe trial. These 12 trials were ran-
198 domly ordered within their respective set. This resulted in 135 visual manipulation trials,
199 15 left probe trials, 15 right probe trials, and 15 null probe trials per condition. Between
200 conditions, participants performed 25 washout trials that were identical to baseline tri-
201 als. The order of conditions was randomized.

202 Visuomotor Feedback Probes:

203 To assess visuomotor feedback gains, we interleaved visuomotor probes trials within
204 the experimental trials.³⁰ In the visuomotor probe trials, participants were constrained
205 within a force channel ($1100N/m$ stiffness and $20N \cdot s/m$ viscosity) imposed by the robot
206 applying effective hand-based loads to the participant. The force channel was aligned
207 to the centerline of the visually displayed channel (**Fig. 1C**). Participants experienced
208 null, left and right probe trials. For null probe trials, the cursor remained aligned with
209 the hand position throughout the reach. The purpose of the null probe trials was to pre-
210 vent a participant from anticipating a cursor jump. For the left and right probe trials, the
211 cursor was initially aligned with the hand position. On left probe trials, once the cursor
212 moved forward by 6.5 cm along the centerline (50% of the reach) the cursor jumped 25
213 mm to the left of the centerline. On right probe trials, once the cursor moved forward
214 by 6.5 along the centerline the cursor jumped 25 mm to the right of the centerline.
215 After 250 ms following the cursor jump, the cursor was realigned with the hand. We
216 recorded the force applied by the participant against the force channel wall during the
217 entire probe trial.

218 Control Experiment: Here we performed a control experiment to verify that our robotic

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219 device and probe channel parameters (stiffness and damping coefficients) could capture
220 changes in visuomotor feedback responses. We replicated the experimental paradigm
221 developed by Franklin and colleagues (2012).³¹ In their experiment, they assessed whether
222 different mechanical environments experienced during reaching would influence visuo-
223 motor feedback responses. Participants performed two conditions: a null forcefield
224 (**Fig. 9A**) or a divergent forcefield. In the null forcefield condition, no external forces
225 were applied to the hand. In the divergent forcefield condition, participants experi-
226 enced a lateral force that scaled linearly with the distance of the hand from the cen-
227 terline of the visually displayed channel. Similar to Franklin and colleagues (2007), we
228 used a higher scaling of the lateral forcefield for males ($75N/m$) than females ($50N/m$).¹¹
229 Unlike **Experiment 1**, we did not apply any visual manipulations to the cursor.

230 The control experiment consisted of 435 total trials. First, participants performed
231 50 baseline trials. For baseline trials, participants reached towards the target without
232 a visually displayed channel. Participants then performed the 2 conditions in separate
233 blocks of 180 experimental trials. The 180 experimental trials were split into 15 sepa-
234 rate sets that each contained 12 trials. Of those 12 trials, there were 9 forcefield trials,
235 one left probe trial, one right probe trial, and one null probe trial. These 12 trials were
236 randomly ordered within their respective set. This resulted in 135 forcefield trials, 15
237 left probe trials, 15 right probe trials, and 15 null probe trials per condition. Between
238 conditions, participants performed 25 washout trials that were identical to baseline tri-
239 als. The order of conditions was randomized.

240 **Data Analysis**

241 Kinematic Data:

242 Hand position data was digitally dual-pass, 2nd order, lowpass (20 Hz cutoff), Butter-
243 worth filtered. Kinematic data were normalized in time, where 0% and 100% corre-
244 sponded to the tangential hand velocity crossing a 50 mm/s threshold⁴ (**Fig. 2A**), where
245 the latter corresponded with the average hand position being within the target.

*Sensorimotor Regulation of Movement Variability*Reaction Time:

Reaction time was calculated as the time between the appearance of the target and movement onset (0%).

Hand Velocity:

Hand velocity was calculated by differentiating position with respect to time using a fourth-order central difference method. We calculated tangential hand velocity by taking the resultant vector from the lateral and forward velocities. We found peak hand velocity between 0% to 100% of the reach.

Trajectory Variability:

A primary focus of our experiment was to examine hand trajectory variability during the reach. We were particularly interested in reach trajectory variability along the lateral direction where we amplified or delayed cursor position. For each condition, trajectory variability was calculated as the lateral position standard deviation across all reaches for each normalized time point.

Muscle Activity:

All EMG data was dual-pass, 6th order, bandpass (20 Hz and 450 Hz cutoff frequencies), Butterworth filtered, and then full wave rectified. From the EMG normalization posture task, for each muscle we calculated the average processed EMG between 5 and 15 s (steady-state period) and across the five repetitions of each joint load (2 $N \cdot m$ elbow flexion, 2 $N \cdot m$ elbow extension, 2 $N \cdot m$ shoulder flexion, 2 $N \cdot m$ shoulder extension). From these averaged EMG, we found the maximal activity of each muscle. We normalized all processed EMG signals to their corresponding maximal muscle activity.^{45,46} Thus, 1 arbitrary unit (a.u.) corresponds to a muscle resisting a 2 $N \cdot m$ load about a preferred rotational direction. After filtering and normalization, EMG data was time-normalized between movement onset and movement end.

Muscular Co-Contraction:

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272 Aligned with past work, we quantified muscular co-contraction as the minimum nor-
273 malized muscle activity between agonist and antagonist muscle pairs at each normal-
274 ized time point.^{47,4} This muscular co-contraction index captures excess muscle activity
275 that would correspond to increased joint stiffness.⁴ We looked at three muscle pairs:
276 monoarticular elbow (lateral head of the triceps and brachioradialis), monoarticular shoul-
277 der muscles (pectoralis major and posterior deltoid), and biarticular shoulder and elbow
278 muscles (the long head of the triceps and the short head of the biceps).

279 Visuomotor Feedback Responses:

280 Kinetic data from the visual probe trials were dual-pass, 2nd order, lowpass (20 Hz cut-
281 off), Butterworth filtered. The recorded forces applied by the robot to the participant
282 during visual probe trials were time-aligned with the cursor jump onset. We define the
283 visuomotor feedback response (N) as the difference between the recorded force during
284 a right cursor probe and a left cursor probe.³⁰ To investigate the involuntary, visuomo-
285 tor feedback response, we calculated the average force response during the 180 to
286 230 ms time window.³⁰ Additionally, we calculated the average visuomotor feedback
287 response during the 230 to 300 ms time window and the 300 to 400 ms time window.
288 The 230 to 300 ms time window may contain a mixture of involuntary and voluntary re-
289 sponses, which we term as the semi-involuntary visuomotor feedback responses.³¹ The
290 300 to 400 ms time window is the voluntary visuomotor feedback response.³⁰ Note that
291 Franklin and colleagues often term the 180 to 230 ms and 230 to 300 ms windows as
292 the early and late visuomotor feedback response, respectively.³¹

293 We also examined muscle co-contraction just prior to the involuntary visuomotor
294 feedback response. Specifically, we averaged elbow, shoulder, and biarticular muscular
295 co-contraction during the 0 - 90 ms time window after cursor jump onset.³⁰ This time
296 window is prior to any involuntary muscular feedback response to a cursor jump.

297 Interplay of Muscular Co-Contraction and Visuomotor Feedback Responses:

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298 We were interested in whether there was a direct or indirect interplay between muscular
299 co-contraction and visuomotor feedback responses. 'Automatic gain-scaling' is a classic
300 example of a direct interplay, where there is a magnitude scaling of the short-latency
301 muscular stretch response with greater background muscle activity prior to a pertur-
302 bation.⁴⁸ Here we considered a direct interplay to be an interaction where visuomotor
303 feedback responses scale as a function of muscular co-contraction to regulate trajectory
304 variability. To test for a direct interplay, we examined the relationship between invol-
305 untary visuomotor feedback responses (180 - 230 ms) and muscular co-contraction (0 -
306 90 ms) within the same probe trials. Conversely, we consider an indirect interplay to be
307 where the sensorimotor system modulates muscular co-contraction and or visuomotor
308 feedback gains relative to one another to obtain a desired level of trajectory variabil-
309 ity. For example, the sensorimotor system could modulate: i) muscular co-contraction
310 relative to their inherent (i.e., default for a task) visuomotor feedback responses, ii) vi-
311 suomotor feedback responses relative to their inherent muscular co-contraction, or iii)
312 both muscular co-contraction and visuomotor feedback responses to regulate trajectory
313 variability. To test for an indirect interplay, we examined the relationship of involuntary
314 visuomotor feedback responses during probe trials and muscular co-contraction during
315 experimental trials. Note that an indirect interplay is the sum of two processes (e.g.,
316 muscular co-contraction and visuomotor feedback gains), whereas a direct interplay oc-
317 curs when one process scales as a function of the other process (e.g., visuomotor feed-
318 back responses scale as a function of muscular co-contraction).

319 Statistical Analyses:

320 All statistical tests were performed in Python 3.8.5. We used repeated measures anal-
321 ysis of variance (rmANOVA) as the omnibus tests to test for main effects and inter-
322 actions for each dependent variable. In **Experiment 1**, we used a 2 (Amplification:
323 non-amplified or amplified) \times 2 (Delay: non-delayed or delayed) rmANOVA for peak
324 velocity, reaction time, and visuomotor feedback responses. For all other dependent

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325 variables (trajectory variability, elbow co-contraction, shoulder co-contraction, biartic-
326 ular co-contraction), we used separate 2 (Amplification: non-amplified or amplified) ×
327 2 (Delay: non-delayed or delayed) × 5 (Time: 0-20%, 20-40%, 40-60%, 60-80%, 80-
328 100%) rmANOVA. Because we were interested in how the sensorimotor system modu-
329 lates trajectory variability, we used an *a priori* approach that only considered significant
330 muscle co- contraction main effects and interactions that corresponded with significant
331 trajectory variability main effects and interactions. This approach also avoided the like-
332 lihood of finding spurious correlations (i.e., type 1 error). For both experiments, we
333 performed nonparametric bootstrap hypothesis testing ($n = 1,000,000$) for mean com-
334 parisons.^{49,50,51,52,53} Holm-Bonferroni corrections were used to control for Type 1 error.
335 We computed Common Language Effect Size ($\hat{\theta}$) for all mean comparisons.⁵⁴ Effect size
336 for follow-up comparisons were made using the common language effect size ($\hat{\theta}$), where
337 values equal to 56.0%, 64.0%, and 72.0% are respectively considered small, medium,
338 and large effects.^{54,55} We used Spearman rank correlation coefficient (ρ) to test the re-
339 lationship between two variables. Here we used bootstrap hypothesis tests, spearman
340 rank correlation, and common language effect sizes because they make no parametric
341 assumptions such as normality, are robust to outliers, are less biased by samples with un-
342 equal sample size or unequal variance, and are better suited to analyze heteroscedastic
343 data that are present in several commonly recorded biological measures such as signal
344 dependent sensorimotor noise. Statistical significance was set to $p < 0.05$.

345 RESULTS

346 Experiment 1

347 Here we examined whether the sensorimotor system responds to altered movement
348 variability by modulating muscular co-contraction and or visuomotor feedback gains.
349 We also considered the potential influence of time delays on the propagation and accu-
350 mulation of movement variability. Participants each performed four experimental con-
351 ditions where we amplified lateral movement variability and or delayed lateral cursor

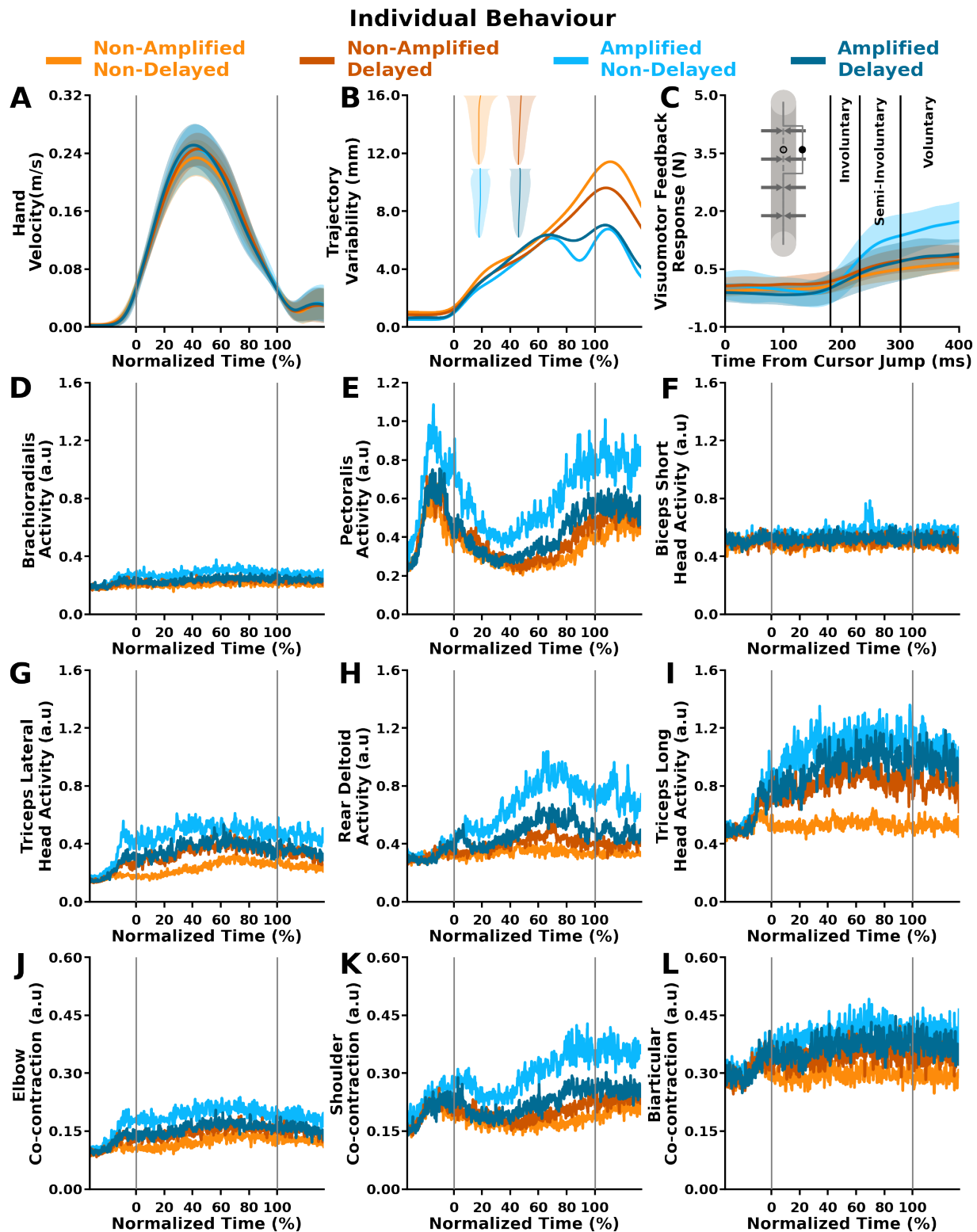
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352 position feedback: (i) non-amplified, non-delayed; (ii) non-amplified, delayed; (iii) am-
353 plified, non-delayed; (iv) amplified, delayed (**Fig. 1B**).

Individual Movement Behaviour and Muscle Activity

355 **Figure 2** shows the behaviour from an individual performing each of the four experimen-
356 tal conditions. Hand velocity was similar throughout the reach across all conditions (**Fig.**
357 **2A**). Similar to other participants, this individual displayed lower hand trajectory vari-
358 ability in the amplified conditions compared to the non-amplified conditions at the end
359 of the reach (**Fig. 2B**). The participant also showed a slight increase in hand trajectory
360 variability as they entered the target ($\approx 100\%$ normalised time), which likely reflected
361 final corrective actions as the participant's hand entered and was within the target.

362 Muscular activity in the amplified conditions was visibly greater compared to the
363 non-amplified conditions for the brachioradialis (**Fig. 2D**), pectoralis (**Fig. 2E**), biceps
364 short head (**Fig. 2F**), triceps lateral head (**Fig. 2G**), rear deltoid (**Fig. 2H**), and triceps
365 long head muscles (**Fig. 2I**). Generally, for the majority of individuals, muscular co-
366 ntraction was greater in the amplified conditions compared to the non-amplified con-
367 ditions for the monoarticular elbow muscles (brachioradialis and triceps lateral head),
368 monoarticular shoulder muscles (pectoralis and rear deltoid), and the biarticular mus-
369 cles (biceps short head and triceps long head). Similarly, muscular co-contraction was
370 greater in the amplified conditions compared to the non-amplified conditions for the
371 monoarticular elbow muscles (brachioradialis and triceps lateral head), monoarticular
372 shoulder muscles (pectoralis and rear deltoid), and the biarticular muscles (biceps short
373 head and triceps long head). Across conditions the participant displayed similar visuo-
374 motor feedback responses during the involuntary epoch (180 - 230 ms) (**Fig. 2C**).



375

376 **Figure 2: Individual Behaviour.** Average data from an individual participant during each condition. **A)**
 377 Hand velocity (y-axis) over normalized time (x-axis), where 0% and 100% (vertical grey lines) respectively
 378 correspond with the start and end of the reach. **B)** Trajectory variability (y-axis) changes over normalized
 379 time (x-axis). The participant displayed lower trajectory variability during amplified conditions (light blue,

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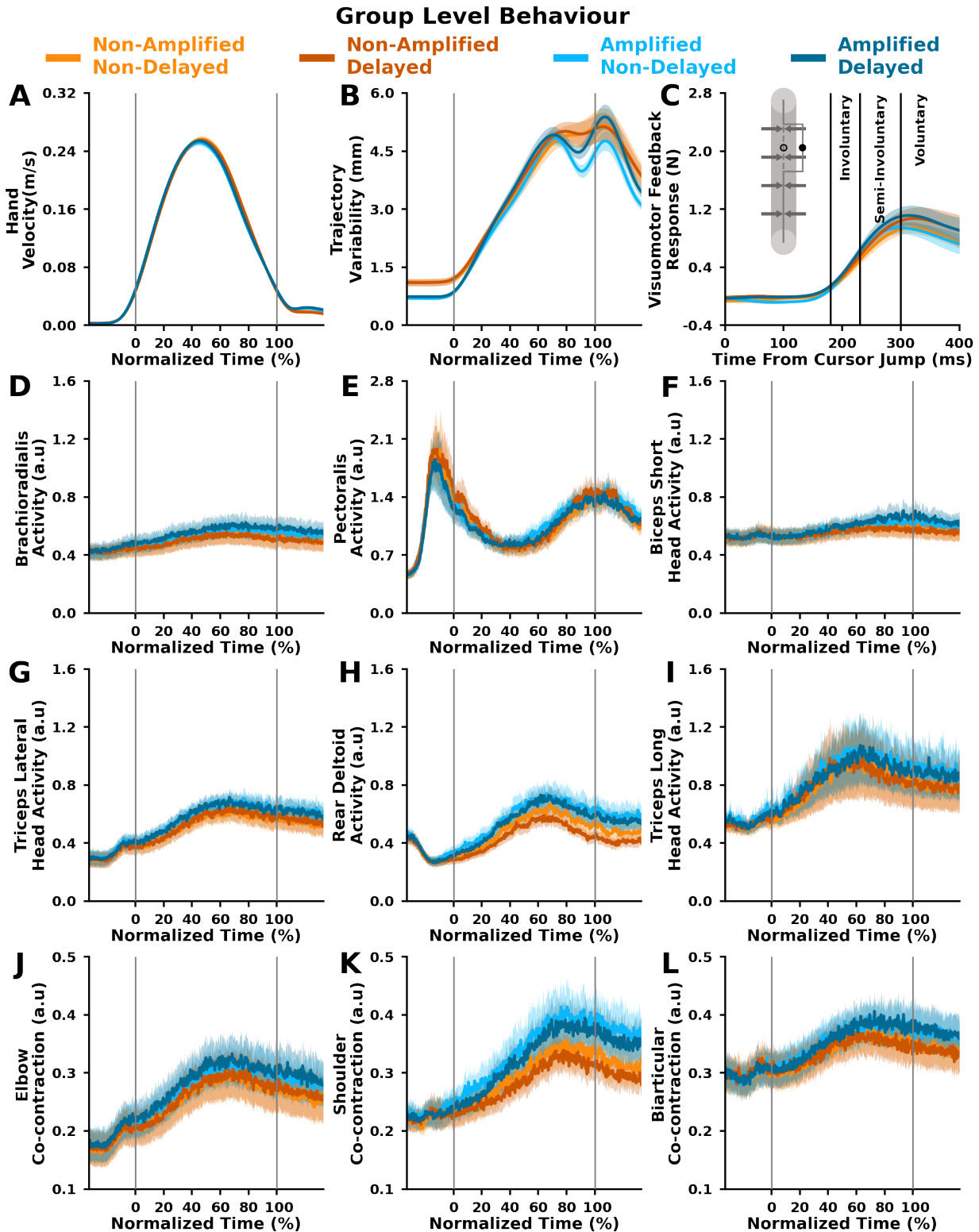
380 dark blue) compared to non-amplified conditions (light orange, dark orange) during the last portion of
381 the reach. The inset displays the corresponding average trajectory and three standard deviation of lateral
382 hand position for each condition. **C**) Visuomotor feedback response (y-axis) over time (x-axis), where 0 ms
383 corresponds to the initial cursor jump. Vertical lines separate involuntary (180 - 230 ms), semi-involuntary
384 (230 - 300 ms), and voluntary (300 - 400 ms) visuomotor feedback responses. Muscle activity (y-axis) over
385 normalized time (x-axis) for **(D)** brachioradialis, **(E)** pectoralis, **(F)** biceps short head, **(G)** triceps lateral
386 head, **(H)** rear deltoid, and **(I)** triceps long head muscles. The participant displayed greater muscular
387 activity in the amplified conditions (blue, dark blue) relative to the non-amplified conditions (orange, dark
388 orange). Muscular co-contraction (y-axis) over normalized time (x-axis) for the **J**) monoarticular elbow
389 muscles (brachioradialis and triceps lateral head), **K**) monoarticular shoulder muscles (pectoralis and rear
390 deltoid), and **L**) biarticular muscles (biceps short head, triceps long head). The participant had greater
391 muscular co-contraction in the amplified conditions (light blue, dark blue) compared to the non-amplified
392 conditions (light orange, dark orange). Shaded areas represents ± 1 standard deviation.

393 Group Movement Behaviour and Muscle Activity

394 **Figure 3** displays average group behaviour for each of the four experimental conditions.
395 As shown, hand velocity profiles were quite similar across all conditions (**Fig. 3A**). Par-
396 ticipants displayed lower trajectory variability prior to and at the start of the reach (\lesssim
397 0-20% normalized time) in the amplified conditions relative to the non-amplified con-
398 ditions, reflecting they initially positioned their hand slightly closer to the centre of the
399 start position in response to the visual amplification (**Fig. 3B**). Similar to past work,⁶
400 trajectory variability increased from the initial to middle portion of reach (\approx 0-60% nor-
401 malized time) and was similar for all conditions. At the end of the reach (\approx 60-100%
402 normalized time) the majority of participants displayed reduced trajectory variability in
403 the amplified conditions relative to the non-amplified conditions. Further below we ad-
404 dress that this reduction in trajectory variability was related to muscular co-contraction.

405

406 The majority of muscles qualitatively displayed greater muscular activity in the am-
407 plified conditions relative to the non-amplified conditions (brachioradialis, **Fig. 3D**; bi-
408 ceps short head, **Fig. 3F**; triceps lateral head, **Fig. 3G**; rear deltoid, **Fig. 3H**; tri-
409 ceps long head, **Fig. 3I**), with the exception of the pectoralis (**Fig. 3E**). Greater mus-
410 cle activity led to greater muscular co-contraction for the mono-articular elbow mus-
411 cles (brachioradialis and triceps lateral head; **Fig. 3J**), mono-articular shoulder muscles
412 (pectoralis and rear deltoid; **Fig. 3K**), and the biarticular muscles (biceps short head



413

414 **Figure 3: Group Behaviour.** Average participant behaviour for each condition. **A)** Hand velocity (y-axis)
 415 over normalized time (x-axis), where 0% and 100% (vertical grey lines) respectively correspond with the
 416 start and end of the reach. **B)** Trajectory variability (y-axis) over normalized time (x-axis). Participants had

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417 lower trajectory variability in the amplified conditions compared to the non-amplified conditions during
418 0-20% and 80-100% of the reach. **C)** Visuomotor feedback response (y-axis) over time (x-axis), where 0 ms
419 corresponds to the initial cursor jump. Vertical lines separate involuntary (180 - 230 ms), semi-involuntary
420 (230 - 300 ms), and voluntary (300 - 400 ms) visuomotor feedback responses. There were no differences
421 in visuomotor feedback responses between conditions. Muscle activity (y-axis) over normalized time (x-
422 axis) for the **(D)** brachioradialis, **(E)** pectoralis, **(F)** biceps short head, **(G)** triceps lateral head, **(H)** rear
423 deltoid, and **(I)** triceps long head muscles. Muscular co-contraction (y-axis) over normalized time (x-
424 axis) for the **(J)** monoarticular elbow muscles (brachioradialis and triceps lateral head), **(K)** monoarticular
425 shoulder muscles (pectoralis and rear deltoid), and **(L)** biarticular muscles (biceps short head, triceps long
426 head). Participants had greater elbow and shoulder co-contraction in the amplified conditions (light blue,
427 dark blue) compared to the non-amplified conditions (light orange, dark orange) throughout the reach.
428 Participants also displayed an increase of biarticular co-contraction during the latter portion of the reach.
429 Shaded areas represent ± 1 standard error.

430 and triceps long head; **Fig. 3L**). Participants displayed involuntary visuomotor feedback
431 responses for each condition (**Fig. 3C**), which were similar across conditions.

Hand Velocities and Reaction Times were Similar Across Conditions

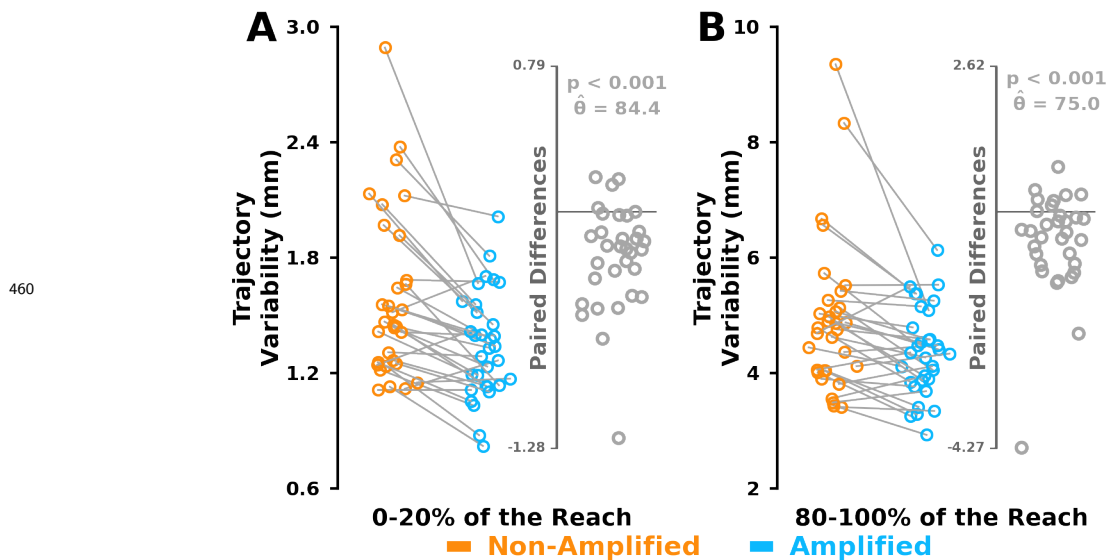
432 As shown in **Fig. 3A** and mentioned above, participants displayed similar hand velocities
433 throughout the reach for each condition. To confirm there were no hand velocity differ-
434 ences between conditions we examined peak tangential hand velocity. From our 2-way
435 rmANOVA, we did not find a significant main effect of amplification [$F(1,15) = 0.368$,
436 $p = 0.553$], main effect of delay [$F(1,15) = 0.281$, $p = 0.604$], or interaction between
437 amplification and delay [$F(1,15) = 2.234$, $p = 0.156$] on peak tangential hand velocity.
438 We also tested whether there were reaction time differences between conditions. We
439 did not find a significant main effect of amplification [$F(1,15) = 1.564$, $p = 0.230$], main
440 effect of delay [$F(1,15) < 0.001$, $p = 0.988$], or interaction between amplification and de-
441 lay [$F(1,15) = 0.117$, $p = 0.737$] for reaction time. This suggests that any differences in
442 trajectory variability or muscle activity between conditions were not due to differences
443 in movement speed or reaction time.

Amplified Conditions Had Lower Trajectory Variability at the Start and End of the Reach

446 We compared trajectory variability between conditions to assess how the sensorimotor
447 system responded to movement variability. For trajectory variability we found a signifi-
448 cant interaction between amplification and time [$F(1.727, 25.901) = 6.2627$, $p = 0.008$],

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449 as well as a main effect of time [$F(0.350, 5.256) = 222.392, p < 0.001$]. We did not find
 450 any other main effects [amplification: $F(1,15) = 1.971, p = 0.181$; delay $F(1,15) = 3.4460,$
 451 $p = 0.083$], two-way interactions [amplification x delay: $F(4, 60) = 1.069, p = 0.318$; delay
 452 x time: $F(0.576, 34.536) = 1.724, p = 0.190$], or a three-way interaction [amplification
 453 x delay x time: $F(1.926, 28.904) = 3.047, p = 0.065$]. For the amplification and time
 454 interaction, we found significantly less trajectory variability in amplified conditions rel-
 455 ative to the non-amplified conditions at 0-20% of the reach ($p < 0.001, \hat{\theta} = 84.4$; **Fig.**
 456 **4A**) and 80-100% of the reach ($p < 0.001, \hat{\theta} = 75.0$; **Fig. 4B**), but not during the other
 457 time periods (20-40%, 40-60%, or 60-80% of the reach; $p > 0.570$ for all comparisons).
 458 These results suggest that the sensorimotor system responded to amplified conditions
 459 by reducing trajectory variability, specifically near the start and end of the movement.



461 **Figure 4. Trajectory Variability:** Trajectory variability (y-axis) for the non-amplified (orange) and amplified
 462 (blue) conditions during (A) 0-20% of the reach, and (B) 80-100% of the reach for each participant (open
 463 circles). A,B The insets display the corresponding paired differences (y-axis) between the non-amplified
 464 and amplified conditions of each participant (open grey circles). Here the horizontal grey line represents
 465 a paired difference of 0. Participants had significantly lower trajectory variability in amplified conditions
 466 relative to the non-amplified conditions during (A) 0-20% of the reach ($p < 0.001$) and (B) 80-100% of the
 467 reach ($p < 0.001$).

468 *Greater Muscular Co-Contraction was Observed during Amplified Conditions*

469 We predicted that the sensorimotor system would increase muscular co-contraction in
 470 response to amplified movement variability. We considered mono-articular muscle pairs

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471 at the elbow joint and the shoulder joint, as well as a biarticular muscle pair that crossed
472 both the elbow and shoulder joints.

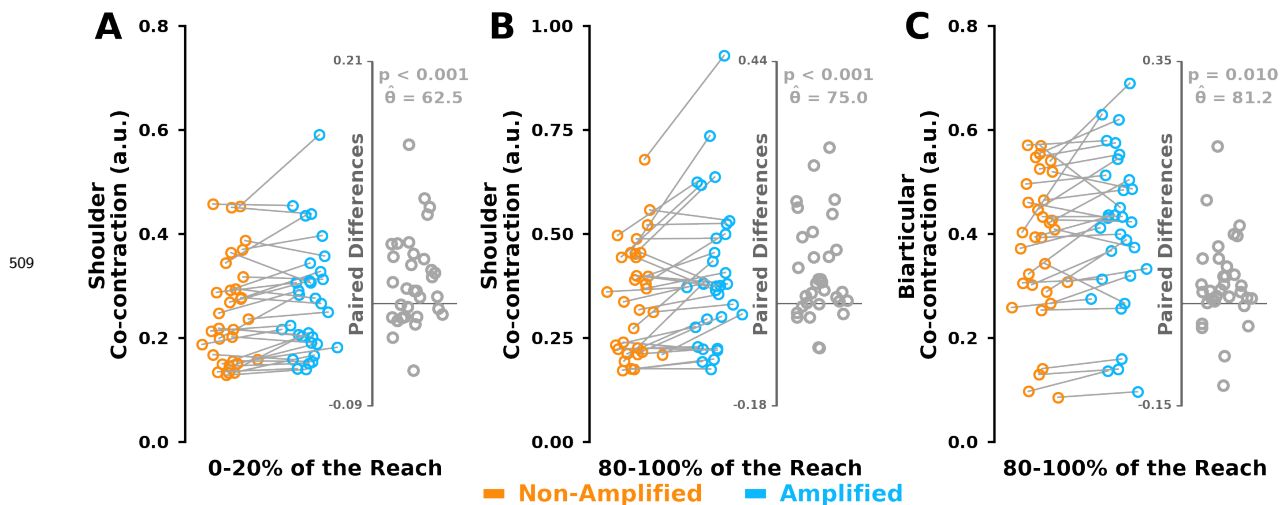
473 Similar to trajectory variability, for muscular co-contraction we found a significant
474 interaction between amplification and time for the mono-articular shoulder muscles
475 [F(1.433, 21.490) = 4.885, $p = 0.027$] and the biarticular muscles [F(1.335, 20.019) =
476 8.876, $p = 0.004$]. We found significantly greater shoulder co-contraction in amplified
477 conditions, relative to the non-amplified conditions, for each block of time ($p < 0.001$, $\hat{\theta} >$
478 62.5, for all comparisons). We also found significantly greater biarticular co-contraction
479 at 60-80% ($p = 0.032$, $\hat{\theta} = 68.8$) and 80-100% ($p = 0.010$, $\hat{\theta} = 81.3$) of the reach. We then
480 examined the number of individuals that had significant differences in biarticular mus-
481 cular co-contraction between amplified and non-amplified conditions by considering all
482 of their trials. At this individual level, we found that 12 out of 16 participants (75%)
483 had a significantly greater biarticular muscular co-contraction in the amplified condi-
484 tions compared to the non-amplified conditions during 80-100% of the reach. **Figure 5**
485 shows shoulder co-contraction and biarticular co-contraction in the amplified and non-
486 amplified conditions at 0-20% and 80-100% of the reach, which temporally align with
487 significantly lower trajectory variability. We did not find an interaction between ampli-
488 fication and time for the mono-articular elbow muscles [F(2.031,30.467) = 2.438, $p =$
489 0.1035]. Collectively, these results suggest that the sensorimotor system modulated
490 muscular co-contraction in response to amplified movement variability throughout the
491 reach.

492 We also considered the possibility that sensorimotor delays may allow movement
493 variability to propagate. One possibility is that muscular co-contraction could act as
494 a feedforward mechanism to prevent the propagation of movement variability due to
495 time delays. However, for elbow, shoulder, and biarticular muscular co-contraction we
496 found no significant main effects or interactions involving delay ($p > 0.290$ for all om-
497 nibus tests). These results do not support the idea that muscular co-contraction is used

498 to mitigate the propagation of movement variability as a result of time delays.

499 *Greater Biarticular Muscular Co-contraction was Related to Lower Trajectory Variability*
500 *at the End of the Reach*

501 We predicted that trajectory variability would be regulated by muscular co-contraction.
502 As shown in **Figure 4** and mentioned above, we found significant lower trajectory vari-
503 ability in amplified conditions during the 0-20% and 80-100% of the reach. Similarly, we
504 found significantly greater shoulder muscular co-contraction (**Fig. 5A,B**) and biarticular
505 muscular co-contraction (**Fig. 5C**) in amplified conditions during 0-20% or 80-100% of
506 the reach. Thus, we examined the relationship between trajectory variability and muscu-
507 lar co-contraction along portions of the reach when both measures displayed significant
508 differences.



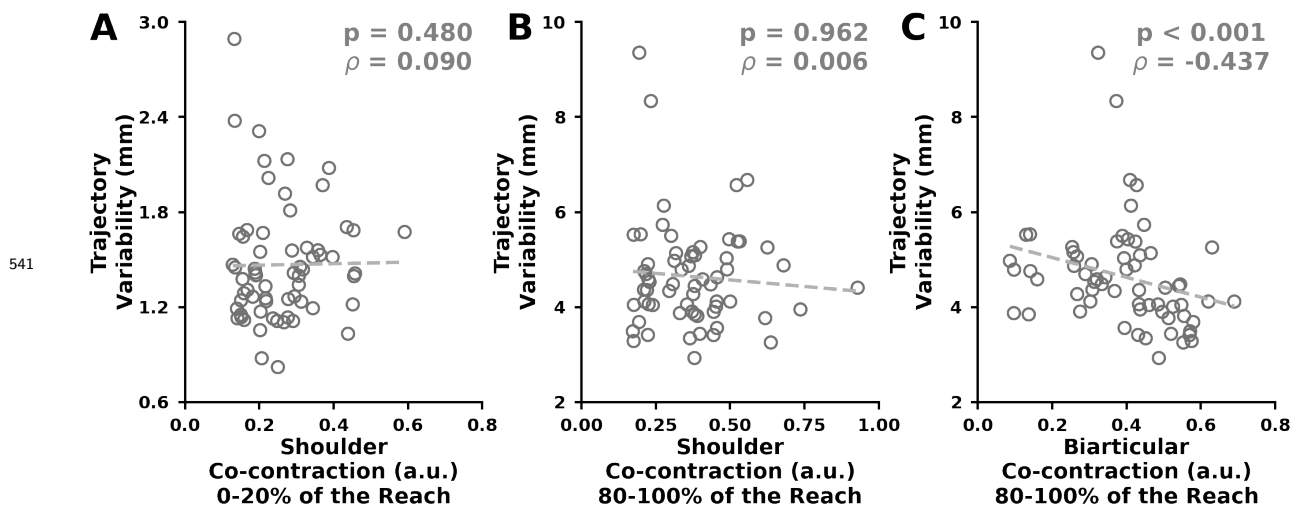
510 **Figure 5. Muscular Co-contraction:** Shoulder co-contraction (y-axis) for the non-amplified (orange) and
511 amplified (blue) conditions during **(A)** 0-20% of the reach, and **(B)** 80-100% of the reach for each participant
512 (open blue or orange circles). **(C)** Biarticular co-contraction (y-axis) for the non-amplified (orange) and
513 amplified (blue) conditions during 80-100% of the reach. **A,B,C** The insets display the paired differences
514 (y-axis) between the non-amplified and amplified conditions for each participant (open grey circles). The
515 horizontal grey line represents a paired difference of 0. Participants had significantly greater shoulder
516 co-contraction in the amplified conditions relative to the non-amplified conditions during **(A)** 0-20% of
517 the reach ($p < 0.001$) and **(B)** 80-100% of the reach ($p < 0.001$). **(C)** Participants also had greater biarticular
518 co-contraction in the amplified conditions relative to the non-amplified conditions during 80-100% of the
519 reach ($p = 0.010$).

520 We found significantly lower trajectory variability and greater shoulder muscle co-
521 contraction in the amplified conditions during 0-20% and 80-100% of the reach. How-

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522 ever, we did not find a correlation between shoulder muscle co-contraction and trajec-
523 tory variability ($p = 0.480$, $\rho = 0.090$) during 0-20% of the reach (**Fig. 6A**). This suggests
524 that lower trajectory variability at the beginning of the reach was not caused by muscular
525 co-contraction. The decreases in trajectory variability in the amplified conditions were
526 likely caused by participants keeping the visually amplified cursor closer to the center of
527 the start position prior to movement onset. Similarly, we found significantly lower trajec-
528 tory variability and greater shoulder muscular co-contraction in the amplified conditions
529 during 80-100% of the reach. Again, however, we did not find a significant correla-
530 tion between shoulder muscular co-contraction and trajectory variability ($p = 0.962$, ρ
531 $= 0.006$) during 80-100% of the reach (**Fig. 6B**). These results suggest the observed
532 decreases in trajectory variability were not related to the observed increases in shoul-
533 der muscular co-contraction, and hence were not due to an impedance control strategy
534 from the monoarticular shoulder muscles.

535 As mentioned, we found both significantly less trajectory variability and greater
536 biarticular muscular co-contraction during 80-100% of the reach. Critically, we found a
537 significant, negative correlation between biarticular muscular co-contraction and trajec-
538 tory variability ($p < 0.001$, $\rho = -0.437$) during the 80-100% time window (**Fig. 6C**). These
539 results support our hypothesis that the sensorimotor system uses impedance control to
540 regulate trajectory movement variability, particularly at the end of the reach.



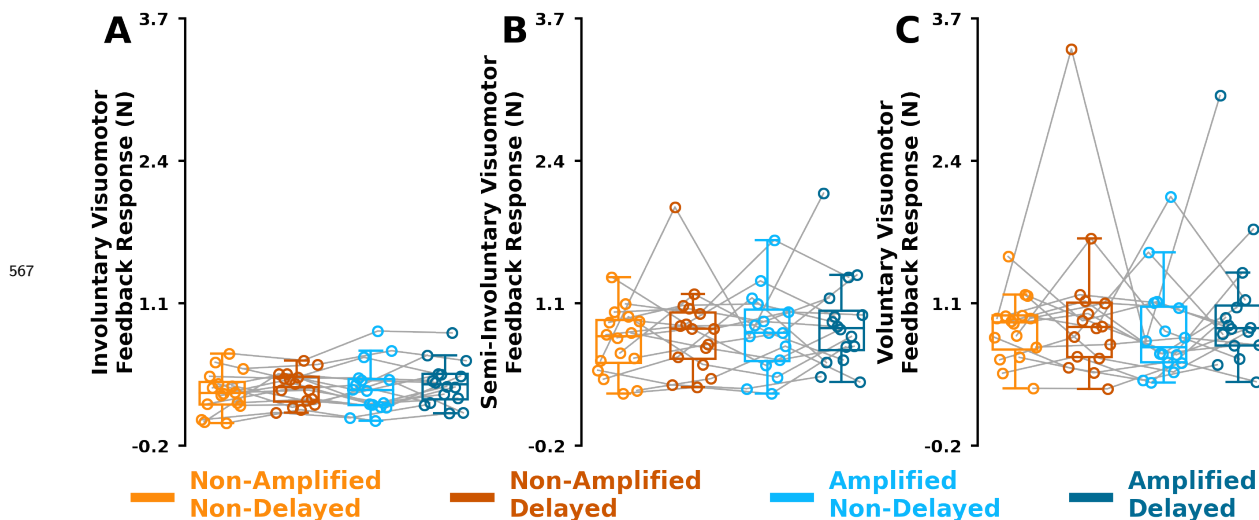
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542 **Figure 6. Relationship between Muscular Co-contraction and Trajectory Variability** **A)** Trajectory vari-
543 ability (y-axis) and shoulder co-contraction (x-axis) during **A)** 0-20% of the reach, and **B)** 80-100% of the
544 reach. **C)** Trajectory variability (y-axis) and biarticular co-contraction (x-axis) were negatively correlated (p
545 < 0.001 , $\rho = -0.437$) during 80-100% of the reach, suggesting that greater biarticular co-contraction may
546 have been used to decrease trajectory variability during the latter portion of the reach. Dashed grey lines
547 show the line-of-best-fit.

548 Visuomotor Feedback Responses Did Not Change Between Conditions

549 We predicted that the sensorimotor system would modulate visuomotor feedback re-
550 sponses in conditions with amplified movement variability and greater time delays. For
551 involuntary visuomotor feedback responses (180 - 230 ms; **Fig. 7A**), we did not find
552 main effects of amplification [$F(1,15) = 2.556$, $p = 0.131$] or delay [$F(1,15) = 1.578$, $p =$
553 0.228], nor an interaction of amplification and delay [$F(1,15) < 0.001$, $p = 0.987$]. The
554 average cursor position across participants during the involuntary visuomotor feedback
555 response was between 88% - 97% along the forward direction during the last portion
556 of the reach. This portion of the reach aligns well with observed condition differences
557 in trajectory variability. Semi-involuntary visuomotor feedback responses (230 - 300 ms;
558 **Fig. 7B**) did not yield main effects of amplification [$F(1,15) = 2.450$, $p = 0.138$] or de-
559 lay [$F(1,15) = 0.878$, $p = 0.364$], nor an interaction between the amplification or delay
560 [$F(1,15) = 0.003$, $p = 0.954$]. Similarly, voluntary visuomotor feedback responses (300 -
561 400 ms; **Fig. 7C**) did not show main effect of amplification [$F(1,15) < 0.001$, $p > 0.999$]
562 or delay [$F(1,15) = 1.069$, $p = 0.317$], nor an interaction between the amplification or
563 delay [$F(1,15) = 0.061$, $p = 0.808$]. It is important to note that we do not suggest that
564 the sensorimotor system did not utilise visuomotor feedback responses during the task.
565 Rather, our results suggest that the sensorimotor system did not modulate visuomotor
566 feedback gains in response to the experimental manipulations.

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568 **Figure 7. Visuomotor Feedback Response:** Visuomotor feedback response (y-axis) for each condition
 569 (x-axis) during the **A**) involuntary (180 - 230 ms), **B**) semi-involuntary (230 - 300 ms) and **C**) voluntary
 570 (300 - 400 ms) time windows. Circles and connected grey lines represent individual participants. Colour
 571 represents the experimental condition. Involuntary, semi-voluntary, and voluntary visuomotor feedback
 572 responses did not change due to the experimental conditions ($p > 0.05$ for all comparisons). These results
 573 suggest that the nervous system does not modulate visuomotor feedback gains to regulate trajectory
 574 variability. Box and whisker plots show 25%, 50%, and 75% quartiles.

575 *Muscular Co-contraction was Related to Inherent Visuomotor Feedback Responses*

576 Next, we explored the interplay between muscular co-contraction and visuomotor feed-
 577 back responses. First we examined whether there was a direct interplay between mus-
 578 cular co-contraction and visuomotor feedback responses. As a reminder, a direct inter-
 579 play is an interaction where visuomotor feedback gains scale as a function of muscular
 580 co-contraction. To this end, we correlated the muscular co-contraction prior to the invol-
 581 untary visuomotor feedback response (0 - 90 ms) and involuntary visuomotor feedback
 582 responses (180 - 230 ms) within the same probe trials. We found that elbow ($p = 0.177$,
 583 $\rho = -0.171$), shoulder ($p = 0.218$, $\rho = -0.156$), and biarticular ($p = 0.114$, $\rho = -0.119$)
 584 muscular co-contraction was not correlated with involuntary visuomotor feedback re-
 585 sponses. We also did not find a significant relationship of semi-involuntary (230 - 300
 586 ms) and voluntary (300 - 400 ms) visuomotor feedback responses to elbow, shoulder, or
 587 biarticular muscular co-contraction ($p > 0.093$, for all correlations). This result suggests
 588 that the muscular co-contraction did not directly interact with the upcoming visuomotor

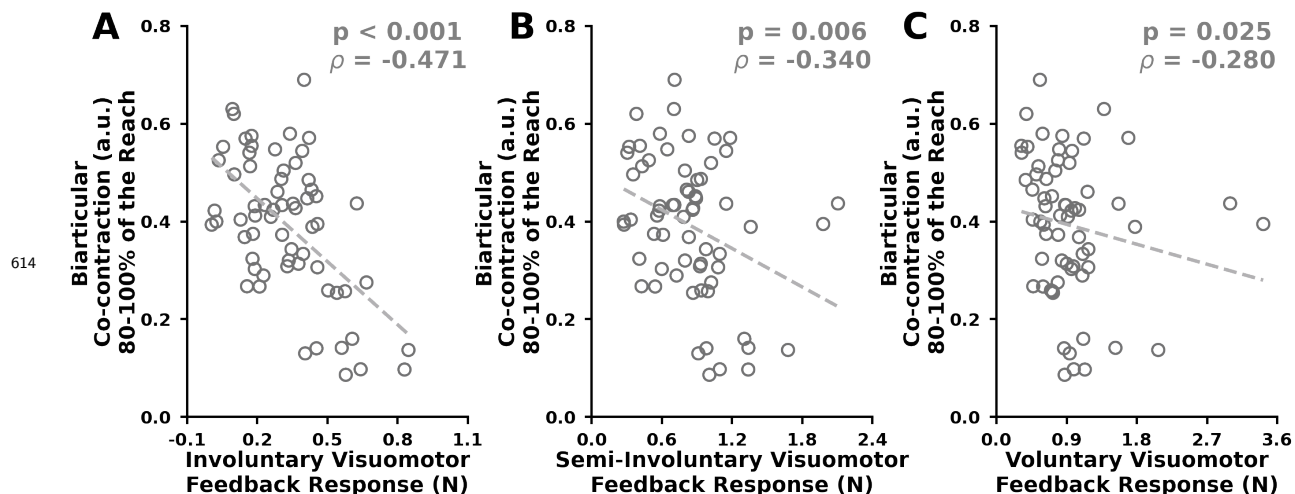
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589 feedback response.

590 We also tested whether there may be an indirect interplay between muscular co-
591 contraction and visuomotor feedback responses. That is, we wanted to examine whether
592 the sensorimotor system scales muscular co-contraction and or visuomotor feedback
593 gains relative to one another when regulating trajectory variability. To examine whether
594 there was an indirect interplay, we correlated visuomotor feedback responses to biartic-
595 ular muscular co-contraction during 80-100% of the reach during the experiment trials
596 (i.e., non-probe trials). Following the *a priori* approach mentioned in the statistical anal-
597 yses section, we focused on biarticular muscular co-contraction during 80-100% of the
598 reach because it was correlated with decreased trajectory variability. Interestingly, we
599 found that biarticular muscular co-contraction during 80-100% of the reach was nega-
600 tively correlated to the involuntary ($p < 0.001$, $\rho = -0.471$; **Fig. 8A**), semi-involuntary
601 ($p = 0.006$, $\rho = -0.340$; **Fig. 8B**), and voluntary ($p = 0.025$, $\rho = -0.280$; **Fig. 8C**) vi-
602 suomotor feedback responses—despite observing no changes to visuomotor feedback
603 responses between experimental conditions. That is, muscular co-contraction was mod-
604 ulated about inherent visuomotor feedback responses, which did not change between
605 conditions, when regulating trajectory variability. We found that biarticular muscular
606 co-contraction remained negatively correlated from the involuntary to voluntary time
607 windows, likely because these visuomotor feedback responses had some temporal de-
608 pendance. Similarly, when averaging across conditions we found biarticular muscular
609 co-contraction during 80 - 100% of the reach was negatively correlated with involuntary
610 ($p = 0.023$, $\rho = -0.565$), semi-involuntary ($p = 0.049$, $\rho = -0.500$), and voluntary ($p = 0.037$,
611 $\rho = -0.524$) visuomotor feedback responses.

612 Our results support the idea that there is an indirect interplay between muscular co-
613 contraction and visuomotor feedback responses when regulating trajectory variability.

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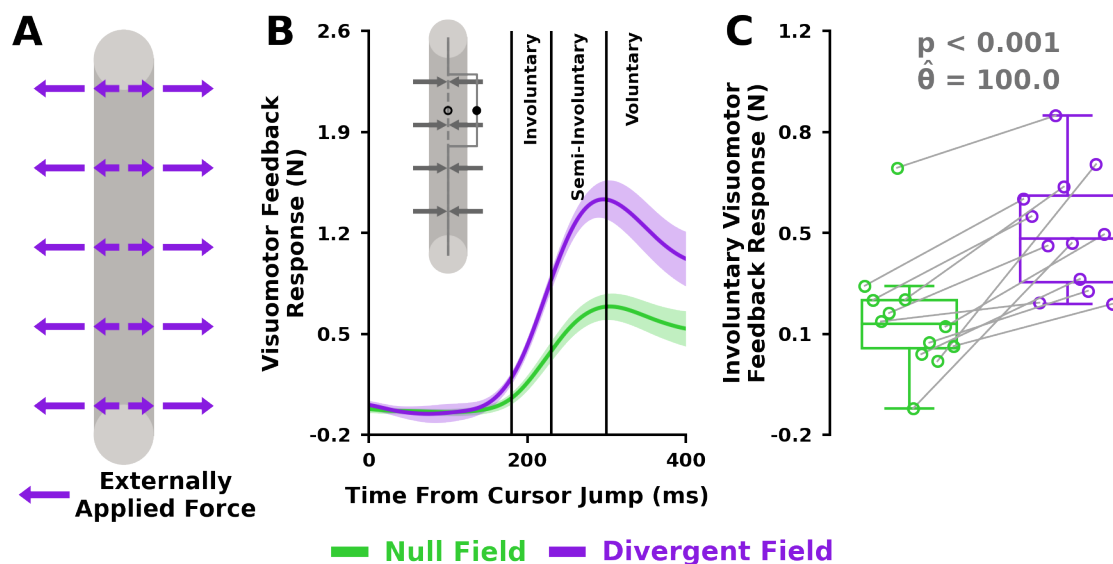


615 **Figure 8. Relationship between Visuomotor Feedback Responses and Muscular Co-contraction:** Bi-
 616 articular co-contraction during 80-100% of the reach was negatively related to **A)** involuntary ($\rho = -0.471$, p
 617 < 0.001), **B)** semi-involuntary ($\rho = -0.340$, $p = 0.006$), and **C)** voluntary ($\rho = -0.280$, $p = 0.025$) visuomotor
 618 feedback responses (x-axes). These results suggest that there is an indirect interplay between muscular
 619 co-contraction and visuomotor feedback responses. The dashed grey line shows the line-of-best-fit.

620 Control Experiment

621 The results of **Experiment 1** show that the sensorimotor system did not modulate vi-
 622 suomotor feedback responses based on our experimental manipulations. The goal for
 623 the control experiment (**Fig. 9A**) was to verify that we could elicit changes in visuomo-
 624 tor feedback responses within individuals when using the exoskeleton robot and force
 625 channel parameters (i.e., stiffness and damping coefficients). The visuomotor feedback
 626 response (**Fig. 9B**) in both conditions begin to increase approximately 170 ms after the
 627 cursor jump. The visuomotor feedback response in the divergent field condition rose
 628 faster and to a higher level than the null field condition. Specifically, we found greater
 629 involuntary (**Fig. 9C**; $p < 0.001$, $\hat{\theta} = 100.0$), semi-voluntary ($p < 0.001$, $\hat{\theta} = 100.0$) and
 630 voluntary ($p < 0.001$, $\hat{\theta} = 100.0$) visuomotor feedback responses in the divergent field
 631 condition compared to the null field condition. Thus, similar to past work (Franklin and
 632 Wolpert, 2008), our experimental setup was able to capture within participant changes
 633 in visuomotor feedback gains between conditions.³⁰

634



635 **Figure 9. Control Experiment: A)** We recruited 12 participants to participate in a second experiment to
 636 verify that our experimental setup can capture changes in visuomotor feedback responses. Participants
 637 experienced two experimental conditions: i) a null field (green) without externally applied forces, and ii) a
 638 divergent force field (purple). For the divergent force field, externally applied forces scaled proportionally
 639 with the lateral distance of the hand from the centerline of the visual channel. We interleaved visuomotor
 640 feedback probe trials to measure involuntary, visuomotor feedback responses. **B)** Visuomotor feedback
 641 response (y-axis) over time (x-axis), where 0 ms corresponds to the initial cursor jump. Solid lines represent
 642 average visuomotor feedback responses for each condition. Shaded regions represent ± 1 standard error.
 643 Vertical lines separate involuntary (180 - 230 ms), semi-involuntary (230 - 300 ms), and voluntary (300 -
 644 400 ms) visuomotor feedback responses. **C)** Average involuntary, visuomotor feedback response (y-axis)
 645 for each condition (x-axis). Circles and connected grey lines represent individual participant data. Box
 646 and whisker plots show 25%, 50% and 75% quartiles. As shown previously (Franklin and Wolpert, 2008),
 647 we found a significant increase in the involuntary visuomotor feedback response in the divergent field
 648 compared to the null field ($p < 0.001$). Thus, we were able to confirm that our exoskeleton robot and
 649 chosen force channel parameters (stiffness and damping coefficients) were able to capture changes in
 650 involuntary, visuomotor feedback responses.

651 Discussion

652 We found that lower trajectory variability was related to greater muscular co-contraction.
 653 This finding supports the hypothesis that the sensorimotor system utilizes impedance
 654 control to regulate movement variability. Conversely, we did not find any change in
 655 visuomotor feedback responses when lateral movement was visually amplified, which
 656 does not support the notion that the sensorimotor system modulates visuomotor feed-
 657 back gains to regulate trajectory variability. Interestingly, despite no changes in visuo-
 658 motor feedback responses between conditions, we found that muscular co-contraction

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659 was related to inherent visuomotor feedback responses. This finding suggests that there
660 is an indirect interplay between impedance control and visuomotor feedback control
661 when regulating trajectory variability.

662 In **Experiment 1**, we found lower trajectory variability at the end (80-100%) of
663 the reach and similar levels of trajectory variability to the work of Gribble and col-
664 leagues (2003). Here we also found greater shoulder and biarticular co-contraction
665 in amplified compared to non-amplified conditions. We found that biarticular muscu-
666 lar co-contraction was negatively correlated to hand trajectory variability during this
667 time period. The negative relationship between biarticular muscular co-contraction sup-
668 ports the hypothesis that the sensorimotor system utilizes impedance control to regulate
669 movement variability. However, we did not find a relationship between shoulder muscle
670 co-contraction and trajectory variability. Unexpectedly, we did not find any modulation
671 of involuntary, semi-involuntary, or voluntary visuomotor feedback responses between
672 any of the experimental conditions. Despite not modulating between conditions, the
673 involuntary visuomotor feedback response was present during the 180 - 230 ms time
674 window. Within probe trials, we did not find a significant relationship between visuo-
675 motor feedback responses and the preceding muscular co-contraction. Interestingly,
676 however, we observed a significant and negative relationship between biarticular mus-
677 cular co-contraction and visuomotor feedback responses during the involuntary, semi-
678 involuntary, and voluntary time windows. Because visuomotor feedback responses did
679 not change with the experimental manipulations, this suggests that the sensorimotor
680 system modulated muscular co-contraction relative to inherent visuomotor feedback
681 responses. For example, a participant that had a low visuomotor feedback response
682 tended to have high muscular co-contraction. This finding supports the notion that
683 there is an indirect interplay between impedance control and visuomotor feedback con-
684 trol when regulating trajectory variability.

685 Movement Variability and Impedance Control

686 In our study, we found that trajectory variability increased over time. During 80-100%
687 of the reach, trajectory variability was lower in the amplified condition compared to the
688 non-amplified condition. During multi-joint reaching, past work has shown that the sen-
689 sorimotor system can increase in muscular co-contraction⁴ or effective hand stiffness¹⁸
690 to perform more accurate movements. These prior studies did not statistically examine
691 the relationship between muscle co-contraction or effective hand stiffness with trajec-
692 tory variability during the reach. During single-joint reaches, it has been found that
693 trajectory variability is modulated during the final portion of the movement.^{5,6} These
694 studies also found lower trajectory variability that corresponded with increased limb
695 stiffness⁶ and muscle activity.⁵ In agreement, we found that trajectory variability was
696 negatively correlated with muscular co-contraction during 80-100% of the reach. Our
697 results align with prior literature that suggests that the sensorimotor system uses mus-
698 cular co-contraction to regulate trajectory variability.

699 The ability of a muscle to provide joint impedance depends on its intrinsic stiffness
700 properties. It is well established that muscle-tendon units resist length changes through
701 short-range and long-range muscle fiber stiffness, as well as through the tendon and
702 parallel elastic component properties.^{56,57} Short-range muscle fiber stiffness arises from
703 bound cross-bridges that strongly resist small length changes prior to exceeding a max-
704 imal cross-bridge bond length and becoming unbound.^{58,59,60,61} Beyond small length
705 changes, such as following a large displacement or during movement, muscle fibers still
706 provide some resistance to length changes through long-range stiffness. Long-range
707 muscle fiber stiffness is related to the active and passive force-length relationships, as
708 well as the muscle fiber velocity that influences cross-bridge (un)binding rates.^{58,60,62,61}
709 Both experiments and theory show with greater muscle fiber velocity there is a decrease
710 in muscle fiber long-range stiffness.^{58,56} A reduction in muscle-tendon stiffness during
711 movement likely contributes to the finding that limb inertia tends to dominate joint

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712 impedance given a large mechanical perturbation of the arm.⁶³ Nevertheless, as in our
713 experiment, long-range muscle fiber stiffness would still be present to some degree
714 during the reaching movements.⁵⁶ Greater muscle activity from muscular co-contraction
715 would further enhance muscle-tendon stiffness and consequently joint impedance,^{64,12,13}
716 which in our study may have led to reduced trajectory variability.

717 In addition to their intrinsic mechanical properties, how muscles are geometri-
718 cally oriented about one or more joints also contributes to their ability to provide joint
719 impedance. The moment arm squared and length of a muscle-tendon unit also deter-
720 mines its contribution to rotational joint impedance.^{65,66} More generally, multiarticular
721 muscles provide impedance about each of the joints they span.⁵⁶ The relationship be-
722 tween joint impedance and effective hand stiffness can be calculated by considering
723 the Jacobian that relates the rate of change of joint movement to the rate of change of
724 hand movement.¹⁵ In our study, participants responded to our amplified conditions by
725 increasing biarticular co-contraction of the biceps short head and triceps long head mus-
726 cles. Biarticular co-contraction would increase joint impedance about both the shoulder
727 and elbow joints. Increasing shoulder and elbow joint impedance would consequently
728 increase effective hand stiffness. Thus, biarticular muscle co-contraction would lead to
729 greater effective hand stiffness that would resist changes in hand position and reduce
730 trajectory variability. Following previous work,⁴ we examined muscular co-contraction
731 separately for monoarticular elbow muscles, monoarticular shoulder muscles, and biar-
732 ticular muscles that span both the elbow and shoulder. However, all muscles would
733 interact to balance joint moments, as well as contribute to joint impedance and effec-
734 tive hand stiffness. For example, the biarticular biceps short head would mechanically
735 interact with the monoarticular rear deltoid. It would be useful for future studies to con-
736 sider the intrinsic mechanical properties and geometric orientation of each muscle, as
737 well as how these muscles interact to stabilize reaching movements.

738 Movement Variability and Feedback Control

739 Optimal feedback control theory predicts that feedback responses change as a function
740 of sensorimotor noise.²³ Here we experimentally tested this idea by visually amplify-
741 ing movement variability and increasing sensory delays. Prior studies have shown that
742 involuntary visuomotor feedback responses are modulated by visual manipulations³⁰
743 or velocity-dependent force fields.³⁴ However, despite being present, we did not find
744 changes in visuomotor feedback responses by visually amplifying movement variabil-
745 ity or imposing delays. A lack of visuomotor feedback response modulation between
746 conditions led us to perform a second experiment. This was a control experiment to
747 confirm our exoskeleton robot and force channel parameters were sensitive to detect
748 differences in visuomotor feedback responses in a position-dependent forcefield. We
749 found higher involuntary visuomotor feedback responses to the divergent-field in com-
750 parison to the null-field, verifying that our experimental paradigm was able to elicit
751 changes in visuomotor feedback responses. A potential reason that we did not ob-
752 serve changes in visuomotor feedback responses between conditions is that we did not
753 apply the probes throughout the reach. It is possible that probes applied later in the
754 reach may have elicited differences in visuomotor feedback responses. However, it is
755 worthwhile to note that the involuntary visuomotor feedback responses we observed
756 would have led to movement changes at the latter portion of the reach, where we
757 found lower trajectory variability between conditions. Another potential reason that
758 we did not see any changes in visuomotor feedback responses is that only modulating
759 muscular co-contraction was sufficient to reduce trajectory variability to a desired level.
760 Perhaps in other more demanding tasks it would be useful to modulate both muscular
761 co-contraction and visuomotor feedback responses, but that is not we found in the cur-
762 rent experiment. Our findings suggests that visuomotor feedback responses may have
763 been used by the sensorimotor system to correct for positional deviations, but did not
764 modulate with amplified movement variability or greater sensory delays.

*Sensorimotor Regulation of Movement Variability***Delays**

In this work we also examined the potential influence of increasing sensory delays on the regulation of trajectory variability. As a reminder, sensorimotor time delays may allow movement variability to both propagate and accumulate before any possible feedback correction. To impose visual delays during a tracking task, prior studies have delayed visual feedback of a cursor that was controlled with a joystick.^{38,39} These studies used visual delays of 200 ms³⁹ and 300 ms.^{38,39} As expected, they showed that increased visual delays led to higher error between the cursor and the moving target. Similarly in standing balance, greater sensory delays led to higher postural variability.⁶⁷ In our study, the 200 ms visual delay did not influence trajectory variability during any portion of the reach. Furthermore, we also found no main effect or interaction of delays on muscular co-contraction or visuomotor feedback responses. The aforementioned studies applied delays across both forward and lateral dimensions^{38,39} or were only measuring movement in the forward dimension.⁶⁷ Unlike past work, we imposed sensory delays along the lateral dimension, but not along the forward direction. One possibility for not finding muscular co-contraction or visuomotor feedback response differences due to imposed lateral position delays is that the sensorimotor system is more responsive to delays along the resultant direction of movement. A task that involves reaching along different paths with various curvatures may provide insight into how the sensorimotor system proportionally weighs delayed visual feedback, parallel and perpendicular to the direction of movement.

Interplay between Visuomotor Feedback Control and Impedance Control

We also explored whether there might be direct and or indirect interplay between muscular co-contraction and visuomotor feedback responses. Here we considered a direct interplay to be an interaction where visuomotor feedback gains scale as a function of muscular co-contraction. Automatic gain-scaling⁴⁸ and a dual agonist-antagonist con-

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791 trol strategy^{68,69} are two potential causes that might lead to a direct interplay between
792 muscular co-contraction and feedback responses. As a reminder, automatic gain-scaling
793 is the magnitude scaling of the muscular stretch response with greater background mus-
794 cle activity prior to a perturbation, which can occur via muscular co-contraction. Auto-
795 matic gain-scaling of short-latency and long-latency muscular feedback responses given
796 a mechanical perturbation is well known.⁴⁸ Although, currently there has not been any
797 statistical evidence to support that automatic gain-scaling occurs for visuomotor feed-
798 back responses.^{31,34,70} Another potential cause of a direct interplay between muscular
799 co-contraction and visuomotor feedback responses is a dual agonist-antagonist control
800 strategy. The principle behind a dual agonist-antagonist control strategy is that the ag-
801 onist and antagonist muscles can simultaneously activate and deactivate, respectively.
802 Such a dual agonist-antagonist control strategy would lead to a larger net change in
803 joint moment compared to only activating the agonist muscles. A larger net change in
804 joint moment would allow for one to respond faster to mechanical perturbation^{68,69} or
805 visuomotor perturbations. In our study, and similar to past work,^{31,34,70} we do not see an
806 increase in visuomotor feedback responses with greater muscular co-contraction. Thus,
807 our current experiments do not support the idea that the visuomotor system uses a di-
808 rect interplay via automatic gain-scaling or a dual agonist-antagonist control strategy.

809 We also considered the possibility that there might be an indirect interplay be-
810 tween impedance control and visuomotor feedback control. That is, we examined
811 whether the sensorimotor system scales muscular co-contraction and or visuomotor
812 feedback gains relative to one another when regulating trajectory variability. In our
813 study, we found that muscular co-contraction increased during the amplified conditions.
814 Conversely, despite being present, we did not find any differences in visuomotor feed-
815 back responses during amplified and non-amplified conditions. Interestingly, we found
816 a negative correlation between muscular co-contraction and visuomotor feedback re-
817 sponses. Taken together, our results suggest that the sensorimotor system modulates

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818 muscular co-contraction relative to inherent visuomotor feedback responses when reg-
819 ulating trajectory variability.

820 Currently, it is unknown what might cause such an indirect interplay. A recent com-
821 putational study has shown that the use of both feedforward muscular co-contraction
822 and feedback control may be more energetically efficient than feedback control alone.¹⁶
823 Thus, an indirect relationship between impedance control and feedback control may
824 arise due to the sensorimotor system minimizing metabolic energy.⁷¹ Past work has
825 shown that muscular co-contraction^{72,14,70} and visuomotor feedback gains⁷⁰ adapt over
826 time when participants learn a novel forcefield. Likewise, Sutter and colleagues (2022)
827 found that trajectory variability reduced with practice.⁷³ Another interesting direction,
828 using a between group experimental design, would be to examine how muscular co-
829 contraction, feedback gains, and their interplay adapt over time to regulate trajectory
830 variability. Further studies are needed to elucidate the control and learning mechanisms
831 that underpin this indirect interplay.

832 **Conclusion**

833 Humans often have to account for movement variability during day-to-day activities to
834 produce accurate movements. Here we amplified movement variability to understand
835 the independent and interacting roles of impedance control and feedback control. We
836 found that humans modulate muscular co-contraction to regulate trajectory variability.
837 Interestingly, our results also suggest that the sensorimotor system scales muscular co-
838 contraction relative to inherent visuomotor feedback gains when regulating trajectory
839 variability. The present work advances our understanding of how the sensorimotor sys-
840 tem utilizes both impedance control and feedback control to regulate trajectory vari-
841 ability. Understanding how humans utilize impedance control and feedback to control
842 movements is important for healthy individuals,⁷⁴ as well as those with different neu-
843 rological disorders that involve muscle spasticity.⁷⁵ Future work should further examine

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844 the mechanisms that underpin the interplay between impedance control and feedback
845 control in both healthy and neurological disease populations.

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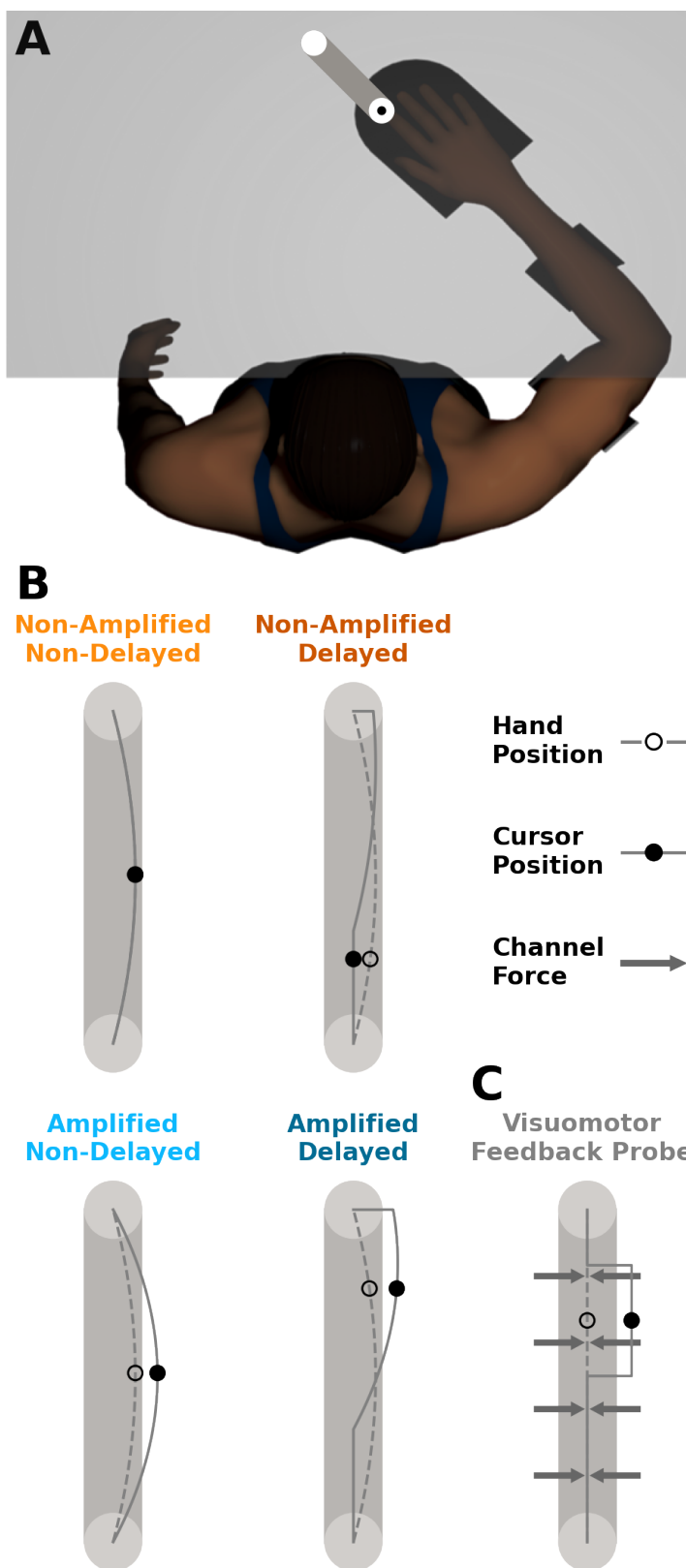
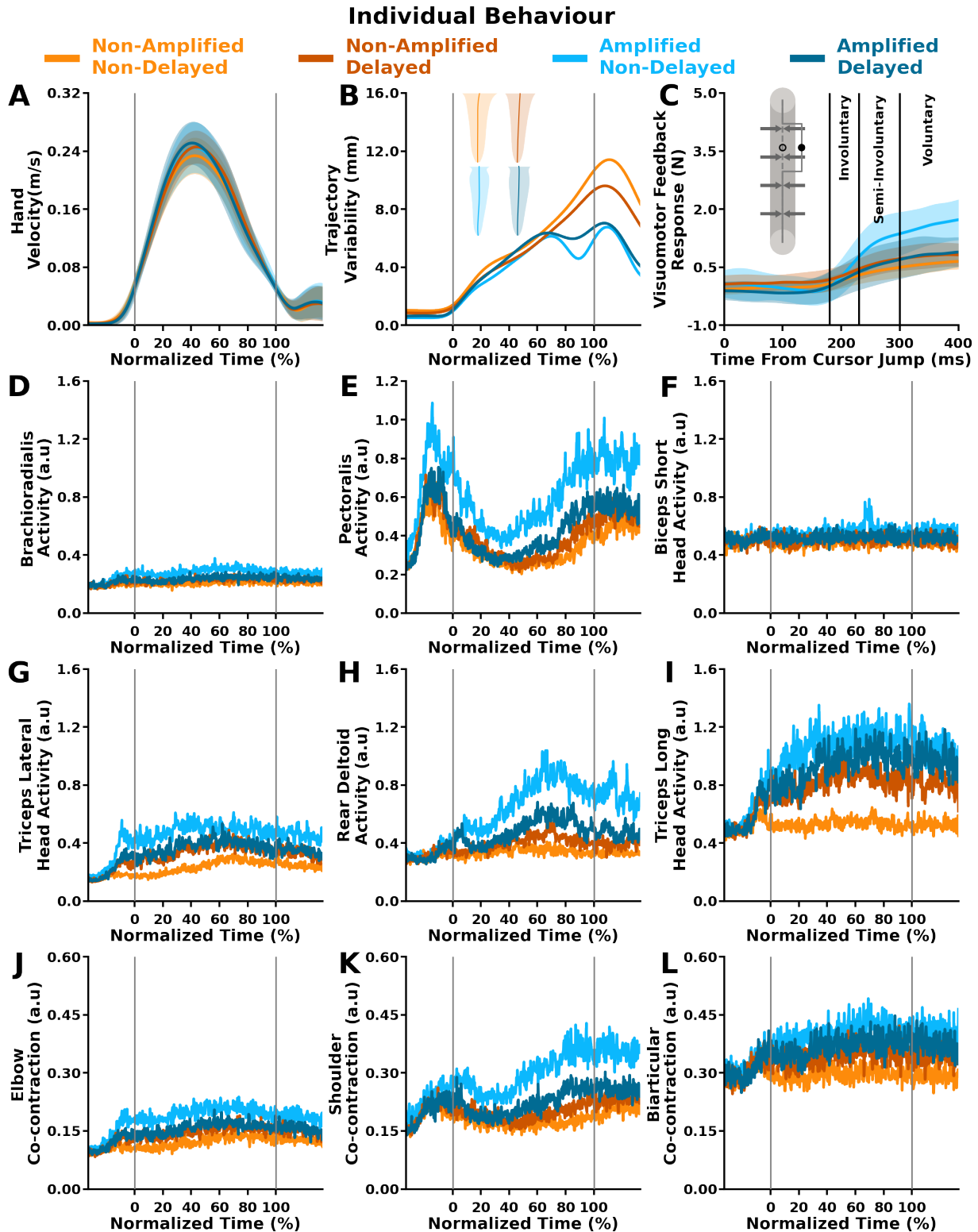


Figure 1: Experimental Design. **A)** Participants had their right arm supported by an exoskeleton (Kinarm). A semi-silvered mirror projected images from an LCD screen and occluded vision of the hand. Participants were told that the visually displayed cursor was aligned with their hand position. Participants were instructed to reach forward from a start position (white circle) to an end target (white circle) while keeping the cursor inside a visually displayed channel (grey). The forward and lateral axes were parallel and perpendicular to the visually displayed channel. We recorded electromyography of six upper limb muscles. **B)** We amplified and or delayed the lateral position of the cursor relative to the hand. Participants performed four experimental conditions in separate blocks of trials. In one condition, the cursor (solid black circle) and hand position (open black circle) were aligned during the reach (non-amplified, non-delayed; light orange). In a second condition, we imposed a 200 ms delay on the lateral cursor position relative to the participant's hand position (non-amplified, delay; dark orange). In a third condition, we amplified the cursor position relative to the hand by doubling its lateral distance from the straight line connecting the start position and target (amplified, non-delayed; light blue). In a fourth condition, we amplified and delayed the lateral cursor position relative to the participant's hand position (amplified, delayed; dark blue). **C)** We interleaved visuomotor feedback probe trials to measure visuomotor feedback responses. Probe trials consisted of participants reaching within a force channel that prevented lateral movement. During probe trials, the hand and cursor were aligned for the initial portion of the reach. Halfway through the reach, the cursor was displaced 25 mm to the left or right of the force channel. After 250 ms, the cursor realigned with the hand. We measured the visuomotor feedback response as the force (N) participants applied to the wall of the stiff force channel.

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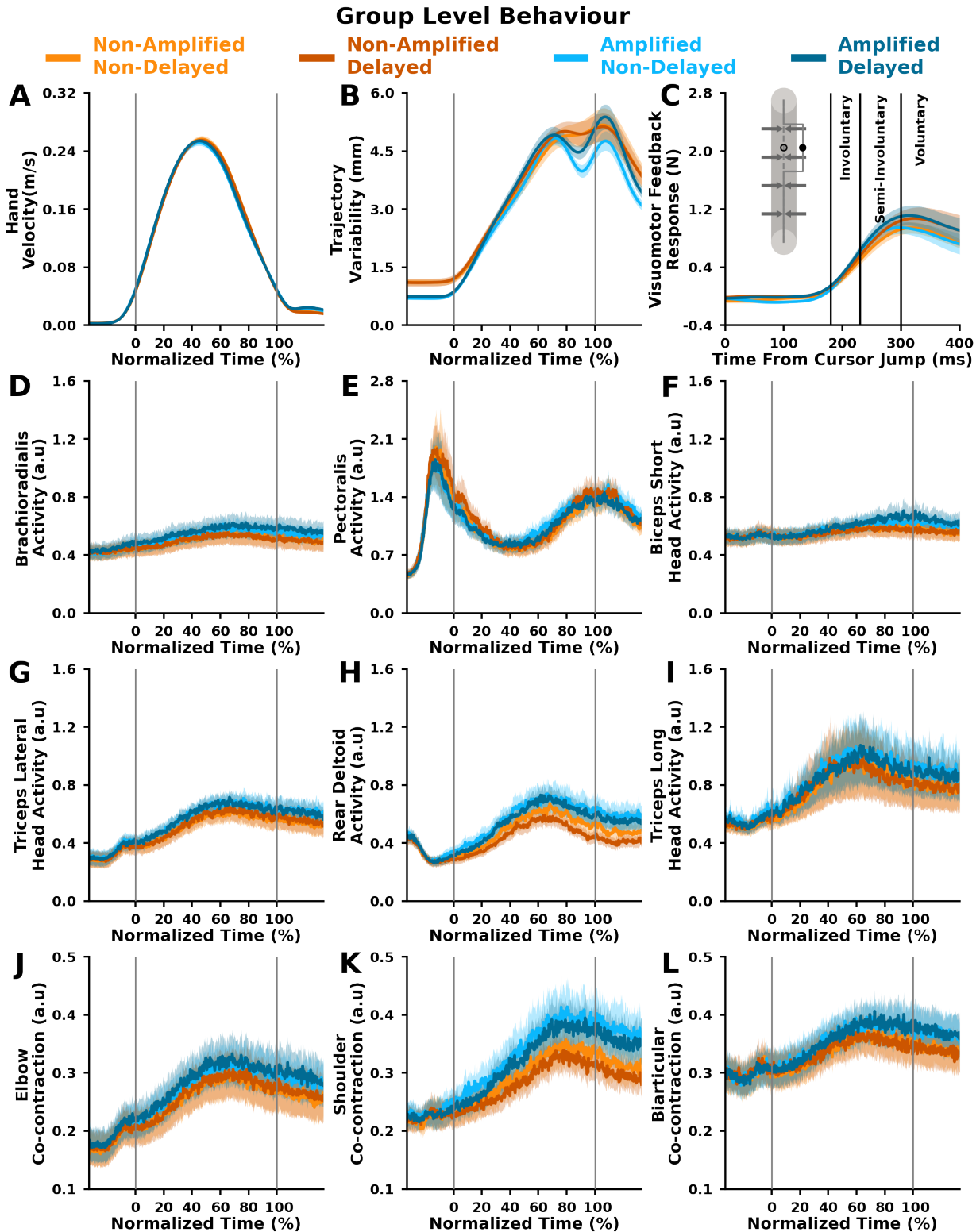


847

848 **Figure 2: Individual Behaviour.** Average data from an individual participant during each condition. **A)**
849 Hand velocity (y-axis) over normalized time (x-axis), where 0% and 100% (vertical grey lines) respectively
850 correspond with the start and end of the reach. **B)** Trajectory variability (y-axis) changes over normalized
851 time (x-axis). The participant displayed lower trajectory variability during amplified conditions (light blue,

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852 dark blue) compared to non-amplified conditions (light orange, dark orange) during the last portion of
853 the reach. The inset displays the corresponding average trajectory and three standard deviation of lateral
854 hand position for each condition. **C**) Visuomotor feedback response (y-axis) over time (x-axis), where 0 ms
855 corresponds to the initial cursor jump. Vertical lines separate involuntary (180 - 230 ms), semi-involuntary
856 (230 - 300 ms), and voluntary (300 - 400 ms) visuomotor feedback responses. Muscle activity (y-axis) over
857 normalized time (x-axis) for **(D)** brachioradialis, **(E)** pectoralis, **(F)** biceps short head, **(G)** triceps lateral
858 head, **(H)** rear deltoid, and **(I)** triceps long head muscles. The participant displayed greater muscular
859 activity in the amplified conditions (blue, dark blue) relative to the non-amplified conditions (orange, dark
860 orange). Muscular co-contraction (y-axis) over normalized time (x-axis) for the **J**) monoarticular elbow
861 muscles (brachioradialis and triceps lateral head), **K**) monoarticular shoulder muscles (pectoralis and rear
862 deltoid), and **L**) biarticular muscles (biceps short head, triceps long head). The participant had greater
863 muscular co-contraction in the amplified conditions (light blue, dark blue) compared to the non-amplified
864 conditions (light orange, dark orange). Shaded areas represents ± 1 standard deviation.



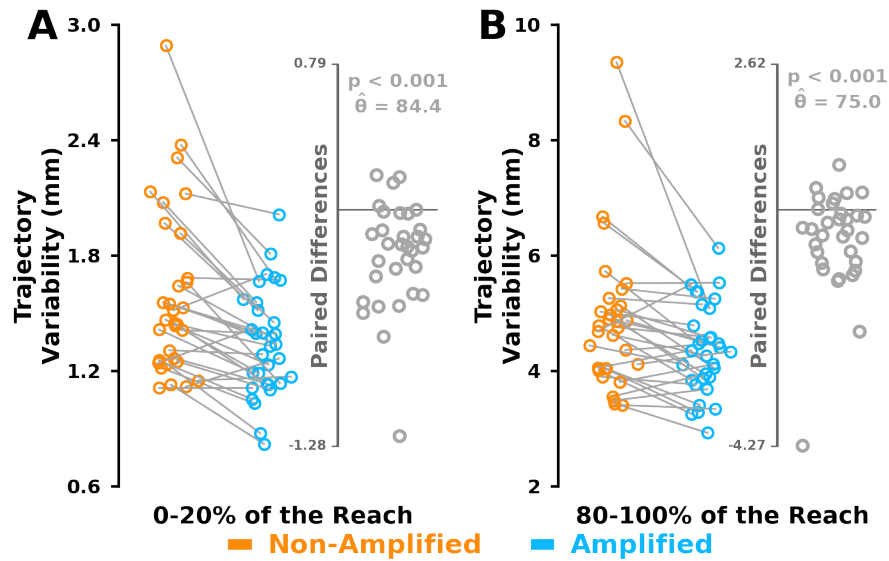
865

866 **Figure 3: Group Behaviour.** Average participant behaviour for each condition. **A)** Hand velocity (y-axis)
 867 over normalized time (x-axis), where 0% and 100% (vertical grey lines) respectively correspond with the
 868 start and end of the reach. **B)** Trajectory variability (y-axis) over normalized time (x-axis). Participants had
 869 lower trajectory variability in the amplified conditions compared to the non-amplified conditions during

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870 0-20% and 80-100% of the reach. **C**) Visuomotor feedback response (y-axis) over time (x-axis), where 0 ms
871 corresponds to the initial cursor jump. Vertical lines separate involuntary (180 - 230 ms), semi-involuntary
872 (230 - 300 ms), and voluntary (300 - 400 ms) visuomotor feedback responses. There were no differences
873 in visuomotor feedback responses between conditions. Muscle activity (y-axis) over normalized time
874 (x-axis) for **(D)** brachioradialis, **(E)** pectoralis, **(F)** biceps short head, **(G)** triceps lateral head, **(H)** rear
875 deltoid, and **(I)** triceps long head muscles. Muscular co-contraction (y-axis) over normalized time (x-
876 axis) for the **(J)** monoarticular elbow muscles (brachioradialis and triceps lateral head), **(K)** monoarticular
877 shoulder muscles (pectoralis and rear deltoid), and **(L)** biarticular muscles (biceps short head, triceps long
878 head). Participants had greater elbow and shoulder co-contraction in the amplified conditions (light blue,
879 dark blue) compared to the non-amplified conditions (light orange, dark orange) throughout the reach.
880 Participants also displayed an increase of biarticular co-contraction during the latter portion of the reach.
881 Shaded areas represent ± 1 standard error.

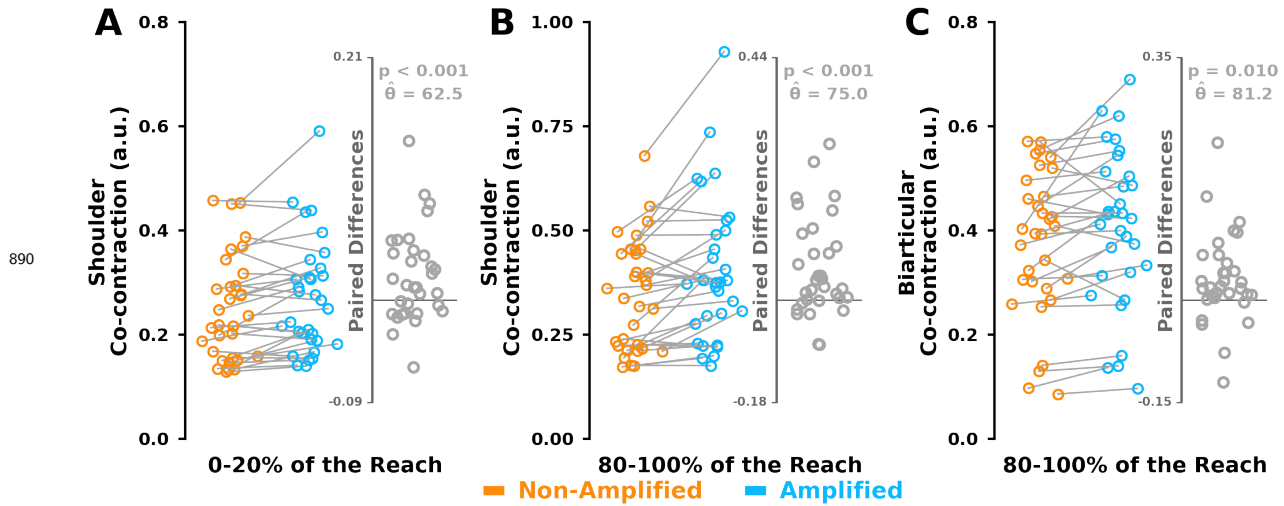
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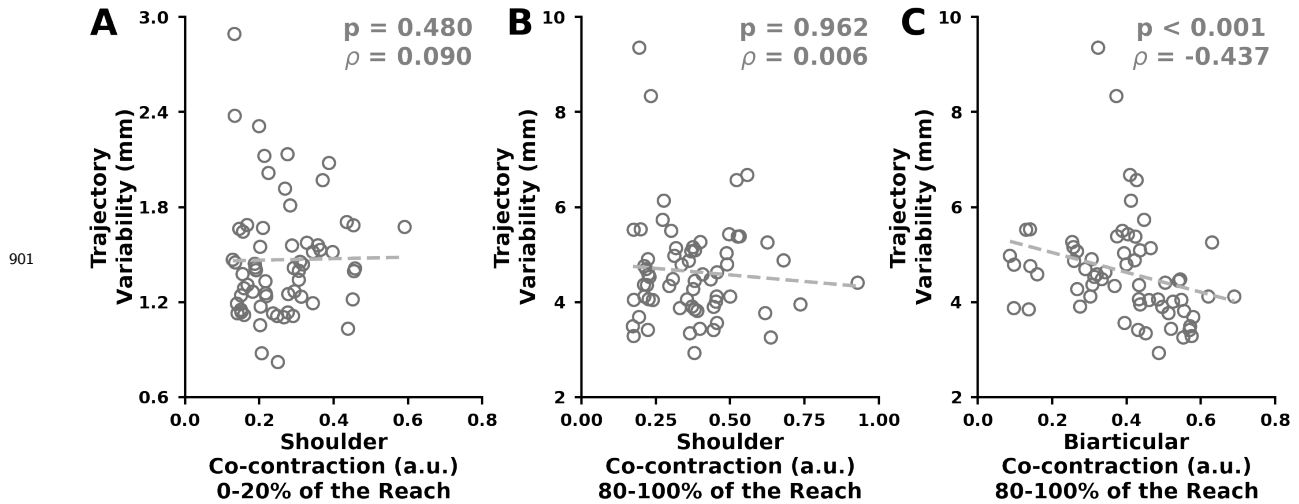
883 **Figure 4. Trajectory Variability:** Trajectory variability (y-axis) for the non-amplified (orange) and amplified
884 (blue) conditions during (A) 0-20% of the reach, and (B) 80-100% of the reach for each participant (open
885 circles). A,B The insets display the corresponding paired differences (y-axis) between the non-amplified
886 and amplified conditions of each participant (open grey circles). Here the horizontal grey line represents
887 a paired difference of 0. Participants had significantly lower trajectory variability in amplified conditions
888 relative to the non-amplified conditions during (A) 0-20% of the reach ($p < 0.001$) and (B) 80-100% of the
889 reach ($p < 0.001$).

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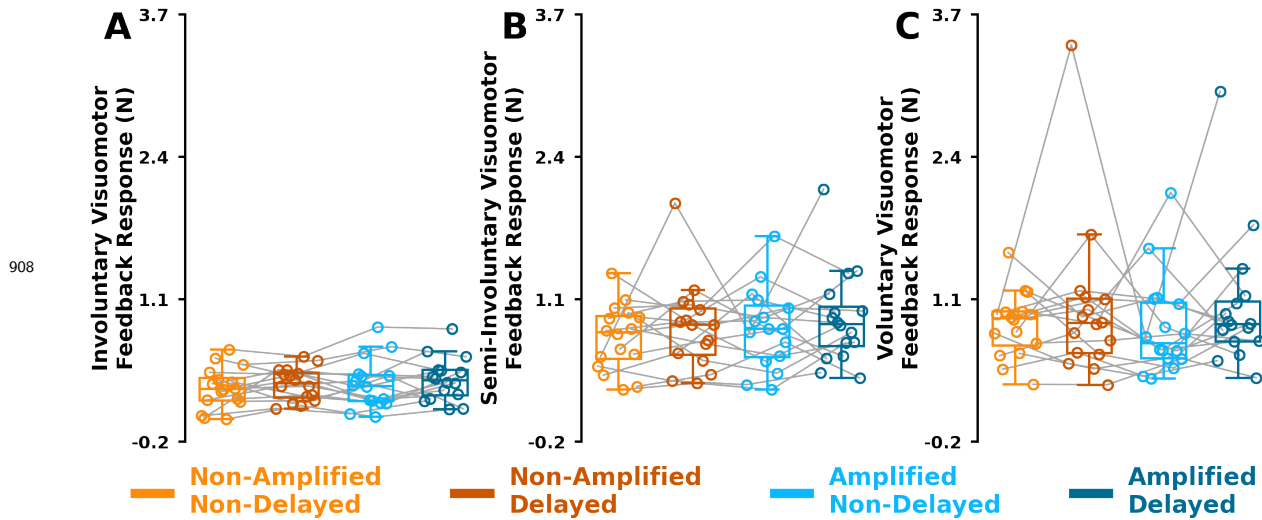
891 **Figure 5. Muscular Co-contraction:** Shoulder co-contraction (y-axis) for the non-amplified (orange) and
 892 amplified (blue) conditions during **(A)** 0-20% of the reach, and **(B)** 80-100% of the reach for each participant
 893 (open blue or orange circles). **(C)** Biarticular co-contraction (y-axis) for the non-amplified (orange) and
 894 amplified (blue) conditions during 80-100% of the reach. **A,B,C)** The insets display the paired differences
 895 (y-axis) between the non-amplified and amplified conditions for each participant (open grey circles). The
 896 horizontal grey line represents a paired difference of 0. Participants had significantly greater shoulder
 897 co-contraction in the amplified conditions relative to the non-amplified conditions during **(A)** 0-20% of
 898 the reach ($p < 0.001$) and **(B)** 80-100% of the reach ($p < 0.001$). **(C)** Participants also had greater biarticular
 899 co-contraction in the amplified conditions relative to the non-amplified conditions during 80-100% of the
 900 reach ($p = 0.010$).

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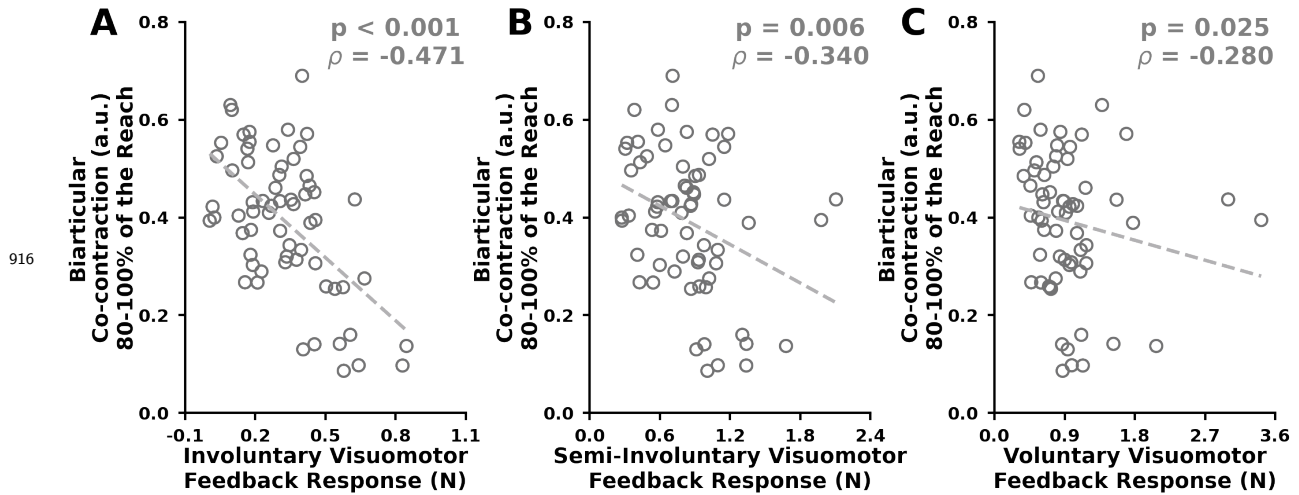
902 **Figure 6. Relationship between Muscular Co-contraction and Trajectory Variability** **A)** Trajectory vari-
 903 ability (y-axis) and shoulder co-contraction (x-axis) during **A)** 0-20% of the reach, and **B)** 80-100% of the
 904 reach. **C)** Trajectory variability (y-axis) and biarticular co-contraction (x-axis) were negatively correlated (p
 905 < 0.001 , $\rho = -0.437$) during 80-100% of the reach, suggesting that greater biarticular co-contraction may
 906 have been used to decrease trajectory variability during the latter portion of the reach. Dashed grey lines
 907 show the line-of-best-fit.

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909 **Figure 7. Visuomotor Feedback Response:** Visuomotor feedback response (y-axis) for each condition
 910 (x-axis) during the **A**) involuntary (180 - 230 ms), **B**) semi-involuntary (230 - 300 ms) and **C**) voluntary
 911 (300 - 400 ms) time windows. Circles and connected grey lines represent individual participants. Colour
 912 represents the experimental condition. Involuntary, semi-voluntary, and voluntary visuomotor feedback
 913 responses did not change due to the experimental conditions ($p > 0.05$ for all comparisons). These results
 914 suggest that the nervous system does not modulate visuomotor feedback gains to regulate trajectory
 915 variability. Box and whisker plots show 25%, 50% and 75% quartiles.

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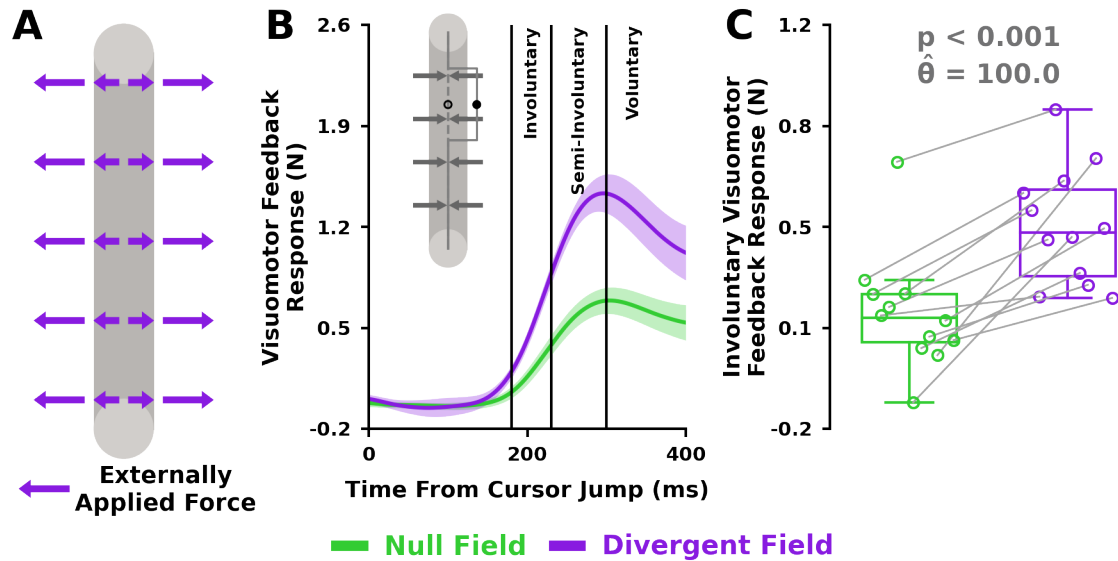


917 **Figure 8. Relationship between Visuomotor Feedback Responses and Muscular Co-contraction:** Biarticular co-contraction during 80-100% of the reach was negatively related to **A**) involuntary ($\rho = -0.471$, $p < 0.001$), **B**) semi-involuntary ($\rho = -0.340$, $p = 0.006$), and **C**) voluntary ($\rho = -0.280$, $p = 0.025$) visuomotor feedback responses (x-axes). These results suggest that there is an indirect interplay between muscular co-contraction and visuomotor feedback responses. The dashed grey line shows the line-of-best-fit.

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923 **Figure 9. Control Experiment:** **A)** We recruited 12 participants to participate in a second experiment to
 924 verify that our experimental setup can capture changes in visuomotor feedback responses. Participants
 925 experienced two experimental conditions: i) a null field (green) without externally applied forces, and ii) a
 926 divergent force field (purple). For the divergent force field, externally applied forces scaled proportionally
 927 with the lateral distance of the hand from the centerline of the visual channel. We interweaved visuomotor
 928 feedback probe trials to measure involuntary, visuomotor feedback responses. **B)** Visuomotor feedback
 929 response (y-axis) over time (x-axis), where 0 ms corresponds to the initial cursor jump. Solid lines represent
 930 average visuomotor feedback responses for each condition. Shaded regions represent ± 1 standard error.
 931 Vertical lines separate involuntary (180 - 230 ms), semi-involuntary (230 - 300 ms), and voluntary (300 -
 932 400 ms) visuomotor feedback responses. **C)** Average involuntary, visuomotor feedback response (y-axis)
 933 for each condition (x-axis). Circles and connected grey lines represent individual participant data. Box
 934 and whisker plots show 25%, 50% and 75% quartiles. As shown previously (Franklin and Wolpert, 2008),
 935 we found a significant increase in the involuntary visuomotor feedback response in the divergent field
 936 compared to the null field ($p < 0.001$). Thus, we were able to confirm that our exoskeleton robot and
 937 chosen force channel parameters (stiffness and damping coefficients) were able to capture changes in
 938 involuntary, visuomotor feedback responses.