Are online corrections to visual targets really a distinct class of movement?

David Y. Mekhaiel[1,2,3], Melvyn A. Goodale[2,3,4], Brian D. Corneil[2,3,4,5]

[1] Graduate Program in Neuroscience, Western University, London, Ontario, Canada.
[2] Western Institute for Neuroscience, Western University, London, Ontario, Canada.
[3] Department of Psychology, Western University, London, Ontario, Canada.
[4] Department of Physiology and Pharmacology, Western University, London, Ontario, Canada.
[5] Robarts Research Institute, London, Ontario, Canada.

*Corresponding Author: Brian D. Corneil, bcorneil(at)uwo.ca

Number of pages: 46
Number of figures: 10

Keywords:

Online correction; Express visuomotor response; Reaching; Electromyography; Force

Abbreviations:

BF	Bayes factor
EMG	Electromyography
EVR	Express visuomotor response
F-RT	Force reaction time
PPC	Posterior parietal cortex
SC	Superior colliculus
TMS	Transcranial magnetic stimulation

Summary

Humans have a remarkable capacity to adjust reaching movements rapidly and accurately when visual targets jump to a new location. The short latency of such online corrections has led to the hypothesis that they constitute a distinct class of movement and arise from an 'automatic pilot' that is selectively engaged only during ongoing movements. However, concrete evidence for this hypothesis is scarce.

Here, we test this idea by measuring muscle recruitment, force, and kinematics in a jumping target reaching task. In separate blocks of trials, participants were instructed to respond to target jumps by (1) following the jumped target, (2) stopping the on-going movement, or (3) ignoring the jumped target. This allowed us to establish the automaticity and timing of responses to target jumps and to compare such measures to the original reaching movement initiated from rest.

We find that the earliest phase of muscle recruitment elicited by the jumped target corresponds to a subcortical reflex, beginning at ~80ms and ending by ~120ms, preceding the onset of voluntary recruitment at ~130ms. This reflex inexorably drives a reaching adjustment towards the new target in all three blocks; it is only somewhat reduced in the 'stop' and 'ignore' blocks. Critically, this earliest phase of muscle recruitment was also present at the exact same latency (80ms) for the original reaching movement initiated from rest. Thus, rather than supporting the model of online corrections as distinct class of movement that is mediated by an 'automatic pilot,' our results suggest that all reaches, whether adjusted in mid-flight or initiated from rest, arise from a common nested control system featuring subcortical and cortical components whose influence can be strategically preset by task demands.

Introduction

It has long been recognized that adjustments in movements in response to suddenly displaced targets, often termed ‘online corrections,’ can be initiated at shorter latencies (~100ms) than movements initiated from rest (~130ms; Brenner & Smeets, 1997; Brière & Proteau, 2011; Carlton, 1981; de Brouwer & Spering, 2022; Fautrelle et al., 2011; Goodale et al., 1986; Oostwoud Wijdenes et al., 2011; Paulignan, Jeannerod, et al., 1991; Paulignan, MacKenzie, et al., 1991; Prablanc & Martin, 1992; Reichenbach et al., 2009). In fact, the short-latency and inexorable stimulus-driven nature of the initial phases of these adjustments are frequently noted as hallmarks differentiating online corrections as a distinct class of movement. These differences are attributed to a rapid 'automatic pilot,' which exclusively modifies movement plans mid-flight but is not engaged during movement from rest (for review, see Gomi, 2008). Debate persists regarding the neural correlates of online corrections, with theories suggesting that processing through either the posterior parietal cortex (PPC; Desmurget et al., 1999; Pisella et al., 2000) or the superior colliculus (SC; Day & Brown, 2001; Reynolds & Day, 2012) instantiates the 'automatic pilot.' Regardless of the exact neural underpinnings, it seems curious that the brain would have a dedicated system that is utilized only in the case of online corrections; if such a rapid system exists, why is it not used for movements from rest? And, what determines the stimulus-driven nature of the first phase of online corrections (Day & Lyon, 2000; Striemer et al., 2010)?

We designed an experiment to study and compare online corrections and movements from rest, using electromyography (EMG) to characterize the timing and pattern of muscle recruitment that precede both types of movement. We also measured reach force using force

transducers in the reach manipulandum. Across three separate blocks, participants performed different reach adjustments in response to a target that jumped unpredictably on a third of the trials. Importantly, all blocks featured identical visual stimuli, ensuring that observed differences in muscle recruitment and behaviour stemmed solely from the task set.

In one block, participants were instructed to 'Follow' the target jump by performing an online correction. This allowed us to compare the timing of muscle recruitment leading up to movements initiated from rest (during the initial reach) and online corrections (during the reach adjustment); an 'automatic pilot' predicts earlier recruitment during online corrections. In another block, participants were instructed to 'Stop' their hand mid-reach if the target jumped. Although some studies suggest that muscle recruitment for action-stopping occurs later (~140ms; Atsma et al., 2018; Raud et al., 2020; Raud & Huster, 2017) than for online corrections, other studies have suggested that action-stopping is produced by the same rapid neural network (Novembre & Iannetti, 2021). If so, then the first phase of muscle recruitment in the 'Follow' and 'Stop' blocks should be linked to the different goals of these tasks. In another block, participants were instructed to 'Ignore' the target jump and continue their reach towards the original target location. This block allowed us to test the automaticity of the muscle activity underlying online corrections.

Our results indicate that the earliest phase of muscle recruitment elicited by the jumped arises from a subcortical reflex that produces express visuomotor responses (EVR; formerly 'stimulus-locked response'; Corneil et al., 2004; Pruszynski et al., 2010) spanning an interval from 80-120ms after target jump, prior to the onset of voluntary recruitment at ~130ms. Remarkably, the EVR defied task set by inexorably driving an online correction towards the new

target in all three blocks; it was only somewhat reduced in the ‘Stop’ and ‘Ignore’ blocks. EVR magnitude was correlated with reaction time across all blocks, eliciting short-latency force and kinematic online corrections towards the target appropriately in the 'Follow' block and erroneously in the other two blocks. Taken together, the similarity of the EVR across all blocks explains why online corrections are inexorably drawn towards displaced targets (Gritsenko & Kalaska, 2010; Striemer et al., 2010).

Upon comparing the reaches initiated from rest and the online corrections, we found that the timing of both the EVR and forces applied to the manipulandum were virtually identical. However, online corrections had much lower movement reaction times than movements initiated from rest, likely because forces rose faster, and hence overcame the arm’s inertia sooner, during online corrections compared to movements from rest. Thus, rather than supporting the idea of an ‘automatic pilot’ that is exclusively engaged during online corrections, our results point to a common nested control system featuring subcortical (EVR) and cortical (voluntary muscle activity) components that can be similarly active during both online corrections and reaches from rest. Our findings call into question the classification of online corrections as a distinct class of movement. This idea was originally based on the differences in the reaction times of online corrections versus movements initiated from rest (Carlton, 1981; Soechting & Lacquaniti, 1983), but our results show that such apparent differences disappear when closely examining the timing of muscle recruitment and applied forces.

Results

Overview

During intermixed blocks of trials, participants were instructed to adjust their ongoing reaches differently in response to the exact same visual stimuli by performing three types of reach adjustments. Targets initially appeared randomly in one of two locations (T1 or T2). In a third of trials, the target jumped to the other location once the participant's hand left the startpoint (fig. 1C). If the target jumped (fig. 1E) during 'Follow' blocks, participants were instructed to reach towards the NEW target, (fig. 1F) during 'Stop' blocks, they were instructed to stop the ongoing movement, (fig. 1G) and during 'Ignore' blocks, they were instructed to reach towards the OLD target.

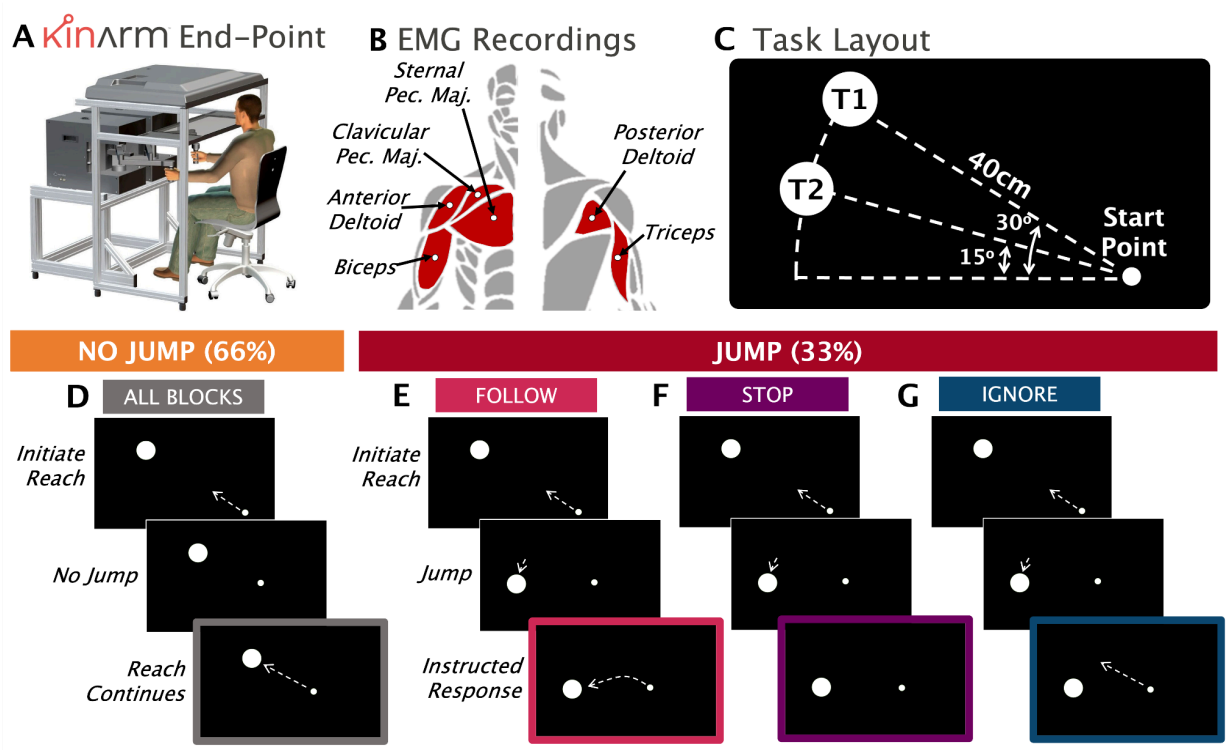

Figure 1. Experimental apparatus & task: *(A) Participants made reaches with their right arm in a Kinarm End-Point Lab. (B) Surface EMG activity was recorded from six right arm muscles. (C) The task layout included a startpoint and two potential targets (T1 and T2). (D-G) Task timelines.*

Below, we report kinematic and force measures obtained from the Kinarm manipulandum (fig. 1A) and describe how error rate and reaction time of force deviation varied across different blocks. We then report surface EMG signals recorded from arm and shoulder muscles (fig. 1B) to investigate how the task set influences the EVR and how the EVR relates to reaction time of force deviation. Finally, we compare the latency of the EVR, mean force onset, and mean kinematic onset during the initial reach (in response to the initial target) and during the online correction (in response to the target jump).

Analysis of performance

We first quantified the error rate and reach trajectory to ensure participants followed block instructions. To clarify, error trials were *not excluded* from future analyses. Given the different instructions in each of the three block types, the criteria for determining an error differed for each block (for exemplar, see fig. 2A). Error trials were defined as the participant reaching the original target in 'Follow' blocks, reaching either target during 'Stop' blocks, or reaching the new target in 'Ignore' blocks. Errors, although defined differently, were highest in the 'Stop' blocks (33.6%), followed by the 'Follow' (13.2%), and 'Ignore' blocks (5.2%; fig. 2C). This largely indicates that participants were at least attempting to perform the task as instructed. It also suggests that countermanding during the 'Stop' condition was the least automatic of the three reach adjustments. Errors were slightly higher when the target jumped away from the participants (T2 to T1; 21.5%) compared to jumps towards the participant (T1 to T2, 13.1%, fig. 2B), perhaps reflecting a marginally more difficult adjustment (fig. 2B).

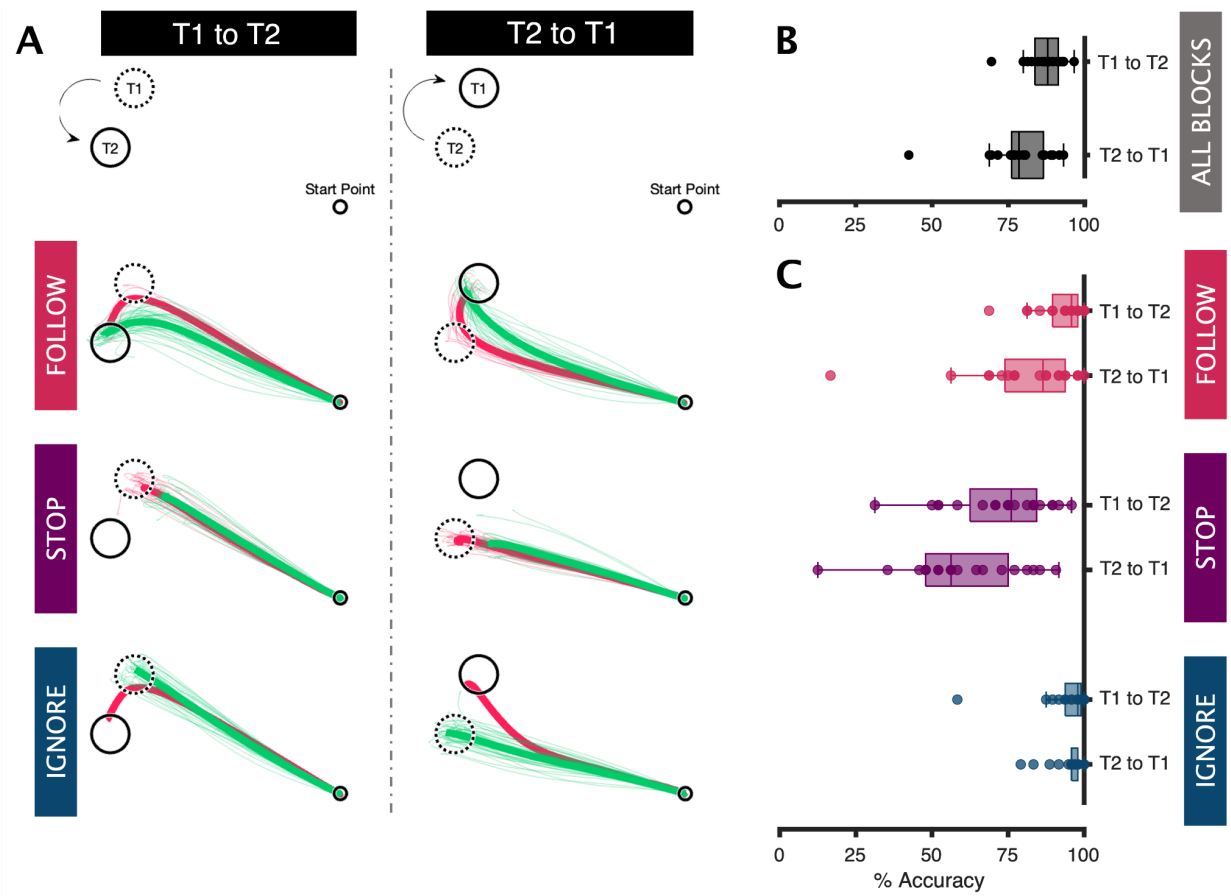

Figure 2. Exemplar reach trajectories & group error rates: *(A) Reach trajectories for correct (green) and error (red) jump trials for the exemplar participant (p6). Error rate by (B) direction of jump and (C) block instruction. Error rate was determined using criteria unique to each block type.*

Initial online correction observed regardless of instruction

We then looked at force and reaction times to compare responses across blocks. To make interpretation of the force and kinematic data easier, we rotated the workspace by -157.5° around the centre of the startpoint (fig. 3A). Doing so aligns the main force moving the arm towards the average position of the two targets with the x-axis and the main force moving the arm between the two targets with the y-axis. Looking first at the force trajectories during the 'Follow' block, we find that the force trajectories appear to diverge in the y-dimension just near

the end of the EVR epoch (~110ms; fig. 3B). At this point, there does not appear to be force deviation in the x-dimension, meaning participants did not notably slow down their outbound movement following a target jump. We observed similar but smaller force deviations in the y-dimension both in the 'Stop' and 'Ignore' blocks, emphasizing a seemingly reflexive deviation in reach force toward the jumped target. In the 'Stop' block only, there was also a clear force deviation in the x-dimension starting at a latency of ~150ms, ~40ms later than the onset of online reach corrections (~110ms). Therefore, in the 'Stop' block, participants only stopped their ongoing reaching movement after an initial deviation toward the jumped target.

To better characterize these observed differences, we then investigated how the target jump impacted force development over time. We used a Bayesian paired t-test to compare the mean Euclidean deviation from control (mean no jump) for both jump and no jump conditions for each time point. In 'Follow' blocks, for each jump direction, there begins to be a 'strong' likelihood of divergence (*BF* > 10) at 140ms (T1 to T2) and 134ms (T2 to T1) and in 'Stop' blocks at 151ms (T1 to T2) and 303ms (T2 to T1). In 'Ignore' blocks, trajectories strongly diverged in only one jump direction (T2 to T1), starting at 321ms. These results demonstrate that our task elicited significant short latency corrections in both jump directions in both the 'Follow' and 'Stop' blocks. Furthermore, countermanding or action stopping appears to begin later than online correction, at a similar latency to voluntary reaching from rest.

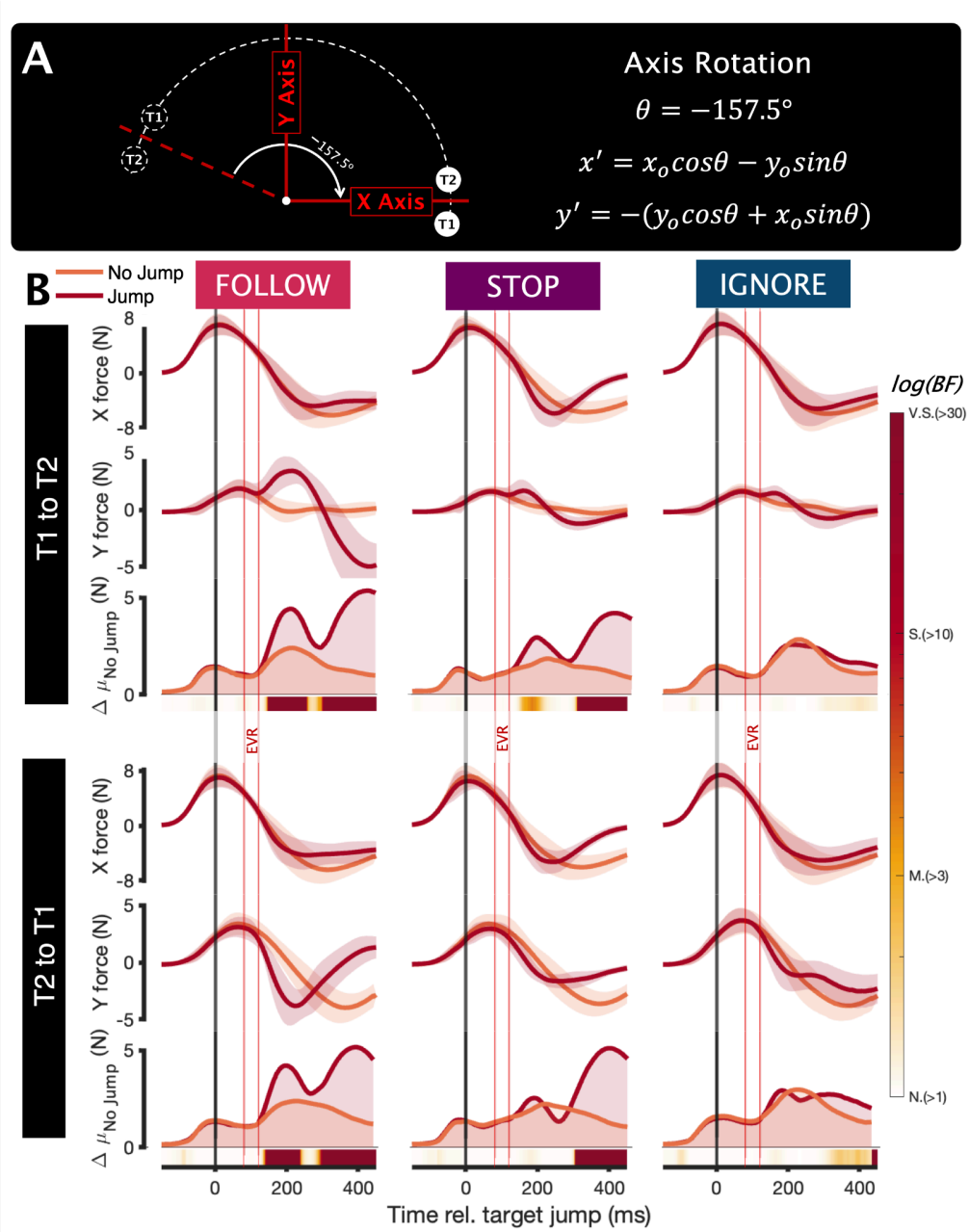

Figure 3. Group force over time: *(A) Alignment of force data to isolate movement between startpoint and targets (x-dimension) and deviation towards each of the two targets (y-dimension). (B) Mean group force trajectories, mean Euclidean deviation from mean no jump trajectory, and Bayesian analysis. For Y and X force trajectories, boundaries indicate standard deviation. BF heatmap denotes the likelihood of the model that jump trials exhibit more deviation from the mean no jump force trajectory, than no jump trials. BF heatmap is qualified by the following standard thresholds (Jeffreys, 1998): N.(> 1) = Negligible, M.(> 3) = Moderate, S.(> 10) = Strong, V.S.(> 30) = Very Strong. EVR epoch (80-120ms) is denoted by vertical red lines to demonstrate the onset of EVR responses (first line) and the onset of voluntary muscle activity (second line).*

To better characterize the aforementioned small deviations in the force trajectories, we next investigated how force reaction times (F-RT) differed across conditions. F-RT denoted the first time point in each trial where the force trajectory was more than one standard deviation away from the mean force trajectory of the complimentary no-jump condition. Therefore, here F-RT is defined agnostically, rather than specifically reflecting block goals. For example, in 'Stop' blocks a F-RT could indicate either a correct stopping action or an erroneous online correction. Since this method of reaction time detection is likely prone to false positives, especially during an ongoing movement, we also conducted the same analysis for no jump trials to serve as control.

Comparing the distributions of F-RTs in jump and no jump trials, we found that we began observing more 'F-RTs' in jump conditions relative to no jump conditions starting at ~100ms after target jumps during 'Follow' blocks (fig. 4). Looking at how those reactions impacted movement, we found that for all blocks the earliest F-RTs (100-150ms) typically resulted in acceleration towards the jumped target (below the control line). This was most prominent in the ‘Follow’ and ‘Stop’ blocks, and to a lesser degree in the T2 to T1 jumps during ‘Ignore’ blocks. While this is expected in 'Follow' blocks, this is counter to the task goals in both the 'Stop' and 'Ignore' blocks. This observation reiterates that online corrections (at least within our task) seem to have a reflexive component that cannot be arbitrarily suppressed by task set.

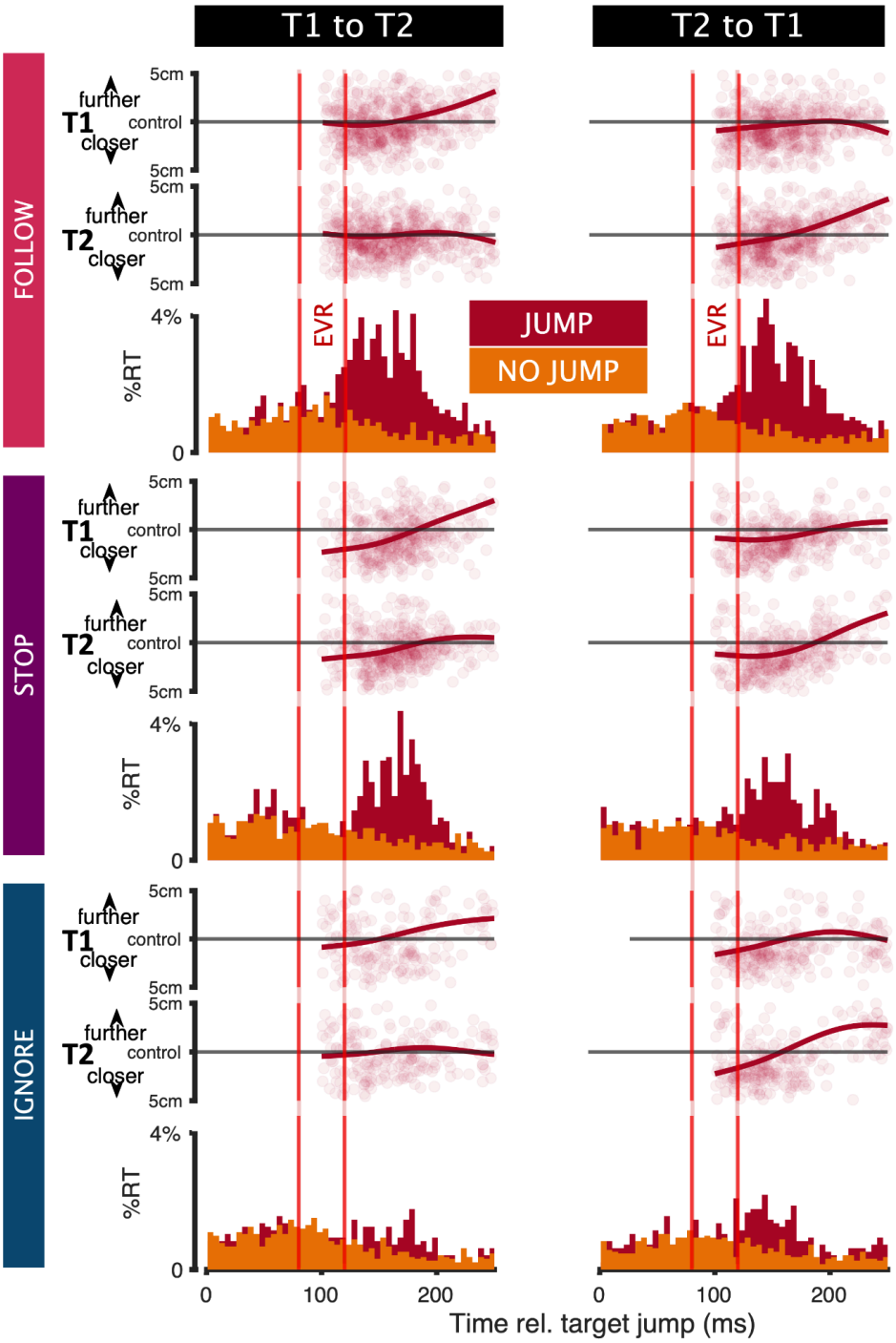

Figure 4. F-RT distribution and deviation: *Histograms of all F-RTs for all participants (5ms bins) for both jump and no jump conditions as a percentage of trial type. F-RTs determined as the first instance force trajectory deviates more than 1 standard deviation from the corresponding no jump (control) condition. Scatter plots denote the Euclidean distance on an individual trial basis relative to each of the two targets (T1 & T2) 20ms following F-RT, normalized based on the distance to each target for the corresponding mean no jump condition.*

EVR present in all three tasks

Next we examined single-trial EMG recordings, to better understand the changes in muscle recruitment related to the profiles of reach forces. We do this by constructing 'heat maps' that depict the magnitude of muscle activity on each trial relative to the timing when the hand left the start point in response to the initial target appearance. This is the time point where the target jumps during jump trials (for exemplar, see fig. 5). When represented in this way, a distinct band of muscle activity during the EVR epoch time (80-120ms) becomes obvious, consisting of a stimulus-locked increase (when T1 jumps to T2) or decrease (when T2 jumps to T1) in muscle activity. This is the EVR (Pruszynski et al., 2010), as its timing is more aligned to stimulus onset rather than movement onset, and since it facilitates arm movement towards the new target. In our exemplar participant, these directional changes in muscle activity, with pectoralis activity either increasing or decreasing for target jumps from T1 to T2 or T2 to T1, respectively, begin ~80ms after the target jump. Like online motor corrections (Striemer et al., 2010), EVRs are known to be spatially locked to stimulus location independent of task (Contemori et al., 2023; Gu et al., 2016). The consistency of the EVR across blocks strongly implies that the initial online corrections observed across blocks (fig. 4), are attributable to the EVR since it is the only distinct phase of muscle activity occurring prior to those short-latency corrections.

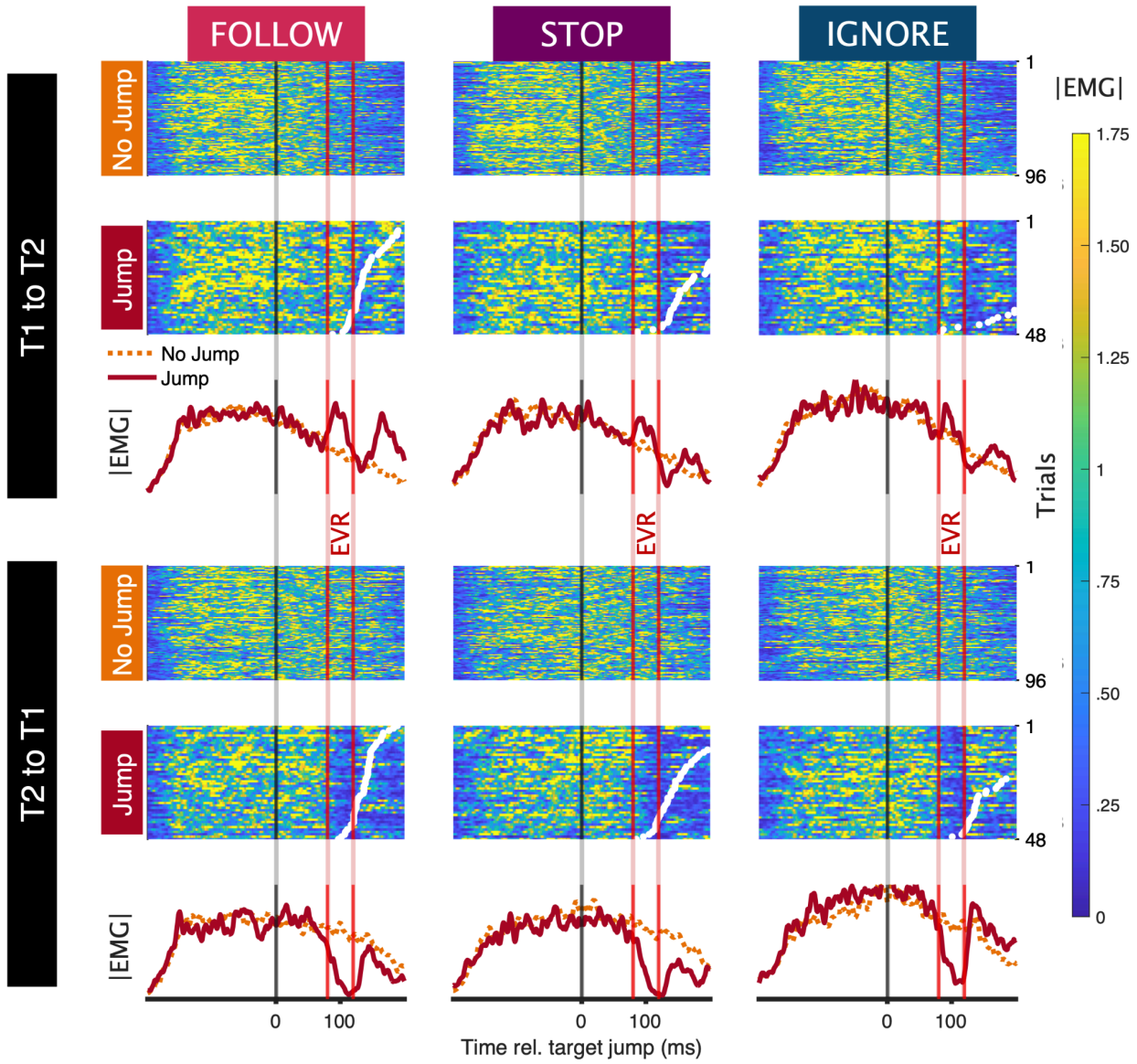

Figure 5. EMG exemplar: *Single trial heatmaps and means of normalized EMG of the right sternal head of pectoralis major of the exemplar participant (p6). Jump trials are organized by F-RT, as denoted by the white dots. EVR epoch (80-120ms) is denoted by vertical red lines.*

Instruction modulates EVR magnitude but not timing

Next, we sought to determine if the magnitude of the EVR differs across block types. As seen in the mean EMG plots (fig. 6A), muscle activity for no jump and jump conditions deviates across all muscles starting at ~80ms. Notably, the EVR magnitude typically changes in the same

direction as the subsequent muscle activity during the 'Follow' blocks, therefore facilitating arm movement in the direction of the new target. This means that across the two jump directions (T1 to T2 vs. T2 to T1), we observe an inversion of the direction of the EVR relative to the control no jump condition.

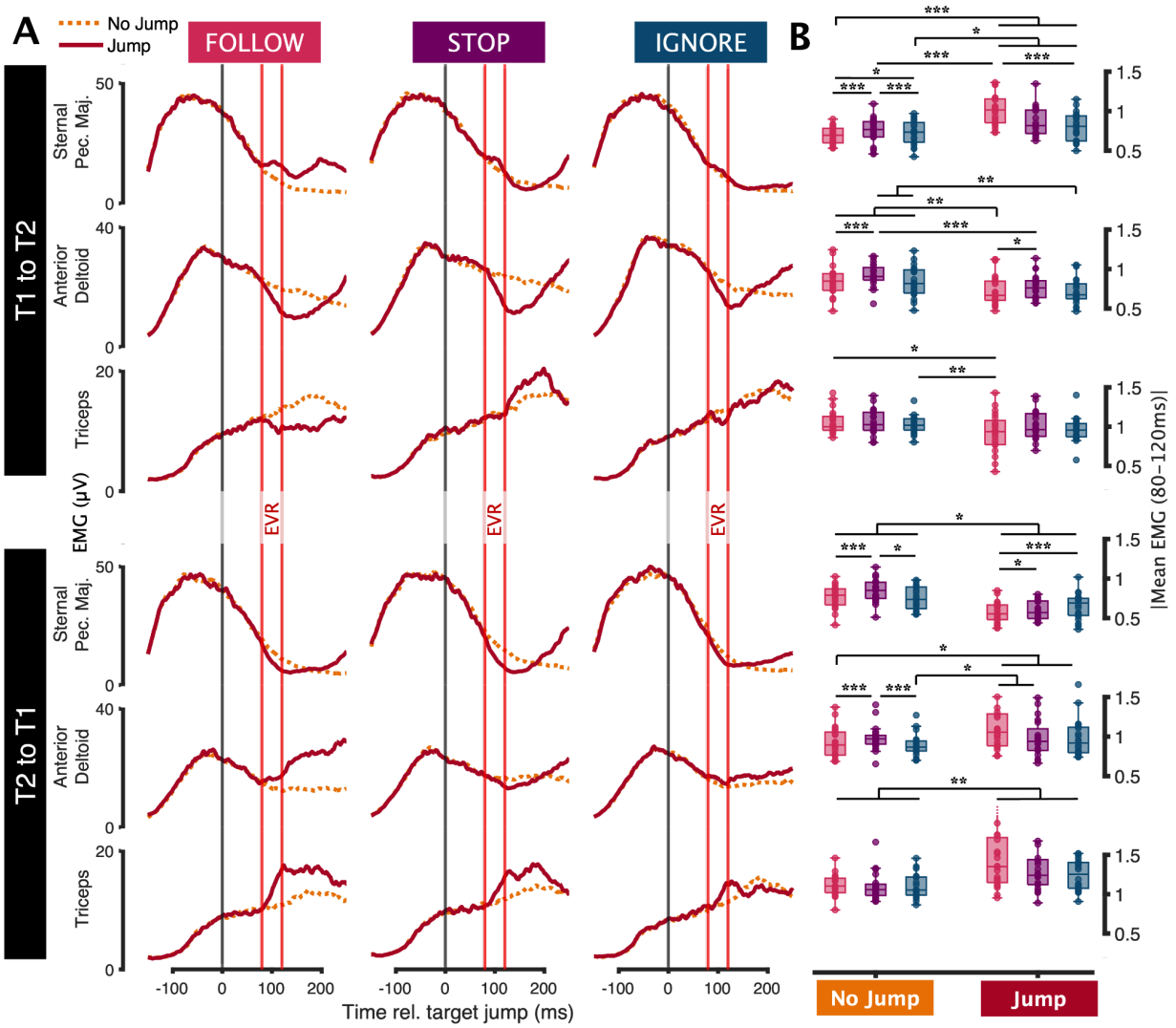

Figure 6. Group EMG: *(A) Mean EMG of all participants across three muscles, for both no jump and jump conditions, including error trials. EVR epoch (80-120ms) is denoted by vertical red lines. (B) Mean EMG magnitude during the EVR epoch. Asterisks indicate significant findings using a contrast of estimated marginal means based on a linear mixed effects model. Due to the size of the dataset, degrees of freedom were estimated asymptotically. The Tukey method was used to adjust p-values. Grouped significance bars denote the least significant p-value.*

Using a linear mixed effects model, we then compared the effects of conditions on muscle activity during the EVR epoch. The model included a four-way interaction between instruction, location of the initial target, target jump, and muscle, with random intercepts for each participant to account for individual variability. Pairwise comparisons were performed on the estimated marginal means to identify significant differences between conditions.

Two statistical patterns emerge from the analysis of mean EMG activity during the EVR epoch (80-120ms; fig. 6B). Firstly, there is a consistently significant difference in EMG between no jump and jump conditions. When arm adduction is required (T1 to T2), adductors exhibit significantly higher activity during jump conditions (i.e. 'Follow,' sternal pec. maj.: $z = 10.28$, $p < .001$) and abductors exhibit significantly lower activity (i.e. 'Follow,' triceps: all $z = -3.33$, $p < .05$). The inverse is true when arm abduction is required (T2 to T1). This occurs across all instruction types to varying degrees, even in 'Ignore' blocks which necessitate no change in trajectory. Secondly, instruction has an impact on the magnitude of the EVR during jump trials, with participants exhibiting the most prominent EVR during 'Follow' jump trials compared to both other blocks (i.e. 'Follow' vs. 'Ignore', T1 to T2, sternal pec. maj.: $z = 3.97$, $p < .001$).

Stronger EVRs precede earlier online corrections

To investigate the relationship between the EVR and F-RT, we then calculated linear mixed models on an individual muscle basis to investigate the effects of EVR magnitude, conditions, and instruction on F-RT, with random intercepts for each participant to account for individual variability. We found that participants exhibited significantly faster F-RT in response to the target jump during 'Follow' blocks than during the other two tasks (all $z < -7.77$, $p < .001$; fig. 7A). This pattern is likely due to the EVR magnitude being significantly larger in the ‘Follow’

block followed by the ‘Stop’ and ‘Ignore’ blocks (fig. 5). Pairwise comparisons were performed on the estimated marginal means to identify significant differences between conditions. In line with the EVR pattern observed relative to no jump conditions (fig. 7B), EVR magnitude was predictive of F-RT. For example, an increase in the EVR in the sternal pectoralis major in the 'Follow' and 'Ignore' blocks was weakly, but significantly, correlated with lower F-RTs in T1 to T2 jumps (all $r^2 > .029$, $z < -2.91$, $p < .001$), with the inverse being true for T2 to T1 jumps for all instructions (all $r^2 > .032$, $z > 2.31$, $p < .05$), as is suggested by the direction of the EVR as seen in the group EMG analysis (fig. 7B). Although individually EVRs in any one muscle only accounted for a maximum 9.5% of variance in F-RT, a multiple regression analysis of the effect of the mean EVR magnitude of all six muscles on F-RT, found that on average EVR magnitude explained on average 24.7% of the variance in F-RT (fig. 7C). Collectively, these findings indicate that low-latency online corrections are predicated on the EVR and explain why online corrections toward the jumped target are initiated regardless of block instruction.

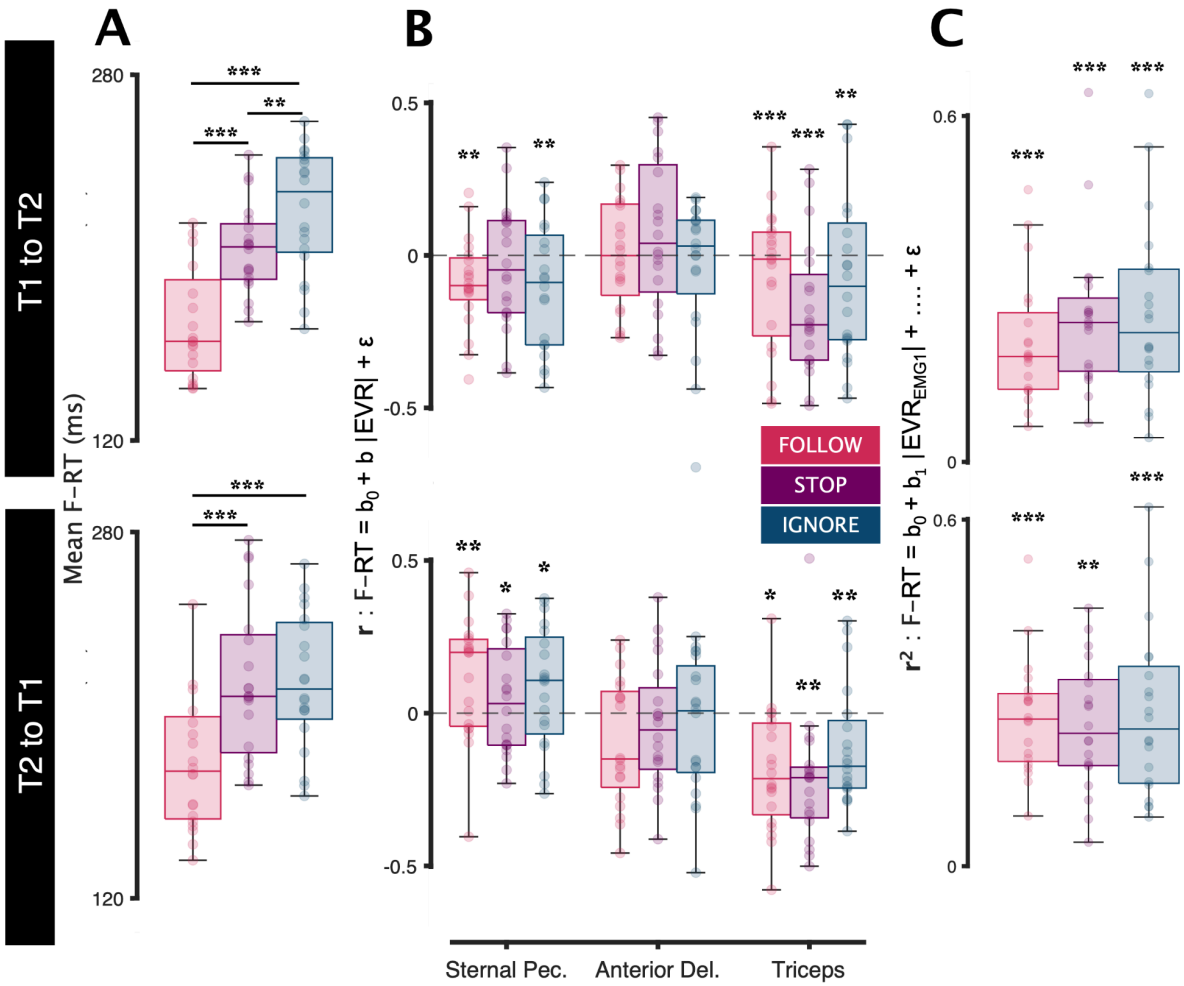

Figure 7. F-RT & EVR magnitude: *(A) Mean F-RT of jump trials for all participants, excluding trials where F-RT was too early (< 100ms) or did not occur. Asterisks indicate significant findings using a contrast of estimated marginal mean based on the linear mixed effects model used in figure 6. (B) Plotted correlation coefficients between F-RT and mean EMG magnitude during the EVR epoch (80-120ms). Asterisks indicate significant findings using a contrast of estimated marginal mean of the trends based on linear mixed effects models of individual muscles. Degrees of freedom were estimated using the kenward-roger method. The Tukey method was used to adjust p-values. (C) r^2 for multiple regression analyses of the effect of mean EVR magnitude of all six muscles on F-RT on an individual trial basis for each participant. Asterisks denote significant findings using a Fisher's combined probability test of the resulting p-values.*

The EVR does not support countermanding

Although we observed that low-latency force changes (100:150ms) typically resulted in kinematic deviation towards the jumped target across all blocks (fig. 4), we also observed that

EVR magnitude correlates with F-RT independent of instruction and that EVR magnitude differs between 'Follow' blocks and 'Stop' blocks (fig 6). This left open the possibility that the EVR may be contributing to countermanding actions in the ‘Stop’ block. To investigate this, we first compared EMG values across the three instruction types. We found that EMG activity between the 'Follow' and 'Stop' block did not significantly differ during the EVR epoch in any of the muscles recorded (BF < 3), with the earliest significant difference beginning at a minimum latency of 138ms (fig. 8A), after the EVR.

As with muscle activity, the initial portion of the force trajectory did not differ between 'Follow' and 'Stop' blocks, with differences only beginning to emerge ~150ms following target jump. Thus, the initial reaction correction beginning ~110ms after target jump is relatively similar on ‘Follow’ and ‘Stop’ blocks, moving the hand towards the jumped target. As an aside, this analysis revealed a slight increase in force in the 'Ignore' block relative to the 'Follow' block during the initial reach (well before the EVR) in one comparison (T2 to T1). This is likely because participants made slightly faster reaches from rest during the 'Ignore' block since they were primed to not respond to the target jump and therefore exercised less caution.

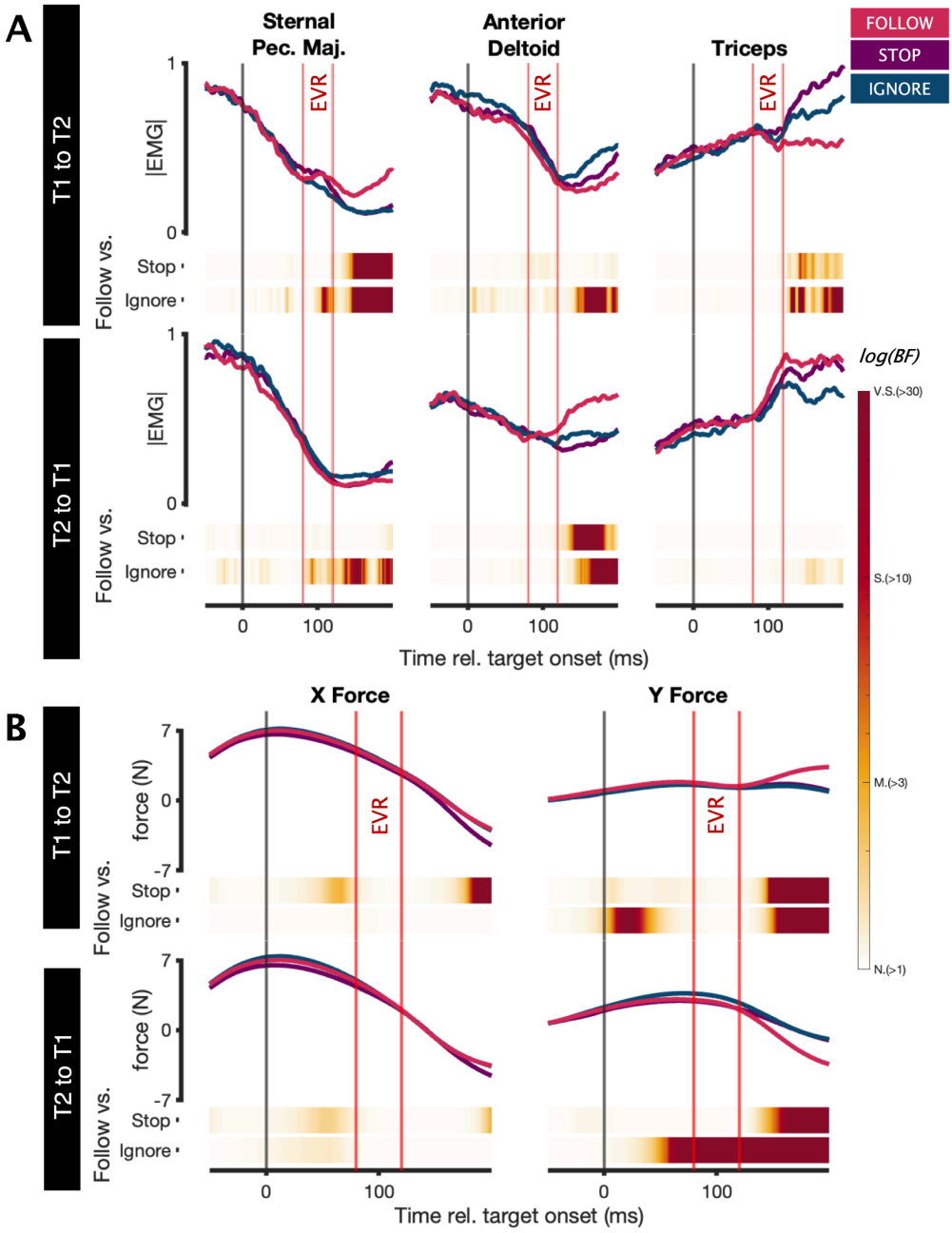

Figure 8. Comparison of jump conditions: *Comparison of (A) mean group EMG for three muscles and (B) mean force across jump conditions. BF heatmaps below each graph indicate comparisons between the 'Follow' block and each of the other two block types, based on Bayesian two-tailed paired t-test. BF is qualified by the following standard thresholds (Jeffreys, 1998): N(> 1) = Negligible, M(> 3) = Moderate, S(> 10) = Strong, VS(> 30) = Very Strong. EVR epoch (80-120ms) is denoted by vertical red lines.*

Similar force onset for online corrections and reaches from rest

Having demonstrated that EVR magnitude is correlated with online correction F-RT, we compared how force and EVR latencies during the initial reach compared with those observed in the online reach correction. To do this, we conducted two sets of analyses. The first replicated the methods of the seminal literature on online reach corrections, which have typically employed either visual inspection (Brenner & Smeets, 1997; Day & Brown, 2001; Paulignan, Jeannerod, et al., 1991; Paulignan, MacKenzie, et al., 1991) or various acceleration and velocity thresholds (Brière & Proteau, 2011; de Brouwer & Spering, 2022; Oostwoud Wijdenes et al., 2011; Prablanc & Martin, 1992; Reichenbach et al., 2009). Indeed, using a common threshold of $2m/s^2$ for acceleration onset, we identified delayed onsets in the initial reach of 202ms (to T1) and 195ms (to T1), compared to earlier onsets during online correction of 147ms (T1 to T2) and 145ms (T2 to T1), in line with previous findings (fig. 9).

We followed up with a second analysis, in which we employed a more objective and sensitive timewise Bayesian analysis to determine force onset in both the initial movement and the correction (fig. 9). To determine the latency of online reach corrections, we compared force data on jump vs no-jump trials. To determine the latency of the reach from rest, we compared force of the initial reach to baseline force (200ms prior). Using this analysis, we found that the latencies for force were nearly identical across both types of movements; 141ms (to T1) and 148ms (to T2) for reaching from rest compared to 146ms (T1 to T2) and 139ms (T2 to T1) for online correction (fig. 3). In short, although more traditional methods of identifying latency found that online corrections occur earlier than reaches from rest, changes in the force applied

to the manipulandum begin nearly simultaneously for online correction vs movements initiated from rest.

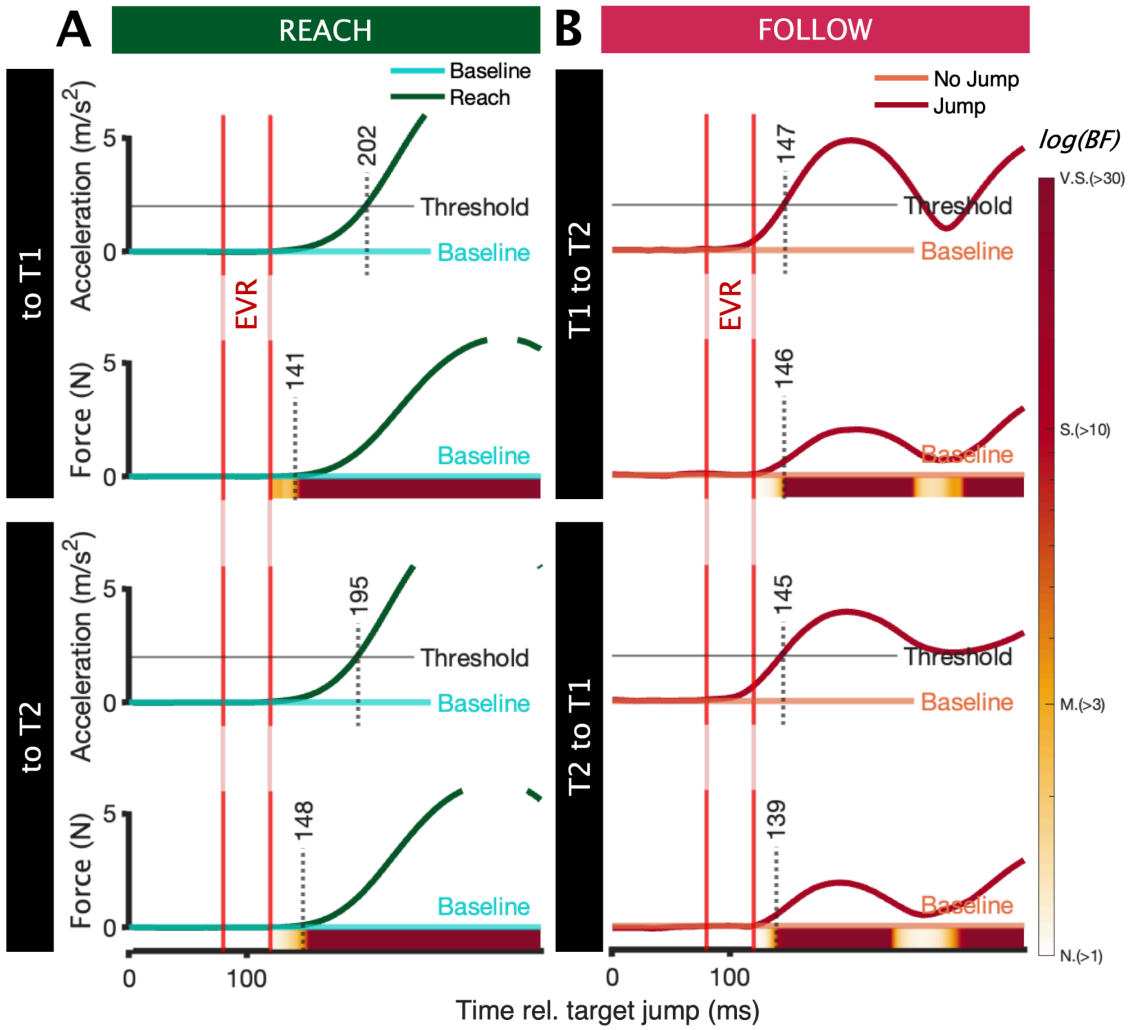

Figure 9. Comparing reaction time analyses : *Mean acceleration (vector sum of x and y acceleration) and mean force deviation from baseline for (A) initial reach and (B) online reach correction. For acceleration plots, dotted vertical lines denote onset determined using a threshold of 2 m/s^2. For force plots, the BF heatmaps denote the likelihood of the model that the force in force deviates significantly from baseline (for the initial reach comparison begins at 120ms, force 200ms prior was used as baseline). Dotted vertical line denotes first instance where BF > 10. BF heatmap is qualified by the following standard thresholds (Jeffreys, 1998): N.(> 1) = Negligible, M.(> 3) = Moderate, S.(> 10) = Strong, V.S.(> 30) = Very Strong. EVR epoch (80-120ms) denoted by vertical red lines.*

Similar EVR latencies for online correction and reaching from rest

We then compared the exemplar participant's EVRs during reaching from rest and online correction (fig. 10A). We find that as with EVRs during online corrections, the initial reach EVRs consistently begin at a latency of ~80ms, and in both cases the EVR is more aligned in time to stimulus onset/jump rather than F-RT. It is not meaningful to directly compare EVR magnitudes, given differences in EMG activity immediately before the EVR. Regardless, a key prediction of the 'automatic pilot' hypothesis is that EVR and force changes should be earlier for online reach corrections versus reaches from rest. Although one study has previously reported this when comparing data collected across two different blocks of trials (Kozak et al., 2019), another study has also documented nearly identical latencies for EMG onset for both the initial reach and the online correction (Soechting & Lacquaniti, 1983). Importantly, our paradigm allows for a direct comparison of EVR timing within the same trials, thereby controlling for target relative to hand location and task set.

To compare the latency of the EVRs, we ran a paired Bayesian t-test on each time point, comparing mean EMG in jump vs. no jump conditions and Initial reach vs. baseline (time point 200ms prior; fig. 10B). We found that EVR latency was functionally identical for both the initial reach and online correction. For the sternal head of pectoralis major, the primary muscle used to make right arm leftward reaches, the BF indicated a strong likelihood of an effect starting on average (across jump directions) at 87ms and 85ms during the initial reach and online correction, respectively. Results were more ambiguous for the anterior deltoid and triceps, due in part to the low vigor of muscle recruitment, however, visually EVR latency appears fairly consistent on all muscles recorded. This finding corroborates the force data (fig. 9),

demonstrating that motor commands arrive at the muscle at ~80ms for both reaches from rest and online corrections.

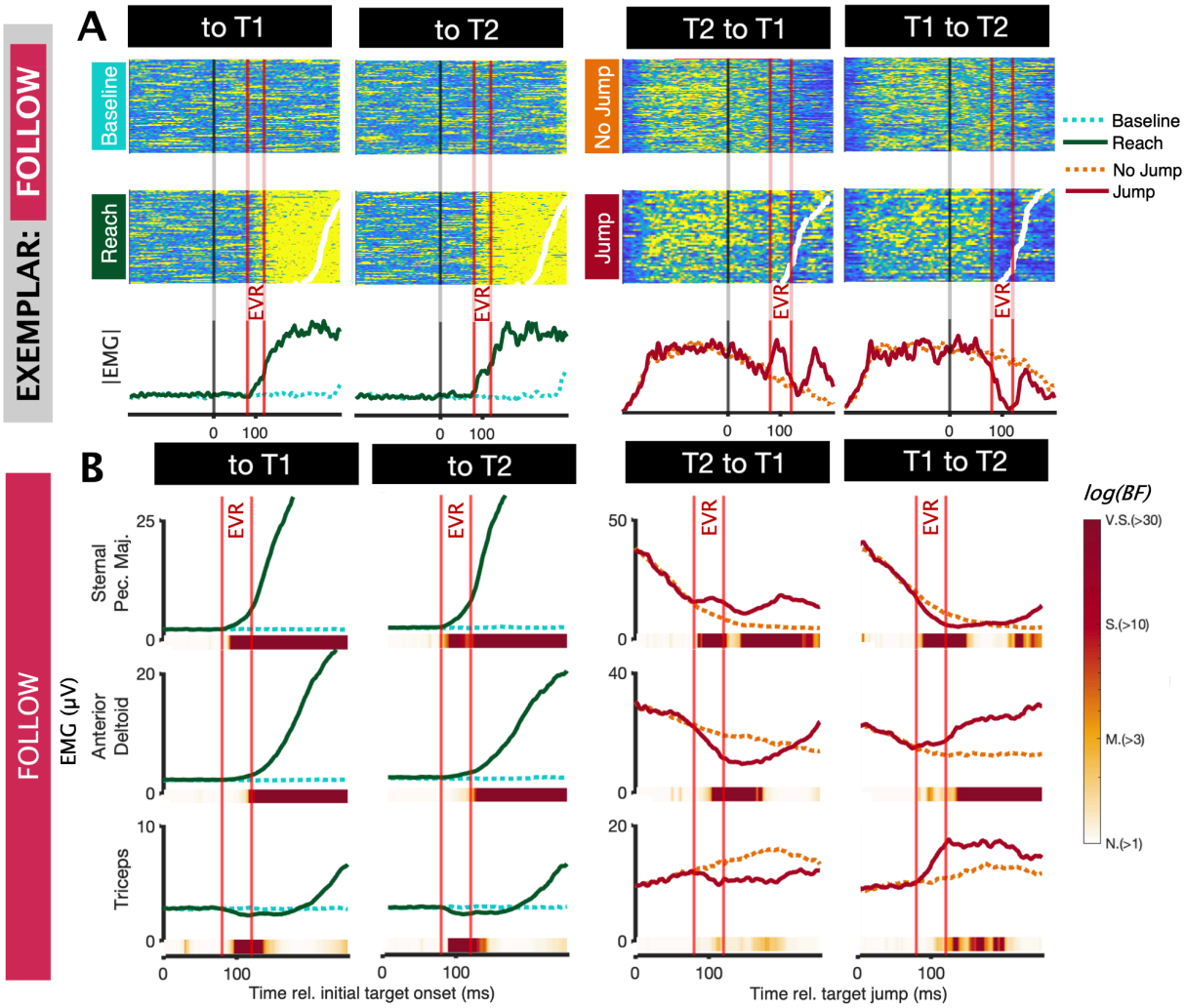

Figure 10. Comparison of EMG during the initial reach and online correction: *(A) Initial reach and baseline single trial heatmaps and means of normalized EMG of the right sternal head of pectoralis major of the exemplar participant (p6). Trials are organized by F-RT, as denoted by the white dots. (B) Group initial reach compared to baseline (200ms prior to target onset) and jump compared to baseline (no jump trials) in 'Follow' blocks. Note differences in y-axis scaling. BF heatmap denotes the likelihood of a difference between two conditions. Standard BF thresholds (Jeffreys, 1998): N.(> 1) = Negligible, M.(> 3) = Moderate, S.(> 10) = Strong, V.S.(> 30) = Very Strong. EVR epoch (80-120ms) is denoted by vertical red lines.*

Discussion

Here, we addressed the hypothesis that online corrections to visual targets constitute a distinct class of movements. Such a conceptualization is based primarily on the low kinematic latency of online corrections relative to reaches from rest. By measuring EMG as well as the hand force on the manipulandum, we find no support for this hypothesis. Instead, our results support a nested model of reaching control, composed of distinct phases of subcortical (80-120ms) and cortical (> 130ms) muscle recruitment which occurred at nearly identical latencies during reaching from rest or online correction. However, only during online corrections did this pattern of muscle recruitment lead to low-latency kinematic changes. Thus, an alternative interpretation of previous kinematic results supporting the notion of an 'automatic pilot' system for the control of online correction, is that they arose not from earlier muscle recruitment, but rather from biomechanical considerations related to how quickly consequent forces overcome the arm's inertia.

The EVR underlies the stimulus driven nature of online corrections to visual targets

We investigated the mechanisms underlying the almost irresistible urge to follow a suddenly displaced target in a reaching task. Our results demonstrate that these short-latency online corrections (< 120ms) are preceded by a distinctive phase of muscle recruitment, the express visuomotor response (EVR), which is time locked to the target jump. Here, we show that the magnitude of the EVR in an online correction predicted the timing and magnitude of forces that direct the arm to the target. Further, while the EVR could be muted in magnitude, it persisted even when counter to task goals in the 'Stop' and 'Ignore' blocks. Thus, both the initial phase of

online correction (Gritsenko & Kalaska, 2010; Striemer et al., 2010) and the EVR (fig. 5 & 6) are automatic and only somewhat muted by task demands.

Despite the automaticity of the EVR, the EVR was more pronounced during the 'Stop' blocks compared to the 'Ignore' block, leading to larger erroneous deviations (fig. 3B) and a shorter latency for those deviations (fig. 7). Presumably, this is because the jumped target still carries behavioral relevance in the 'Stop' block, but not in the 'Ignore' block; in other words EVRs to task-irrelevant stimuli are easier to restrain. This result complements findings that both spatial (Contemori et al., 2023; Gu et al., 2018; Selen et al., 2023) and temporal (Contemori et al., 2021; Kozak & Corneil, 2021) factors can impact EVR magnitude, and EVRs persistently direct the arm along a path toward a salient visual stimulus in tasks with incongruous stimulus-response mappings (Gu et al., 2016, 2018). Thus, the EVR develops task-relevant forces capable of deviating the arm toward the jumped stimulus in our task.

Re-evaluating the model of online corrections

A core prediction of the 'automatic pilot' hypothesis is that muscle activity should change sooner after target displacement for online corrections compared to reaches from rest. For example, Smeets, Oostwoud, and Brenner (2016) suggested that online corrections are earlier because there is no need to detect the target de novo following its displacement [but see Brenner and Smeets (2022) for different results from a rapid pointing task]. Conversely, Cluff and Scott (2016) suggested that online corrections are expedited due to the earlier expression of postural adjustments that must precede movements from rest.

When we analyzed movement onset using conventional kinematic measures like acceleration, we did indeed find earlier onsets for online corrections than movements from rest

(Fig. 9). However, a close inspection of muscle activity and force revealed essentially identical latencies but larger magnitudes for online corrections and for movements from rest (Figs. 9, 10). This discrepancy highlights the importance of limb biomechanics, and particularly an appreciation of how quickly the forces that arise from changes in muscle recruitment overcome the limb's inertia. Critically, the impetus (Carlton, 1981; Soechting & Lacquaniti, 1983) and criterion for categorizing online corrections as a distinct class of movement in the previous literature is that they are 'quick' (Gomi, 2008), 'fast' (Archambault et al., 2015; Gaveau et al., 2014), or 'rapid' (Sarlegna & Mutha, 2015). Our EMG and force findings undermine this conception and, by extension, the idea of an 'automatic pilot' which functions exclusively in the context of an ongoing movement (Brière & Proteau, 2011; Gaveau et al., 2014; Gosselin-Kessiby et al., 2008; Pisella et al., 2000; Prablanc & Martin, 1992).

Why then was the EVR not observed during previous studies of online corrections, despite occasional use of EMG? Certainly task features appear critical, as noted above, and it is well documented that the EVR (Pruszynski et al., 2010; Weerdesteyn et al., 2024) and other subcortical reflexes such as express saccades (Oor et al., 2023), are more prevalent during tasks with a degree of urgency. Further, the study of EVRs is predicated on a trial-by-trial analysis of EMG activity (Corneil et al., 2004; Kozak et al., 2019; Pruszynski et al., 2010); the averaging of EMG activity across multiple trials regardless of reaction time will obscure the EVR and compromise the conclusions that can be drawn. This issue is particularly problematic during online corrections, as any EVRs would evolve on-top of a pre-existing dynamic of muscle recruitment related to the initial reaching movement (Kozak et al., 2019), and because of the

potential for ‘voluntary’ or even anticipatory recruitment to merge into the EVR interval for short-latency trials.

In our study, the EVR was easier to characterize due to the dissociation of the EVR from the subsequent phases of recruitment in the ‘Ignore’ and ‘Stop’ blocks (fig. 5 & 6). Finally, trial-by-trial analyses of EMG activity emphasize that the EVR need not be all-or-none even in a given task (Contemori et al., 2021); instead, the phenomenon of EVRs has a probabilistic nature akin to express saccades, where expression also is likely impacted by such things as previous-trial effects, motivation, and vigilance.

A common nested system for visually-guided reaches

Our findings of equivalent timing for reaches whether initiated from rest or during an ongoing movement resonate with models of a nested system for the control of reaching, made up of subcortical and cortical pathways contributing distinct phases of muscle recruitment (Contemori et al., 2023). In this model the first phase of recruitment, the EVR, is mediated through the superior colliculus (SC) via the tecto-reticulo-spinal pathway. This subcortical pathway has the advantage of being extremely short-latency but the disadvantage of being inexorably stimulus-driven. In monkeys, EVR latency, which is shorter relative to humans (Cecala et al., 2023; Goonetilleke et al., 2015), is correlated with and preceded by visual bursts in the movement-related layers of the SC (Rezvani & Corneil, 2008). Certain stimuli, including high-contrast (Chen & Hafed, 2018; Kozak & Corneil, 2021; Schneider & Kastner, 2005), low-spatial frequency (Chen et al., 2018; Kozak et al., 2019; Zhang et al., 2015), and evolutionarily relevant images, like faces (Mekhaiel et al., 2024; Wang et al., 2020; Yu et al., 2024), preferentially evoke the EVR, activate the human SC, and robustly activate monkey SC

neurons within < 50ms. Our observations here add to the evidence that the EVR, and by extension the initial phase of low-latency online corrections to visual targets, are mediated through the tecto-reticulo-spinal pathway. While the nested architecture we propose may well be recruited to targets of other modalities, we speculate that the strong visual response in the SC engenders the stimulus-directed nature to "express" responses which is not seen for auditory (Shafiq et al., 1998) or tactile (Reschechtko & Pruszynski, 2020) modalities.

The second voluntary phase of muscle recruitment, which lags the EVR, is mediated via the canonical cortical motor pathway which, although being slightly slower, has the benefit of being fully flexible to permit any stimulus-response association. This includes the PPC which, through transcranial magnetic stimulation (TMS) and lesions studies, has been classically regarded as the most likely candidate for the 'automatic pilot' (Archambault et al., 2015; Gaveau et al., 2014; Gomi, 2008; Sarlegna & Mutha, 2015). Although TMS of human PPC disrupts both online reaching (Breveglieri et al., 2023; Della-Maggiore et al., 2004; Desmurget et al., 1999; Johnson & Haggard, 2005; Reichenbach et al., 2011) and grasping (Glover et al., 2005; Rice et al., 2006, 2007; Tunik et al., 2005) [except when TMS is applied > 100ms after target jump (Marigold et al., 2019; Savoie et al., 2020)], in studies where reaction time was measured, no change was found (Desmurget et al., 1999; Reichenbach et al., 2011). Instead, TMS of the PPC increased total movement time. The lack of an effect on reaction time suggests that the initial phase of online corrections may have been preserved, possibly because PPC stimulation disrupted the second phase of recruitment without influencing the EVR. It is during this latter interval where muscle recruitment starts to differ if the task demands an incongruent stimulus-response mapping, as an anti-reach paradigm (Gu et al., 2016), or in the 'Stop' block

studied here. In the ‘Stop’ block, the earliest change in muscle recruitment related to actively braking the reach movement occurred ~20-30ms after the EVR, or ~140-150ms after the jumped target (fig. 8A). This later latency resembles the timing of an active braking signal on limb muscles when reaching movements are abruptly canceled in standard stop-signal tasks (Atsma et al., 2018).

Individuals with optic ataxia following PPC damage exhibit deficits during both online corrections (Gréa et al., 2002; Pisella et al., 2000; Rossit et al., 2012; Schaefer et al., 2012) and reaching from rest (for review, see Andersen et. al, 2014 & Goodale and Milner, 2008), particularly to peripheral targets but also, to a lesser degree, central targets. Can these results be reconciled with the notion of nested pathways? As stated in Pisella and colleagues’ (2000) seminal study on the topic, in their experimental design they were compelled to increase the distance between the initial target (which appeared centrally) and the jumped target because of the patients' high pointing variability from rest. Notably, none of these studies recorded muscle activity; hence the effect of PPC damage muscle recruitment is unknown. Muscle recordings in patients with optic ataxia, in conjunction with tasks promoting response urgency, are particularly important given recent work in Parkinson's Disease attributing a preservation of eye and hand movements in interceptive tasks to signalling through the superior colliculus (Fooken et al., 2022). This work is consistent with other emerging work showing that the pathophysiology of Parkinson’s disease spares EVRs but selectively impacts muscle recruitment during the voluntary interval (Billen et al., 2024; Gilchrist et al., 2024). Whether such selective sparing of EVRs also happens following damage to the PPC and in the context of optic ataxia remains to be determined.

The importance of movement biomechanics and the notion of nested pathways, helps resolve a critical problem in the 'automatic pilot' hypothesis pointed out by Sarlegna and Mutha (2015). The authors questioned why a continuously updated 'automatic pilot' capable of implementing an anti-reach task set for reaching movements initiated from rest would not be able to do so during an ongoing movement; recall that the initial phase of anti-reaches during online corrections is drawn toward the jumped stimulus (Day & Lyon, 2000). This question is prescient, since it suggests two different modules; one capable and the other incapable of facilitating anti-reaching. The EVR erroneously directs movements toward the target during anti reaching tasks both from rest (Gu et al., 2016) and during an ongoing movement as seen here in the 'Stop' block. During an ongoing movement, the EVR leads to sizable kinematic deviations. From rest, however, the EVR's consequent forces are relatively small so that, in conjunction with the arm's inertia, the kinematic deviation toward the stimulus is modest and rapidly corrected by the subsequent voluntary recruitment. The possibility that EVR magnitude is scaled depending on when a target is displaced may help explain the progressive increase in response robustness for target displacements introduced later in an ongoing movement (Gritsenko et al., 2009). Thus, the apparent differences between online corrections and movement from rest are resolved with EMG recordings, and with consideration of movement kinetics and biomechanics. Considerations of task demands are also essential, as EVRs can be generated either well before (Wood et al., 2015) or even without subsequent voluntary muscle recruitment (Kearsley et al., 2022). Conversely, robust voluntary recruitment can precede a muted (as seen in the 'Ignore' block) or entirely absent EVR, particularly in non-urgent response tasks that favour movement accuracy over speed.

Limitations

Our results do not support the conception of online corrections to visual targets as a distinct class of movements mediated by a rapid 'automatic pilot' system. Our main evidence is the equivalent timing of EMG recruitment and onset of manipulandum force regardless of whether reaching movements are initiated from rest or adjusted in mid-flight, which we argue support a nested system wherein distinct subcortical and cortical loops can be engaged during visually-guided reaching. In terms of limitations, future studies could employ causal neurostimulation techniques like transcranial magnetic stimulation to test this architecture. Further, subjects knew that relevant visual stimuli would only be presented at two fairly adjacent spatial locations; future extensions of this work should explore workspaces with a higher degree of target uncertainty. Finally, we did not measure eye movements, which may be informative in the future to see if there are any relationships with the EVR. Regardless, our results emphasize the importance of recording muscle activity and/or force measures in addition to movement kinematics to ensure accurate interpretation of experimental data.

Methods

Participants

All procedures were approved by the Health and Science Research Ethics Board at Western University, London, Ontario, Canada, and conformed to standards set by the Declaration of Helsinki. Twenty university students (female: 15, male: 5; mean age: 19.15 ± 2.08; right-handed: 19, left-handed: 1) were recruited using the Psychology Research Participant Pool, with compensation provided as credits required for course completion. All provided written consent,

reported normal or corrected to normal vision and no neurological disorders, completed the experiment, and are included in the analysis.

Apparatus

Participants made visually-guided reaching movements in a Kinarm Endpoint Robot (fig. 1A; BKIN technologies, Kingston, Ontario, Canada) integrated with a high-performance Propixx projector (VPixx, Saint-Bruno, Quebec, Canada) that ensured reliable event timing. A photodiode provided additional verification of stimulus timing. Behavioural tasks were generated using Stateflow and Simulink within MATLAB (version R2015a, MathWorks Inc., Natick, Massachusetts, United States of America).

All participants, regardless of handedness, completed the task with their right arm using a manipulandum under a horizontal display surface at approximately shoulder level when seated. The display occluded the participants' hand, but did not impact their ability to perform online reach corrections (Goodale et al., 1986; Gosselin-Kessiby et al., 2008). Surface electromyography (EMG; Delsys Inc. Bagnoli-8 system, Boston, Massachusetts, United States of America) recordings of the following six right arm muscles, identified through palpation, were acquired: clavicular and sternal heads of pectoralis major, anterior and posterior deltoids, short head of biceps, and medial head of triceps (fig. 1B). EMG data was filtered using a high and low pass filter of 20 and 450Hz. All data was recorded at 1000Hz by the Kinarm computer.

Behavioural task

Participants initiated trials by aligning their cursor (r = 1cm), controlled by the Kinarm manipulandum, within the startpoint (r = 1cm). Following a hold of 750ms, the startpoint disappeared. Following a randomised time of 250ms + 1:1000ms (total hold = 1000:2000ms), a

target (r = 3cm) appeared randomly in either the T1 or T2 location (fig. 1C). Temporal uncertainty was used to reduce anticipatory reaches. If the participant's hand left the startpoint location before target onset, the trial was terminated and repeated. In 66% of trials, no jump occurred and the trial ended when the cursor reached the target (fig. 1D). In 33% of trials, upon movement initiation (centre of cursor > 1cm away from centre of startpoint) the target jumped to the other location (fig. 1E-G).

In different blocks, we used identical visual stimuli but instructed participants to perform different motor adjustments in response to a target jump. By using the same stimuli, we could ensure that observed differences stemmed solely from top-down cognitive task setting rather than bottom-up stimuli related factors. If the target jumped (E) during 'Follow' blocks, participants were instructed to 'Reach to **NEW** target,' (F) during 'Stop' blocks, they were instructed to '**STOP**' the ongoing movement, (G) and during 'Ignore' blocks, they were instructed to 'Reach to **OLD** target.' On jump trials, the trial ended in 'Follow' blocks when the cursor touched the new target (fig. 1E), in 'Stop' blocks 1500ms following target jump (fig. 1F), and in 'Ignore' blocks when the cursor touched the old target location (fig. 1G).

A practice session of 78 trials was completed before the experiment, including all trial types broken over 6 blocks with alternating instructions, followed by a timed 3-minute break. The experiment consisted of 864 trials, including 192 no jump (66%) and 96 jump (33%) trials for each instruction type. The experiment was broken up into 9 blocks of 96 trials, after each of which the instruction was alternated. The order of the block instructions was pseudorandomized across participants, then repeated sequentially over the experiment,

resulting in 3 blocks for each instruction type. A timed 5-minute break followed every 3 blocks of the experiment.

Data alignment

All preprocessing and analyses, unless otherwise stated, were completed using MATLAB (version R2021a, MathWorks Inc., Natick, Massachusetts, United States of America). On each trial, an unseen white stimulus appeared simultaneously with the first target onset and disappeared once the participant's cursor left the startpoint (the same time the second target appeared and the first target disappeared on jump trials). The onset and offset of this white stimulus was detected by a diode. Kinematic and EMG data were aligned on a per-trial basis to the diode onset (initial target onset) or offset (target jump), depending on whether we wished to investigate the initial reach or the online reach correction, respectively.

Analyses of movement kinematics and forces

We evaluated performance to ensure participants completed the task as instructed. Jump trials were denoted as error trials if the participant failed to follow the block instruction. Using coordinates from the Kinarm manipulandum, trials were marked as error in 'Follow' blocks if the cursor made contact with the initial target location, in 'Stop' blocks if the cursor made contact with either of the target locations, and in 'Ignore' blocks if the cursor made contact with the new target (fig. 2A). No trials were excluded on the basis of these performance classifications in any of our analyses.

In addition to recording kinematic measures such as position data and its derivatives, we also analyzed the force exerted by the hand on the manipulandum, which was measured via force transducers. Force data was filtered using a second-order low-pass Butterworth filter of

60Hz. Force and kinematic data was then transformed spatially by rotating the workspace -157.5° around the centre of the startpoint (see fig. 3A for a graphical depiction of this rotation). This ensured that the x-axis denoted movement between the startpoint and midpoint between the targets, while the perpendicular y-axis denoted deviation of the trajectory towards one of the two targets.

For each participant, we used data from no jump trials to determine the mean force trajectory in the x and y dimensions, as well as the standard deviation of the Euclidean differences relative to this mean. Force reaction time (F-RT) of each jump trial was determined by identifying the time point when the Euclidean difference exceeded one standard deviation, relative to the complementary no jump condition. We calculated F-RTs following target jumps for both jump and no jump trials (as a control) to determine the earliest F-RT onset latency. We found that the earliest discernible difference between the two distributions was ~100ms. Therefore, for all analyses we excluded trials where F-RT occurred prior to 100ms, excluding on average 14.6% of jump trials in 'Follow' blocks, 16.7% in 'Stop' blocks, and 14.7% in 'Ignore' blocks. Inclusion or exclusion of these trials did not change our result, however, we opted to exclude them as a control of anticipatory reach adjustments. Notably, these anticipatory adjustments were approximately just as likely (~15%) during jump and no jump trials since conditions were intermixed and randomized.

We did not exclude any trials due to any task-specific factors such as any error in the reach adjustment (reaching to the wrong target or performing the wrong reach adjustment) or a delay or absence of a response. By removing any subjective criteria, we aimed to objectively assess the impact of muscle recruitment on force and kinematics. The exception to this is for

the analysis of F-RT, where we excluded trials without a detected F-RT (which happened when the participant's hand did not deviate from the no-jump trajectory). This happened on average in an additional 1.3% of jump trials in 'Follow' blocks, 3.4% in 'Stop' blocks, and 24.3% in 'Ignore' blocks.

For each participant the mean Euclidean difference of force was then calculated for both no jump and jump trials, relative to the mean no jump trajectory. A group analysis was conducted with a timewise one-tailed paired t-test using the function BayesFactor v.2.3.0 (Krekelberg, 2022), to quantify the likelihood of the model that force in jump trials deviated more than no jump trials, relative to the mean no jump force trajectory. The same analysis was used to compare the force of the initial reach with baseline force.

Analysis of muscle activity

Offline, EMG data was full-wave rectified and then filtered by a 7-point moving average filter. Since participants initiated a target jump during jump trials when their hand left the startpoint, we aligned each trial's data to the time point for both trials when the target did jump on jump trials, and when it would have jumped on no-jump trials. This allowed us to compare EMG data during the EVR epoch (80-120ms) of jump trials with the same time point during trials where the target did not jump. The relationship between the mean EMG magnitude during the EVR epoch, muscle, condition, and F-RT was analyzed using linear mixed effects models, performed using R (v4.4.0, R Foundation for Statistical Computing, Vienna, Austria). Specific models are discussed in the results section. A Pearson's correlation was used to visualize the relationship between EMG magnitude on F-RT. Additionally, group analyses were conducted using a

timewise two-tailed paired Bayesian t-test, to quantify the likelihood of a difference of these in EMG magnitude across trial types.

Acknowledgements

This work is supported by Discovery Grants from the Natural Sciences and Engineering Research Council of Canada (NSERC) to BDC (RGPIN 311680 and 04394-2021) and MAG (RGPIN-2017-04088).

Conflicts of Interest

The authors declare no competing interests.

References

Andersen, R. A., Andersen, K. N., Hwang, E. J., & Hauschild, M. (2014). Optic ataxia: from Balint's syndrome to the parietal reach region. *Neuron*, *81*(5), 967–983.

Archambault, P. S., Ferrari-Toniolo, S., Caminiti, R., & Battaglia-Mayer, A. (2015). Visually-guided correction of hand reaching movements: The neurophysiological bases in the cerebral cortex. *Vision Research*, *110*(Pt B), 244–256.

Atsma, J., Maij, F., Gu, C., Medendorp, W. P., & Corneil, B. D. (2018). Active Braking of Whole-Arm Reaching Movements Provides Single-Trial Neuromuscular Measures of Movement Cancellation. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *38*(18), 4367–4382.

Billen, L. S., Nonnekes, J., Corneil, B. D., & Weerdesteyn, V. (2024). Lower-limb express visuomotor

responses are spared in Parkinson's Disease during step initiation from a stable position. In *bioRxiv* (p. 2024.11.29.625631). https://doi.org/10.1101/2024.11.29.625631

Brenner, E., & Smeets, J. B. (1997). Fast Responses of the Human Hand to Changes in Target Position. *Journal of Motor Behavior*, *29*(4), 297–310.

Brenner, E., & Smeets, J. B. J. (2022). Having several options does not increase the time it takes to make a movement to an adequate end point. *Experimental Brain Research*, *240*(6), 1849–1871.

Breveglieri, R., Borgomaneri, S., Filippini, M., Tessari, A., Galletti, C., Davare, M., & Fattori, P. (2023). Complementary contribution of the medial and lateral human parietal cortex to grasping: a repetitive TMS study. *Cerebral Cortex* , *33*(9), 5122–5134.

Brière, J., & Proteau, L. (2011). Automatic movement error detection and correction processes in reaching movements. *Experimental Brain Research*, *208*(1), 39–50.

Carlton, L. G. (1981). Processing visual feedback information for movement control. *Journal of Experimental Psychology. Human Perception and Performance*, *7*(5), 1019–1030.

Cecala, A. L., Kozak, R. A., Pruszynski, J. A., & Corneil, B. D. (2023). Done in 65 ms: Express Visuomotor Responses in Upper Limb Muscles in Rhesus Macaques. *eNeuro*, *10*(8). https://doi.org/10.1523/ENEURO.0078-23.2023

Chen, C.-Y., & Hafed, Z. M. (2018). Orientation and Contrast Tuning Properties and Temporal Flicker Fusion Characteristics of Primate Superior Colliculus Neurons. *Frontiers in Neural Circuits*, *12*, 58.

Chen, C.-Y., Sonnenberg, L., Weller, S., Witschel, T., & Hafed, Z. M. (2018). Spatial frequency sensitivity in macaque midbrain. *Nature Communications*, *9*(1), 2852.

Cluff, T., & Scott, S. H. (2016). Online Corrections are Faster Because Movement Initiation Must Disengage Postural Control. *Motor Control*, *20*(2), 162–170.

Contemori, S., Loeb, G. E., Corneil, B. D., Wallis, G., & Carroll, T. J. (2021). Trial-by-trial modulation of express visuomotor responses induced by symbolic or barely detectable cues. *Journal of*

Neurophysiology, *126*(5), 1507–1523.

Contemori, S., Loeb, G. E., Corneil, B. D., Wallis, G., & Carroll, T. J. (2023). Express Visuomotor Responses Reflect Knowledge of Both Target Locations and Contextual Rules during Reaches of Different Amplitudes. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *43*(42), 7041–7055.

Corneil, B. D., Olivier, E., & Munoz, D. P. (2004). Visual responses on neck muscles reveal selective gating that prevents express saccades. *Neuron*, *42*(5), 831–841.

Day, B. L., & Brown, P. (2001). Evidence for subcortical involvement in the visual control of human reaching. *Brain: A Journal of Neurology*, *124*(Pt 9), 1832–1840.

Day, B. L., & Lyon, I. N. (2000). Voluntary modification of automatic arm movements evoked by motion of a visual target. *Experimental Brain Research*, *130*(2), 159–168.

de Brouwer, A. J., & Spering, M. (2022). Eye-hand coordination during online reach corrections is task dependent. *Journal of Neurophysiology*, *127*(4), 885–895.

Della-Maggiore, V., Malfait, N., Ostry, D. J., & Paus, T. (2004). Stimulation of the posterior parietal cortex interferes with arm trajectory adjustments during the learning of new dynamics. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *24*(44), 9971–9976.

Desmurget, M., Epstein, C. M., Turner, R. S., Prablanc, C., Alexander, G. E., & Grafton, S. T. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nature Neuroscience*, *2*(6), 563–567.

Fautrelle, L., Barbieri, G., Ballay, Y., & Bonnetblanc, F. (2011). Pointing to double-step visual stimuli from a standing position: motor corrections when the speed-accuracy trade-off is unexpectedly modified in-flight. A breakdown of the perception-action coupling. *Neuroscience*, *194*, 124–135.

Fooken, J., Patel, P., Jones, C. B., McKeown, M. J., & Spering, M. (2022). Preservation of Eye Movements in Parkinson's Disease Is Stimulus- and Task-Specific. *The Journal of Neuroscience : The Official*

Journal of the Society for Neuroscience, *42*(3), 487–499.

Gaveau, V., Pisella, L., Priot, A.-E., Fukui, T., Rossetti, Y. R., Pélisson, D., & Prablanc, C. (2014). Automatic online control of motor adjustments in reaching and grasping. *Neuropsychologia*, *55*, 25–40.

Gilchrist, M., Kozak, R. A., Prenger, M., Anello, M., Van Hedger, K., MacDonald, P. A., & Corneil, B. D. (2024). Parkinson's Disease affects the contextual control, but not the expression, of a rapid visuomotor response that initiates visually-guided reaching: Evidence for multiple, interacting motor pathways and implications for motor symptoms in Parkinson's Disease. In *bioRxiv* (p. 2024.11.27.625399). https://doi.org/10.1101/2024.11.27.625399

Glover, S., Miall, R. C., & Rushworth, M. F. S. (2005). Parietal rTMS disrupts the initiation but not the execution of on-line adjustments to a perturbation of object size. *Journal of Cognitive Neuroscience*, *17*(1), 124–136.

Gomi, H. (2008). Implicit online corrections of reaching movements. *Current Opinion in Neurobiology*, *18*(6), 558–564.

Goodale, M. A., Pelisson, D., & Prablanc, C. (1986). Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature*, *320*(6064), 748–750.

Goonetilleke, S. C., Katz, L., Wood, D. K., Gu, C., Huk, A. C., & Corneil, B. D. (2015). Cross-species comparison of anticipatory and stimulus-driven neck muscle activity well before saccadic gaze shifts in humans and nonhuman primates. *Journal of Neurophysiology*, *114*(2), 902–913.

Gosselin-Kessiby, N., Messier, J., & Kalaska, J. F. (2008). Evidence for automatic on-line adjustments of hand orientation during natural reaching movements to stationary targets. *Journal of Neurophysiology*, *99*(4), 1653–1671.

Gréa, H., Pisella, L., Rossetti, Y., Desmurget, M., Tilikete, C., Grafton, S., Prablanc, C., & Vighetto, A. (2002). A lesion of the posterior parietal cortex disrupts on-line adjustments during aiming movements. *Neuropsychologia*, *40*(13), 2471–2480.

Gritsenko, V., & Kalaska, J. F. (2010). Rapid online correction is selectively suppressed during movement with a visuomotor transformation. *Journal of Neurophysiology*, *104*(6), 3084–3104.

Gritsenko, V., Yakovenko, S., & Kalaska, J. F. (2009). Integration of predictive feedforward and sensory feedback signals for online control of visually guided movement. *Journal of Neurophysiology*, *102*(2), 914–930.

Gu, C., Pruszynski, J. A., Gribble, P. L., & Corneil, B. D. (2018). Done in 100 ms: path-dependent visuomotor transformation in the human upper limb. *Journal of Neurophysiology*, *119*(4), 1319–1328.

Gu, C., Wood, D. K., Gribble, P. L., & Corneil, B. D. (2016). A Trial-by-Trial Window into Sensorimotor Transformations in the Human Motor Periphery. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *36*(31), 8273–8282.

Jeffreys, H. (1998). *The Theory of Probability*. OUP Oxford.

Johnson, H., & Haggard, P. (2005). Motor awareness without perceptual awareness. *Neuropsychologia*, *43*(2), 227–237.

Kearsley, S. L., Cecala, A. L., Kozak, R. A., & Corneil, B. D. (2022). Express arm responses appear bilaterally on upper-limb muscles in an arm choice reaching task. *Journal of Neurophysiology*, *127*(4), 969–983.

Kozak, R. A., & Corneil, B. D. (2021). High-contrast, moving targets in an emerging target paradigm promote fast visuomotor responses during visually guided reaching. *Journal of Neurophysiology*, *126*(1), 68–81.

Kozak, R. A., Kreyenmeier, P., Gu, C., Johnston, K., & Corneil, B. D. (2019). Stimulus-Locked Responses on Human Upper Limb Muscles and Corrective Reaches Are Preferentially Evoked by Low Spatial Frequencies. *eNeuro*, *6*(5). https://doi.org/10.1523/ENEURO.0301-19.2019

Krekelberg, B. (2022). *BayesFactor: Release 2022 (v2.3.0)*. Zenodo.

https://doi.org/10.5281/ZENODO.7006300

Marigold, D. S., Lajoie, K., & Heed, T. (2019). No effect of triple-pulse TMS medial to intraparietal sulcus on online correction for target perturbations during goal-directed hand and foot reaches. *PloS One*, *14*(10), e0223986.

Mekhaiel, D. Y., Goodale, M. A., & Corneil, B. D. (2024). Rapid integration of face detection and task set in visually guided reaching. *The European Journal of Neuroscience*, *60*(6), 5328–5347.

Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia*, *46*(3), 774–785.

Novembre, G., & Iannetti, G. D. (2021). Towards a unified neural mechanism for reactive adaptive behaviour. *Progress in Neurobiology*, *204*, 102115.

Oor, E. E., Stanford, T. R., & Salinas, E. (2023). Stimulus salience conflicts and colludes with endogenous goals during urgent choices. *iScience*, *26*(3), 106253.

Oostwoud Wijdenes, L., Brenner, E., & Smeets, J. B. J. (2011). Fast and fine-tuned corrections when the target of a hand movement is displaced. *Experimental Brain Research*, *214*(3), 453–462.

Paulignan, Y., Jeannerod, M., MacKenzie, C., & Marteniuk, R. (1991). Selective perturbation of visual input during prehension movements. 2. The effects of changing object size. *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*, *87*(2), 407–420.

Paulignan, Y., MacKenzie, C., Marteniuk, R., & Jeannerod, M. (1991). Selective perturbation of visual input during prehension movements. 1. The effects of changing object position. *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*, *83*(3), 502–512.

Pisella, L., Gréa, H., Tilikete, C., Vighetto, A., Desmurget, M., Rode, G., Boisson, D., & Rossetti, Y. (2000). An “automatic pilot” for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia. *Nature Neuroscience*, *3*(7), 729–736.

Prablanc, C., & Martin, O. (1992). Automatic control during hand reaching at undetected two-dimensional target displacements. *Journal of Neurophysiology*, *67*(2), 455–469.

Pruszynski, J. A., King, G. L., Boisse, L., Scott, S. H., Flanagan, J. R., & Munoz, D. P. (2010). Stimulus-locked responses on human arm muscles reveal a rapid neural pathway linking visual input to arm motor output. *The European Journal of Neuroscience*, *32*(6), 1049–1057.

Raud, L., & Huster, R. J. (2017). The Temporal Dynamics of Response Inhibition and their Modulation by Cognitive Control. *Brain Topography*, *30*(4), 486–501.

Raud, L., Westerhausen, R., Dooley, N., & Huster, R. J. (2020). Differences in unity: The go/no-go and stop signal tasks rely on different mechanisms. *NeuroImage*, *210*, 116582.

Reichenbach, A., Bresciani, J.-P., Peer, A., Bülthoff, H. H., & Thielscher, A. (2011). Contributions of the PPC to online control of visually guided reaching movements assessed with fMRI-guided TMS. *Cerebral Cortex* , *21*(7), 1602–1612.

Reichenbach, A., Thielscher, A., Peer, A., Bülthoff, H. H., & Bresciani, J.-P. (2009). Seeing the hand while reaching speeds up on-line responses to a sudden change in target position. *The Journal of Physiology*, *587*(Pt 19), 4605–4616.

Reschechtko, S., & Pruszynski, J. A. (2020). Voluntary modification of rapid tactile-motor responses during reaching differs from its visuomotor counterpart. *Journal of Neurophysiology*, *124*(1), 284–294.

Reynolds, R. F., & Day, B. L. (2012). Direct visuomotor mapping for fast visually-evoked arm movements. *Neuropsychologia*, *50*(14), 3169–3173.

Rezvani, S., & Corneil, B. D. (2008). Recruitment of a head-turning synergy by low-frequency activity in the primate superior colliculus. *Journal of Neurophysiology*, *100*(1), 397–411.

Rice, N. J., Tunik, E., Cross, E. S., & Grafton, S. T. (2007). On-line grasp control is mediated by the contralateral hemisphere. *Brain Research*, *1175*, 76–84.

Rice, N. J., Tunik, E., & Grafton, S. T. (2006). The anterior intraparietal sulcus mediates grasp execution, independent of requirement to update: new insights from transcranial magnetic stimulation. *The*

Journal of Neuroscience: The Official Journal of the Society for Neuroscience, *26*(31), 8176–8182.

Rossit, S., McIntosh, R. D., Malhotra, P., Butler, S. H., Muir, K., & Harvey, M. (2012). Attention in action: evidence from on-line corrections in left visual neglect. *Neuropsychologia*, *50*(6), 1124–1135.

Sarlegna, F. R., & Mutha, P. K. (2015). The influence of visual target information on the online control of movements. *Vision Research*, *110*(Pt B), 144–154.

Savoie, F.-A., Dallaire-Jean, L., Thénault, F., Whittingstall, K., & Bernier, P.-M. (2020). Single-Pulse TMS over the Parietal Cortex Does Not Impair Sensorimotor Perturbation-Induced Changes in Motor Commands. *eNeuro*, *7*(2). https://doi.org/10.1523/ENEURO.0209-19.2020

Schaefer, S. Y., Mutha, P. K., Haaland, K. Y., & Sainburg, R. L. (2012). Hemispheric specialization for movement control produces dissociable differences in online corrections after stroke. *Cerebral Cortex (New York, N.Y. : 1991)*, *22*(6), 1407–1419.

Schneider, K. A., & Kastner, S. (2005). Visual responses of the human superior colliculus: a high-resolution functional magnetic resonance imaging study. *Journal of Neurophysiology*, *94*(4), 2491–2503.

Selen, L. P. J., Corneil, B. D., & Medendorp, W. P. (2023). Single-Trial Dynamics of Competing Reach Plans in the Human Motor Periphery. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *43*(15), 2782–2793.

Shafiq, R., Stuart, G. W., Sandbach, J., Maruff, P., & Currie, J. (1998). The gap effect and express saccades in the auditory modality. *Experimental Brain Research*, *118*(2), 221–229.

Smeets, J. B. J., Wijdenes, L. O., & Brenner, E. (2016). Movement Adjustments Have Short Latencies Because There is No Need to Detect Anything. *Motor Control*, *20*(2), 137–148.

Soechting, J. F., & Lacquaniti, F. (1983). Modification of trajectory of a pointing movement in response to a change in target location. *Journal of Neurophysiology*, *49*(2), 548–564.

Striemer, C. L., Yukovsky, J., & Goodale, M. A. (2010). Can intention override the “automatic pilot”? *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*, *202*(3),

623–632.

Tunik, E., Frey, S. H., & Grafton, S. T. (2005). Virtual lesions of the anterior intraparietal area disrupt goal-dependent on-line adjustments of grasp. *Nature Neuroscience*, *8*(4), 505–511.

Wang, Y. C., Bianciardi, M., Chanes, L., & Satpute, A. B. (2020). Ultra High Field fMRI of Human Superior Colliculi Activity during Affective Visual Processing. *Scientific Reports*, *10*(1), 1331.

Weerdesteyn, V., Kearsley, S. L., Cecala, A. L., Macpherson, E. A., & Corneil, B. D. (2024). Startling acoustic stimuli hasten reflexive choice reaching tasks by strengthening, but not changing the timing of, express visuomotor responses. In *bioRxiv* (p. 2024.07.01.601510). https://doi.org/10.1101/2024.07.01.601510

Wood, D. K., Gu, C., Corneil, B. D., Gribble, P. L., & Goodale, M. A. (2015). Transient visual responses reset the phase of low-frequency oscillations in the skeletomotor periphery. *The European Journal of Neuroscience*, *42*(3), 1919–1932.

Yu, G., Katz, L. N., Quaia, C., Messinger, A., & Krauzlis, R. J. (2024). Short-latency preference for faces in primate superior colliculus depends on visual cortex. *Neuron*, *112*(16), 2814–2822.e4.

Zhang, P., Zhou, H., Wen, W., & He, S. (2015). Layer-specific response properties of the human lateral geniculate nucleus and superior colliculus. *NeuroImage*, *111*, 159–166.