Single-trial dynamics of competing reach plans in the human motor periphery

Abbreviated title: Competing reach plans in the motor periphery

Luc P. J. Selen[1], Brian D. Corneil[2-5] and W. Pieter Medendorp[1]

[1]Radboud University, Donders Institute for Brain, Cognition and Behaviour; 6500 HB Nijmegen, The Netherlands

Departments of [2]Psychology and [4]Physiology & Pharmacology; University of Western Ontario; London, ON, N6A 5B7; Canada

The [3]Brain and Mind Institute and [5]Robarts Research Institute;

Corresponding Author:

Dr. Luc Selen

luc.selen@donders.ru.nl

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ABSTRACT

Contemporary theories of motor control propose that multiple motor plans compete for selection before the winning command is executed. While most competitions are completed prior to movement onset, movements are often initiated before the competition has been resolved. An example of this is saccadic averaging, wherein the eyes land at an intermediate location between two visual targets. Behavioral and neurophysiological signatures of competing motor commands have been reported for reaching movements, but debate remains about whether such signatures attest to an unresolved competition, arise from averaging across many trials, or reflect a strategy to optimize behavior given task constraints. Here, we recorded electromyographic (EMG) activity from an upper limb muscle while human participants performed a reach analogue of a task that elicits saccadic averaging, freely choosing to reach to one of two identical and suddenly presented visual targets. On each trial, muscle recruitment showed two distinct phases of directionally-tuned activity. In the first wave, time-locked ~100 ms of target presentation, EMG activity was clearly influenced by the non-chosen target, reflecting a competition between two reach commands that was biased in favor of the ultimately chosen target. This resulted in an initial movement direction intermediate between the two targets. In contrast, the second wave of EMG activity, time-locked to voluntary reach onset, was not biased toward the non-chosen target, showing that the competition between targets was resolved by the time of movement initiation. Instead, this second wave of activity was already compensating for the averaging induced by the first wave. Thus, single-trial analysis reveals an evolution in how the non-chosen target differentially influences the first and second wave of EMG activity. Ongoing debates about the interaction between competing reach commands may arise, at least in part, from the use of behavioural tasks that mute the magnitude of the earliest wave of EMG activity.

SIGNIFICANCE STATEMENT

Contemporary theories of motor control suggest that multiple motor plans compete for selection before the winning command is executed. Evidence for this is found in intermediate reach movements towards two potential target locations, but recent findings have challenged this notion by arguing that they attest to an optimal response strategy. By examining upper limb muscle recruitment during a free-choice reach task, we show early recruitment of a sub-optimal averaged motor command to the two targets that subsequently transitions to a single motor command that compensates for the initially averaged motor command. Thus, recording limb muscle activity permits single-trial resolution of the dynamic influence of the non-chosen target through time

INTRODUCTION

The external environment offers multiple goals for action, but ultimately only one action can be selected. How does the brain decide between these potential actions? Classic theories of decision-making assume a two-stage process, where the brain first selects an appropriate action, and then plans and executes the desired motor commands (Donders, 1969; McClelland, 1979). However, neurophysiological studies have suggested that multiple potential motor plans can be concurrently encoded and compete for selection within brain regions involved in eye (Christopoulos et al., 2018; McPeek and Keller, 2004; Port and Wurtz, 2003) or reach movements (Cisek and Kalaska, 2005; Klaes et al., 2011). Competition may also influence behavioral output. For example, when participants are free to look to either one of two suddenly appearing visual targets, they sometimes look to an in-between position (Chou et al., 1999; Findlay, 1982). Because such saccadic averaging is most prominent for short-latency saccades (Ottes et al., 1984; Walker et al., 1997), it is thought that representations of multiple saccade targets initially compete for selection before resolving into a final decision (Kim and Basso, 2008; McPeek and Keller, 2002).

There is currently a debate as to whether motor plans can be represented concurrently within the reaching system. A recent neurophysiological study (Dekleva et al., 2018) proposed that the apparent concurrent encoding of multiple reach plans reported by Cisek and Kalaska (2005) arose from averaging of neural activity across many trials; while the represented alternative can vary trial-to-trial, only a single alternative is represented on any given trial. Behaviorally, reach trajectories that launch in a direction between two alternatives have been observed in ‘go-before-you-know’ paradigms (Chapman et al., 2010), where reach movements are launched before the ‘correct’ target is unveiled. The intermediate reach movements observed

in such a paradigm have been proposed to arise either from an averaging of two competing reach plans (Gallivan et al., 2017; Stewart et al., 2014; Enachescu et al., 2021), or from a strategy that optimizes task success given the nature of the paradigm (Haith et al., 2015; Hudson et al., 2007; Wong and Haith, 2017; Alhussein and Smith, 2021).

In the reaching domain, studies of target selection and potential competition often impose a time delay between target presentation and either movement initiation or target identification (as in the 'go-before-you-know' paradigm). Such methodological features differ from oculomotor tasks that elicit saccadic averaging. Here, we explore whether evidence for a competition between potential reach targets can be observed at the individual trial level if we adopt an immediate and free response paradigm, like in the saccade averaging tasks. Accordingly, we studied humans reaching in a *free-choice, double-target task* that requires an immediate response (**Fig. 1b,c**). Unlike the 'go-before-you-know' paradigm, there is no correct target and thus nothing is gained by strategically aiming between the two targets. We recorded electromyographic (EMG) activity from an upper limb muscle, and focus on the timing and magnitude of EMG recruitment in response to the presentation of the two targets.

Previous studies (Glover and Baker, 2019; Pruszynski et al., 2010; Wood et al., 2015) have shown that two waves of directionally-tuned EMG activity are evoked during reaches to a single visual target: an initial *stimulus-locked response* (SLR) that occurs ~100 ms after visual target onset, followed by a larger wave of EMG activity associated with the onset of the reach movement (MOV, ~200-300 ms after the SLR). The processes governing muscle recruitment during the SLR and MOV intervals are known to differ. For example, the SLR is directed towards the stimulus location even during anti-reaches (Gu et al., 2016), is only influenced by the implicit but not explicit component of motor learning (Gu et al., 2019), and is strongly

influenced by stimulus properties (Glover and Baker, 2019; Kozak et al., 2019; Wood et al., 2015; Kozak and Corneil, 2021). In contrast, EMG during the MOV interval reflects the kinematics of the actual reaching response and is fully determined by the reach geometry, but not influenced by task instructions or stimulus properties.

By examining EMG activity in these intervals during our free choice, double-target reaching task, we found evidence for a dynamic and evolving interaction between the chosen and non-chosen target that plays out on individual trials. During the SLR interval, the non-chosen target influences EMG, attesting to a form of averaging that is biased in favor of the ultimately selected target. This averaging is also observed as an attraction to the non-chosen target in the early reach kinematics. Subsequently, this influence of the non-chosen target yields into a goal-directed motor command during the MOV interval that compensates for the earlier subtle attraction from the non-chosen target and bows the reach trajectory away from the non-chosen target.

MATERIALS AND METHODS

Participants and Procedures

The experiment was conducted with approval from the institutional ethics committee from the Social Sciences faculty at Radboud University Nijmegen, The Netherlands. 12 participants (eight females and four males), between 18 and 33 years of age (mean ±SD = 24 ±5), gave their written consent prior to participating in the experiment. Three participants (one female and two males) were self-declared left-handed, while the remaining participants were self-declared right-handed. All participants were compensated for their time with either course credits or a monetary

payment and they were free to withdraw from the experiment at any time. All participants had normal or corrected-to-normal vision and had no know motor impairments.

Reach Apparatus and Kinematic Acquisition

Participants were seated in a chair in front of a robotic rig. The participant's right arm was supported by an air-sled floating on top of a glass table. All participants performed right-handed horizontal planar reaching movements while holding the handle of the planar vBOT robotic manipulandum (Howard et al., 2009). The vBOT measured both the *x*- and *y*-positions of the handle at a 1 kHz sampling rate. Throughout the whole experiment a constant load of 5 N in the rightward direction, relative to the participant, was applied to increase the baseline activity for the right pectoralis muscle (see below). All visual stimuli were presented within the plane of the horizontal reach movements via a semi-silver mirror, which reflected the display of a downward facing LCD monitor (Asus – model VG278H, Taipei, Taiwan). The start position and the peripheral visual targets were presented as white circles (0.5 and 1.0 cm radii, respectively) onto a black background. Real-time visual feedback of the participant's hand position was given throughout the experiment and was represented by a yellow cursor (0.25 cm in radius).

EMG Acquisition

EMG activity was recorded from the clavicular head of the right pectoralis major (PEC) muscle using wireless surface EMG electrodes (Trigno sensors, Delsys Inc., Natick, MA, USA). The electrodes were placed ~1 cm inferior to the inflection point of the participant's right clavicle. Concurrent with the EMG recordings, we also recorded a photodiode signal that indicated the

precise onset of the peripheral visual targets on the LCD screen. Both the EMG and photodiode signals were digitized and sampled at 1.11 kHz.

Experimental Paradigm

Each trial began with the onset of the start position located at the center of the screen, which was also aligned with the participant's midline. Participants had to move their cursor into the start position and after a randomized delay period (1-1.5 sec) either one (*Single Target*, 25% of all trials, **Fig. 1a**) or two peripheral targets appeared (*Double Targets*, 75%, **Fig. 1b,c**). All peripheral targets were presented 10 cm away from the start position and at one of 12 equally spaced locations around the start position (dotted circles in **Fig. 1a**). The onset of the peripheral targets occurred concurrently with the offset of the start position. Participants were explicitly instructed to reach as fast as possible towards one of the peripheral target locations during *Double Target* trials. To ensure that the participants reached as fast as possible, the peripheral targets turned red if the cursor had not moved out of the start position within 500 ms after the onset of the peripheral targets. The trial ended as soon as the cursor entered one of the peripheral targets.

Each experiment consisted of eight blocks, each block contained 240 trials, with 60 *Single Target* and 180 *Double Target* trials, pseudo-randomly interleaved. For the *Double Target* trials, the two targets appeared either 60°, 120°, or 180° apart in equal likelihood. Each possible single and double target configuration was presented five times in every block, resulting in 40 repeats over the whole experiment.

Data Analyses

All data were analyzed using custom-written scripts in Matlab (version R2014b, Mathworks Inc., Natick, MA, USA). For both the 60° and 120° *Double Target* trials, we sorted trials based on whether the final reach was directed to either the CW (**Fig. 1b**, red arrow) or CCW target location (blue arrow). Thus, for all CW and CCW reach trials the non-chosen target location was in the CCW and CW direction, respectively. Trials from the 180° *Double Target* condition cannot be sorted in this way, since the non-chosen target location was always 180° away.

Reach onset detection and initial reach error: Reach onset was identified as the first time-point after the onset of the peripheral targets at which the tangential hand velocity exceeded 2 cm/sec. Reach reaction time (RT) was calculated as the time between the onset of the peripheral targets and the initiation of the reach movement. Initial reach direction was quantified as the angular direction of the vector between the start position and the location of the hand at the time of reach onset. From this, initial reach error was defined as the angular difference between the initial reach direction and the direction of the final chosen target.

EMG processing and trial inclusion criteria: All EMG data were first rectified and aligned to both the onset of the peripheral targets (as measured by the onset of the photodiode) and reach initiation. To account for the difference in EMG recordings across the participants, we first normalized EMG activity for each participant by dividing against their own mean baseline activity (i.e. mean EMG activity over the 40 ms window prior to the stimuli onset). We then log-normalized each participant's EMG activity to account for the non-linearity of EMG activity. We specifically examined two distinct epochs of EMG activity: (1) The initial *SLR* that occurs 85-

125 ms evoked by the onset of the visual stimuli (Gu et al., 2016, 2018, 2019), and (2) the later movement-related response (MOV, -20 to 20 ms around reach initiation) associated with reach onset. To prevent any overlap between these two different epochs, we excluded all trials with RTs less than 185 ms (~7% all trials). We also excluded with RTs greater than 500 ms (<0.1% of all trials).

Receiver-Operating Characteristic Analysis: As done previously (Corneil et al., 2004; Pruszynski et al., 2010), we used a time-series receiver-operating characteristic (ROC) analysis to quantitatively detect the presence of a SLR. To do this, we first separated leftward (target locations between 120° and 240° from straight right) and rightward (-60° to 60°) *Single Target* trials. For each timepoint from 100 ms before to 300 ms after target onset, we calculated the area under the ROC curve between the EMG activity for leftward compared to rightward trials. This metric indicates the probability that an ideal observer could discriminate the target location based solely on the distribution of EMG activity at that given timepoint. A value of 0.5 indicates chance discrimination, whereas a value of 1 or 0 indicates perfect correct or incorrect discrimination, respectively. We set the threshold for discrimination at 0.6, as this criterion exceeds the 95% confidence intervals for EMG data that has been randomly shuffled through a bootstrapping procedure (Chapman and Corneil, 2011). The discrimination time was defined as the first timepoint after target onset at which the ROC was above 0.6 and remained above that threshold for at least five out of the next 10 timepoints. We defined any participant with a discrimination time less than 125 ms as a participant exhibiting a SLR. Based on this criterion, 11 of the 12 participants had a detectable SLR. All subsequent analyses were done on the 11 participants with a SLR.

Directional tuning of EMG activity: We assumed cosine tuning (**Eq. 1**) between the log-normalized EMG activity and the chosen target location for both the SLR and MOV epochs:

$$EMG(x) = A \times cos(x - \theta) \quad \textbf{(1)}$$

in which x is the chosen target location in degrees, starting CCW from straight right; $EMG(x)$ is the log-normalized EMG activity for the given target location; A is the amplitude of the cosine tuning; and θ is the preferred direction (PD) of the EMG activity. We used Matlab's curve fitting toolbox *fit* function to estimate both the A and θ parameters. We constrained our search parameters such that $A > 0$ and $0° \leq \theta < 360°$. The initial search parameters were $A = 1$ and $\theta = 180°$. PDs of 0° and 180° would represent straight rightward and leftward, respectively.

Model predictions: Previous studies have proposed different models of how the brain converts multiple visual targets into a single motor command. Here we assumed a constant non-linear cosine tuning between target location and reach direction to generate the predicted responses during *Double Target* trials. Each model used parameters derived from each participant's own *Single Target* data (**Fig. 2a**) to predict both the PD and amplitude of the cosine tuning curves for *Double Target* trials. Thus, no free parameters were fitted in any of these four models.

Model 1: The *winner-take-all model* (**Fig. 4a**) assumes that only the target location that the participant reaches towards is converted into a motor command. Therefore,

$EMG(x_1|x_1, x_2) = EMG(x_1)$, where x_1 and x_2 are the chosen and non-chosen target locations, respectively.

Model 2: The *spatial averaging model* (**Fig. 4b**) assumes that the two potential target locations are first spatially averaged into an intermediate target location. Then that target location is converted into a motor command. Therefore, $EMG(x_1|x_1, x_2) = EMG\left(\frac{x_1+x_2}{2}\right)$.

Model 3: The *motor averaging model* (**Fig. 4c**) assumes that the two potential target locations are first converted into their own distinct motor commands and then averaged into a single motor command. Therefore, $EMG(x_1|x_1, x_2) = 0.5 \times EMG(x_1) + 0.5 \times EMG(x_2)$.

Model 4: The *weighted motor averaging model* (**Fig. 4d**) is a variation of the motor averaging model. It assumes that the two target locations are first converted into their associated motor commands, which are then differentially weighted before being averaged into a single motor command. A higher weight is assigned to the chosen target compared to the non-chosen target location. To estimate these weights indirectly, we used each participant's own *Single Target* data. Previous studies have shown that the SLR magnitude is negatively correlated with the ensuing RT for single target visually-guided reaches (Pruszynski et al., 2010; Gu et al., 2016). We assumed that the trial-by-trial magnitude of the SLR reflected the 'readiness' to move towards the target location. Thus, we did a median RT split of the *Single Target* data to get cosine tuning for both *Fast* and *Slow RT* trials. This results in *Fast RT* and *Slow RT* amplitude and PD estimates, which were used to compute the tuning curves for the *Double Target* trials. The *Fast RT* and *Slow RT* parameters were used for the chosen and non-chosen target location,

respectively. Therefore, $EMG(x_1|x_1, x_2) = 0.5 \times EMG_{Fast}(x_1) + 0.5 \times EMG_{Slow}(x_2)$.

To quantify the goodness-of-fit for each model, due to the non-linear interaction between PD and normalized amplitude, we evaluated the total fit error between the predicted and observed tuning curves. To do this, we took the sum of mean squared error for each of the 12 different reach directions (i.e. x_1 = 0°, 30°, 60°, … 330°) between the predicted and observed tuning curves.

Statistical Analyses

Statistical analyses were performed using either one or two-sample *t*-tests or a one-way ANOVA. For all post-hoc comparisons, we used a Tukey's HSD correction. The statistical significance was set as $P < 0.05$. For the model comparison, significance was set at $P < 0.0083$, Bonferroni corrected for the six possible comparisons between the four different models.

RESULTS

Under continuous EMG recording of the right PEC muscle, participants performed a free-choice goal-directed center-out right-handed reach movement in response to the onset of either one (**Fig. 1a**, *Single Target*) or two visual targets (**Fig. 1b** and **c**, *Double Target* trials) that appeared concurrently. The visual targets pseudo-randomly appeared at 12 different possible directions equally spaced around the start position. For *Double Target* trials, the two visual stimuli had an angular separation of either 60°, 120°, or 180°.

Prior to examining the *Double Target* trials, we will first describe PEC EMG activity during the *Single Target* trials. **Figure 1a** shows the individual (middle panel) and mean log-

normalized EMG activity (right) during left-outward (orange trace), straight outward (gray), and right-outward *Single Target* trials (green) from a representative participant. All trials are aligned to visual target onset and the individual trials were sorted based on the reach RTs (color squares). Note, the increase and decrease of activity for the right PEC muscle for left-outward and right-outward reach movement, respectively. Consistent with previous studies (Pruszynski et al., 2010; Wood et al., 2015; Glover and Baker, 2019), we observed a reliable difference in EMG activity for the three different reach directions at two epochs: an initial SLR epoch that occurs ~100 ms after stimulus onset and a later MOV epoch associated with reach RT (stochastically occurring ~200 ms after stimulus onset). Across our participants, the mean ±SEM discrimination time (see **Materials and Methods**) for the SLR was 87.7 ±2.7 ms and the corresponding reach RT was 232 ±3.3 ms. We calculated the SLR magnitude for a given trial as the mean log-normalized EMG activity during the SLR epoch, 85-125 ms after stimulus onset (Gu et al., 2018, 2019) indicated by the white dashed boxes and shaded panels in **Figure 1**. For this participant, we found a reliable increase and decrease in SLR magnitude for left-outward and right-outward trials, respectively, when compared to straight outward trials (1-way ANOVA, $F_{(2,105)} = 37.41$, $P < 10^{-12}$, post-hoc Tukey's HSD, both $P < 0.001$).

Having established the profile of EMG activity during the SLR epoch on *Single Target* trials, we next examined if the presence of a second non-chosen target during the *Double Target* trials changed the SLR. For a direct comparison with **Figure 1a**, we first examined trials with the same reach direction (i.e. straight outward) but with a different non-chosen target location (60° CW, blue, or 60° CCW, red, from the target, **Figure 1b**). If the non-chosen target location has no influence (i.e. no averaging), we would predict that the SLR magnitude would resemble that observed during outward reach movement during *Single Target* trials, which we overlaid in gray

in **Figure 1b**. Despite the same reach direction, we observed both an increase and a decrease of EMG activity during SLR epoch for *Double Target* trials relative to the *Single Target* trials (1-way ANOVA, $F_{(2,83)} = 16.17$, $P < 10^{-5}$, post-hoc Tukey's HSD, $P = 0.01$ and $P = 0.004$, respectively) when the non-chosen target was in the left-outward and right-outward locations, respectively. This result suggests that EMG activity during the SLR is systematically altered by the presence of a second non-chosen target.

A second way to examine the SLR during *Double Target* trials is to compare SLR magnitude on trials with the same two visual targets, but different reach directions. **Figure 1c** shows the EMG activity when both the left-outward (blue) and right-outward (red) targets were presented to the representative participant. If the SLR averaged the locations of the two visual targets completely, then we would predict that the resulting EMG activity would not differ regardless of the final reach direction. However, we observed a reliable difference in SLR depending on whether the participant chose either the left-outward or right-outward target (1-way ANOVA, $F_{(2,72)} = 7.06$, $P = 0.002$, post-hoc Tukey's HSD, $P = 0.01$). This result suggests that EMG activity during the SLR is modulated by the chosen reach direction, even when the same two visual targets are presented.

Systematic shifts in tuning of SLR during Double Target trials

The results from **Figure 1b** and **c** demonstrated that the magnitude of the SLR during *Double Target* trials depended on both the target configuration and the eventual reach direction. To quantify the extent of averaging that occurred, we sought to compare how the directional tuning of the SLR changed between *Single* and *Double Target* trials. Previously, it has been shown that the SLR magnitude can be described by a cosine tuning function (Gu et al., 2019; **Eq. 1**). For

each tuning function we can extract both the preferred direction (PD) and the amplitude of the fit. **Figure 2a** shows both individual trial data (dots) and the cosine tuning fit (line) for the *Single Target* trials from the representative participant in **Figure 1a**. The PD of this fit was 173° CCW (arrow) from straight rightward, indicating that the largest SLR magnitude could be evoked by a visual target presented straight leftward of the start position. Importantly, this cosine tuning between SLR magnitude and target location was not simply due to movement-related EMG activity from trials with the shortest RTs, as this relation was still present when we performed a median RT split and re-fitted the data on either *Fast RT* (**Figure 2b**, dark line) or *Slow RT* trials (light), separately. Across our participants, we found no systematic difference in the PDs between *Fast* and *Slow RT* trials (**Figure 2c**, group mean ±SEM: PD = 169 ± °3 and 162 ± °5°, respectively, paired *t*-test, $t_{(10)} = 1.30$, $P = 0.22$). We did find larger amplitudes (i.e. larger SLR magnitudes) for *Fast* compared to *Slow RT* trials (**Figure 2d**, paired *t*-test, $t_{(10)} = 7.89$, $P < 10^{-4}$), which is consistent with previous studies demonstrating a negative correlation between SLR magnitudes and RTs on a trial-by-trial basis (Pruszynski et al., 2010; Gu et al., 2016). Note, we will leverage this relationship later in the modeling portion of the **RESULTS**.

We next fitted the SLR cosine tuning for the *Double Target* trials. For this we chose to align the trials based on the participant's reach direction (**Figure 1b**) rather than controlling for the visual target locations (**Figure 1c**) to accentuate the effect of the non-chosen target location. **Figure 3a** shows the fits for the three different angular separations for the representative participant. For both the 60° and 120° conditions, we generated two separate fits for when the non-chosen target location was either CW (red) or CCW (blue) relative to the reach direction. To give a little more intuition of how this figure relates to individual trials, the highlighted data (shaded box in the left panel of **Figure 3a**) corresponds to the same trials as **Figure 1b**. The right

panel of **Figure 3a** shows the fit of SLR magnitude to the 180° *Double Target* condition. Note, the data cannot be split because the non-chosen target location is always 180° away from the reach direction. Despite the two targets being in diametrically opposite directions, the SLR was still reliably tuned for the 180° condition ($r^2 = 0.19$, for this participant). Across participants, the directional tuning of the SLR during the 180° *Double Target* trials was not reliably different from that observed in the *Single Target* trials (paired *t*-test, $t_{(10)} = 1.92$, $P = 0.08$), although we did find a systematic decrease in the amplitude of the fits (see below).

For both the 60° and 120° conditions, since we aligned our data relative to the final reach direction, the only difference between CW and CCW trials was the non-chosen target location. If the EMG activity was the result of a perfect averaging between the two target locations, then we would predict the difference in PD between CW and CCW trials (ΔPD) to be equal to the angular separation between the two targets (i.e. ΔPD = 60° and 120°, respectively). If the EMG activity was only influenced by the chosen target direction, then we would predict no difference between CW and CCW conditions (ΔPD = 0°). Consistent with the individual trial data from **Figure 1b**, we observed signs of averaging, albeit incomplete, for the representative participant for both the 60° and 120° conditions, with ΔPDs of 49.3° and 53.0°, respectively (**Figure 3a**).

We found similar results of partial averaging across our participants for both the 60° (**Figure 3b**, left panel, mean ±SEM, ΔPD = 38.6 ± °3.5°, one sample *t*-test against zero, $t_{(10)} = 10.9$, $P < 10^{-6}$) and 120° *Double Target* conditions (ΔPD = 47.2 ±5.4°, one sample *t*-test, $t_{(10)} = 8.7$, $P < 10^{-5}$). To fairly compare the extent of averaging between the conditions, we converted the ΔPD into an averaging ratio (**Figure 3b**, right panel): a value of 1 indicates complete averaging (ΔPD = 60° and 120°, dashed lines) and a value of 0 indicates no averaging (ΔPD = 0°). Overall, we found that the extent of averaging decreases as the angular separation increased

from 60° to 120° (averaging ratio = 0.64 ±0.06 and 0.39 ±0.05 a.u., respectively, paired *t*-test, $t_{(10)} = 3.81$, $P = 0.003$).

In addition to the changes in PD of the SLR tuning, we also quantified the changes in the amplitude during *Double Target* trials. **Figure 3c** shows the mean amplitude for the three conditions, normalized to each participant's own *Single Target* amplitude as a baseline. We observed a systematic decrease in amplitude as a function of angular separation: 1.13 ± 0.04, 0.88 ± 0.04, and 0.63 ± 0.05 a.u. for the 60°, 120°, and 180° conditions, respectively (repeated measures 1-way ANOVA, $F_{(2,20)} = 41.1$, $P < 10^{-7}$, post-hoc paired *t*-test, all $t_{(10)} > 5.5$, $P < 10^{-3}$). The systematic changes in PD and amplitude will be interpreted based on different possible averaging models tested below.

Model predictions of EMG activity during the SLR epoch for Double Target trials

Previous studies examining averaging behavior for both eye and reach movements have proposed different models for how the two visual targets may be integrated into a single motor command. These models make distinct predictions for how the PD and amplitude of the tuning curves should change between *Single* and *Double Target* trials (see **Materials and Methods** for exact details). **Figure 4e** shows the predicted tuning curves generated from the four different proposed models for both the 120° CW and CCW conditions, using the *Single Target* data (dashed gray line) from the representative participants. **Model 1** is the *winner-takes-all model* (**Figure 4a**), which proposes that the two visual targets compete for selection in a winner-takes-all process, resulting in a motor command that is generated towards the winning target location (Donders, 1969; McClelland, 1979). Effectively, there is no integration between the two target locations at any stage of the process. Note this model is agnostic about whether the competition

for selection occurs at either a spatial or motor representation. **Model 2** is the *spatial averaging model* (**Figure 4b**), which proposes that the two targets are first averaged into a spatial representation, resulting in a motor command towards the intermediate spatial direction (Findlay, 1982; Glimcher and Sparks, 1993; Walker et al., 1997; Chou et al., 1999). **Model 3** is the *motor averaging model* (**Figure 4c**), which proposes that the two targets are first converted into two independent motor commands (Edelman and Keller, 1998; Port and Wurtz, 2003; Cisek and Kalaska, 2005) and then averaged into a single motor command (Katnani and Gandhi, 2011; Stewart et al., 2014; Gallivan et al., 2017). Finally, **Model 4** is the *weighted motor averaging model* (**Figure 4d**), which is a variation of the motor averaging model. Once again, the two targets are first converted into two separate motor commands, but a stronger weighting is given towards the chosen compared to the non-chosen target location (Kim and Basso, 2008, 2010; Pastor-Bernier and Cisek, 2011). The final motor command is then an average of these two differentially weighted motor commands. This model can be conceptualized as a race between two accumulators (Schall, 2001, Enachescu et al., 2021), with the eventual chosen target location accumulating at a faster rate compared to the non-chosen target location. Instead of fitting the weights of the chosen and non-chosen target locations, we decided to indirectly estimate them by using the *Fast* and *Slow RT* tuning curves from the *Single Target* trials, respectively (**Figure 2b)**. Previous studies (Pruszynski et al., 2010; Gu et al., 2016, 2018) have linked trial-by-trial SLR magnitude to the ʻreadiness’ of the motor system towards a specific target location. Here, we assumed that during *Double Target* trials the motor system reach towards the more ʻready ’target location.

Weighted motor averaging model best explains SLR-related EMG activity

Figure 5a and **b** summarize the four different model predictions (color lines) for both the ΔPD averaging ratio and normalized amplitude fits across the three different *Double Target* angular separation conditions relative to *Single Target* trials. The *winner-takes-all model* predicted no change in either ΔPD (i.e. averaging ratio = 0 a.u.) or amplitude (i.e. normalized amplitude = 1 a.u.). Both the *spatial* and *motor averaging models* predicted complete averaging (averaging ratio = 1 a.u.) for both the 60° and 120° conditions. The key difference between the two models was in the predicted amplitude, where the *spatial averaging model* predicted no change (amplitude = 1 a.u.), while the *motor averaging model* predicted a systematic decrease (amplitude < 1 a.u.). Finally, the *weighted motor averaging model* predicted both a partial averaging (0 < averaging ratio < 1) and a decrease in amplitude. The extent of these changes depended on each participant's own *Fast* and *Slow RT* fits.

Figure 5a and **b** also show our observed group data (open bars) plotted against the predictions from the four models during the SLR epoch. Note only the *weighted motor averaging model* (green lines) captured both the systematic decrease in averaging ratio and amplitude that was in the observed data. Since the parameters of all four models were derived from each participant's own *Single Target* trials and contained no free parameters, we can directly compare the four different models. **Figure 5c** illustrates the mean ± SEM of the fit error between the observed and predicted fits across the participants. We found that the *weighted motor averaging model* best predicted the observed tuning curves compared to the other three models during the SLR epoch (repeated measures 1-way ANOVA, $F_{(3,30)} = 7.7$, $P < 10^{-3}$, post-hoc paired *t*-test, $t_{(10)} = 3.6$, 4.1, and 4.8, $P = 0.005$, 0.002, and 0.0001, compared to the *winner-takes-all*, *spatial*, and *motor averaging models*, respectively).

Winner-takes-all model best explains MOV-related EMG activity

Up to this point, we have only examined the initial wave of EMG activity time-locked to the onset of the two visual targets (i.e. during the SLR epoch). But are there also signatures of averaging in the tuning of EMG activity associated with movement onset (MOV epoch) in the *Double Target* trials? We therefore examined EMG activity during the MOV epoch, i.e. mean EMG activity -20 to 20 ms around reach onset.

Figure 5d and **e** show both the averaging ratio and amplitude across participants, based on fits to the EMG activity during the MOV epoch. Unlike the SLR epoch, the *winner-takes-all model* best predicted EMG activity around reach onset (**Fig. 5f**, repeated measures 1-way ANOVA, $F_{(3,30)} = 348.8$, $P < 10^{-22}$, post-hoc paired *t*-test, $t_{(10)} = 28.6, 21.8, 29.0$, all $P < 10^{-9}$, compared to the *spatial, motor,* and *weighted motor averaging models*, respectively). Although the *winner-takes-all* model provides the best explanation for our MOV epoch data, we still observed an influence of the non-chosen target location with an averaging ratio shifting in the opposite direction, suggesting a *repulsion* from the non-chosen target location (averaging ratio = –0.13 ±0.03 and –0.11 ±0.01 a.u., for 60° and 120° *Double Target* trials, respectively, one sample *t*-test against zero, $t_{(10)} = –4.2$ and –11.7, both $P < 0.05$, **Fig. 5d**). However, in the next section we will argue that this is not a genuine repulsion from the non-chosen target, but a compensation for the earlier attraction by the non-chosen target in the SLR epoch.

Early kinematics show attraction to the non-chosen target location

Having established an opposite influence of the non-chosen target on the tuning of EMG activity during the SLR and MOV epoch, we next determined whether the brief burst of muscle

recruitment during the SLR interval carried any behavioral consequences. **Figure 6a** shows the representative participant's initial reach error (i.e. the difference between the chosen target location and the initial reach direction at the time of reach onset) for both *Single* and *Double Target* trials. For the *Single Target* trials the distribution of initial reach direction is nicely centered on the actual target direction. However, for the *Double Target* trials the distributions of initial reach direction are clearly shifted toward the non-chosen target. **Figure 6b** shows the median initial reach error direction, averaged across participants. This initial reach error differed significantly from zero for both target separations (Initial Reach Error = 15.2 ± °4.3° and 13.9 ° ±5.5°, paired *t*-test, $t_{(10)}$ = -11.7 and -8.4, both $P < 10^{-5}$, respectively). These initial reach errors indicate an early attraction toward the non-chosen target, which is consistent with the averaging of EMG activity during the SLR interval. Following this averaging during the SLR interval, we subsequently observed a repulsion effect in the tuning of the EMG activity in the MOV epoch for the *Double Target* trials. This is highlighted by a significant negative averaging ratio (**Figure 5d**), We surmise that this repulsion corresponds to compensatory muscular activity that corrects for the initial attraction of the arm toward the non-chosen target, bowing the arm back toward the chosen target location (**Figure 6c).**

DISCUSSION

Contemporary theories of decision-making posit that multiple potential motor plans compete for action selection (Cisek, 2007; Schall, 2001). Behavioral and neurophysiological results show that such competition plays out within the oculomotor system (Chou et al., 1999; Coren and Hoenig, 1971; Findlay, 1982; Ottes et al., 1984; Walker et al., 1997), but due to differences in analytical techniques and tasks, it is unclear whether such results generalize to the reaching system. Here,

by measuring upper limb EMG while human subjects perform a reaching task that demands an immediate response, we demonstrate that the non-chosen target influences the earliest wave of muscle recruitment following target onset. Such evidence is apparent on a single trial, implicating competitive interactions between the chosen and non-chosen target within upstream premotor areas soon after target appearance. Competitive interactions in the first wave of EMG were biased in favor of the ultimately selected target, perhaps indicating a random or strategic preference established before target onset. This initial biased motor averaging had behavioral consequences in terms of the reach angle at reach onset, but subsequently gave way to a single goal-directed motor command that subtly bowed the arm onto a straight trajectory to the chosen target.

The SLR is a trial-by-trial weighted average of two different motor commands

We tested different models of how the brain could have integrated the two visual targets. Classic saccadic averaging studies have suggested that *spatial averaging* of the target locations occurs first and a motor command is then generated towards the intermediate location (Coren and Hoenig, 1971; Walker et al., 1997). In contrast, reaching studies have hinted towards *motor averaging*, where the intermediate reach movement is composed of two different reach plans (Gallivan et al., 2017; Stewart et al., 2014). Here, we found that a *weighted motor averaging* model best explained the partial averaging during the SLR epoch. Such weighted motor averaging is apparent on a single trial, hence our results are inconsistent with a recent interpretation (Dekleva et al., 2018) that the apparent encoding of multiple alternatives in premotor cortex during a delay period may be attributable to the averaging of different alternatives across multiple trials. Instead, our result is consistent with contemporary theories for

a deliberation process in which multiple motor plans compete for selection (Cisek, 2007; Schall, 2001; Enachescu et al., 2021). For example, previous neurophysiological studies have shown that experimentally manipulating the decision variable, via either target uncertainty (Basso and Wurtz, 1997; Dorris and Munoz, 1998), target expectation (Basso and Wurtz, 1998; Bichot et al., 1996), or reward expectation (Pastor-Bernier and Cisek, 2011; Rezvani and Corneil, 2008), modulates the neural representation of the competing motor plans. Similarly, signatures of an evolving decision variable have been shown in the long latency reflex, when subjects must indicate the direction of a random-dot motion stimulus (Selen et al., 2012). Here, rather than experimentally manipulating the decision variable, we exploited the fact that participants randomly choose one of the two visual targets and demonstrated post-hoc that the averaged SLR magnitude was biased towards the final reach direction. This suggests that either fluctuations along the sensorimotor pathway (Faisal et al., 2008; Siegel et al., 2015) or idiosyncratic preferences based on previous choices (Urai et al., 2019) biased both the initial average motor command during the SLR and the final choice. Interestingly, the influence of time varying idiosyncratic preferences on the initial representation of alternatives was also reported recently in the study by Dekleva et al. (2018), with influences of what can loosely be termed 'preference' apparent on the first neural representation of multiple targets.

While the weighted motor averaging model best explained the SLR, the fits were by no means perfect (**Figure 5**). This is likely due to the arbitrary weighting of the strength of the SLR for the chosen vs. non-chosen target, exploiting the known inverse relationship between SLR magnitude and reach RT (Gu et al., 2016; Pruszynski et al., 2010; Wood et al., 2015). Our logic parallels that used in race models (Ratcliff and Rouder, 1997; Rowe et al., 2010), which assume an independent race between the motor programs to each of the two targets, with the one

proceeding faster (drawn from the shorter-than-average subset, so endowed with a larger SLR) 'winning' over the non-chosen alternative. This process is admittedly coarse, as there is no way of inferring what the RT and associated SLR of the non-chosen alternative would have actually been. Our logic also assumes a degree of independence between competing alternatives, which may not be occurring in reality. Regardless, the weighted motor averaging model was the only model that captured the dual influence of the non-chosen target on both the tuning and magnitude of the SLR (**Figure 5**), and hence this model best captures the essence, if not the magnitude, of the interaction between competing motor plans.

Our findings require discussion in relation to recent findings and modeling by Enachescu et al. (2021). Subjects made reaching movements towards two competing targets in a classic '*go-before-you-know*' paradigm. At short reaction times, where the correct target was still unknown, reaches were directed toward one of the two targets. However, as reaction time increased the initial direction of the reach became more intermediate. The authors interpret this observation in terms of a dynamic neural field model, representing the competition as inhibitory interactions between the targets, connected to a stochastic optimal control framework. This model executes a weighted average of a continuum of control policies for all possible reach directions, but only after the competition has crossed the reach onset threshold. In addition, this competition and weighing of control policies continues as the reach unfolds. Our results are in correspondence with this framework and extend it to an immediate and free response task. If we split our data on the median RT, we also observe that short RT trials are associated with an SLR that is more tuned towards the chosen target, whereas the SLR is tuned toward an intermediate direction for the longer RT trials (data not shown). We suggest that for short RTs the neuronal state of the sensorimotor network was closer to either of the two targets and thus the competition was

quickly resolved. However, for the longer RTs the state of the sensorimotor network was less biased and thus resolution of the competition took longer and the initial movement decision less clear.

Influence of task design on the SLR

Our EMG results illustrate that different stages of decision-making influence distinct epochs of neuromuscular activity in the human motor periphery. An important corollary of this perspective is the influence of task design or stimulus properties on these distinct epochs. Previous work has established that the SLR is either muted (Wood et al., 2015) or abolished (Pruszynski et al., 2010) in paradigms that impose a delay between stimulus presentation and movement onset, and recent work shows that SLR expression is augmented when targets are temporally predictable (Contemori et al., 2021). Given this, it is likely that the SLR to the initially presented stimuli may be negligible or absent in delayed response tasks (Cisek and Kalaska, 2005; Dekleva et al., 2018; Thura and Cisek, 2014), or in variants of the go-before-you-know task that introduces a delay between the presentation of the alternatives and the initiation of the reaching movement. When an immediate response is required in the go-before-you-know paradigm, the intermediate reaching movements skew toward the more salient stimulus (Wood et al., 2011). Such results parallel recent findings showing that earlier and larger-magnitude SLRs are evoked by high-contrast (Wood et al., 2015; Kozak and Corneil, 2021) or low-spatial frequency stimuli (Kozak et al., 2019).

Recently, Wong and Haith (2017) have shown that the instruction to move rapidly reduces the production of intermediate reach trajectories and attributed this to the adoption of a control policy that maximizes task success. While the impact of such a velocity instruction on the

SLR is unknown and should be studied in the future, we suspect from previous results that the magnitude but not timing of the SLR would be modulated by the adoption of a different control policy (Gu et al., 2018, 2016). Furthermore, the short-latency of the SLR likely precludes an interpretation where a control policy is established after target onset, but the influence of task instructions on the SLR is consistent with a scenario where an established control policy presets the relevant circuitry prior to stimulus onset. This parallels the influence of task instructions on long-latency reflexes (Pruszynski and Scott, 2012; Scott, 2016).

Kinetic consequences of the SLR

EMG recordings permit the resolution of a decision-making dynamic at a level that would be difficult, if not impossible, to resolve based on kinematics alone. In our results, while EMG activity during the SLR was biased *toward* the non-chosen target, EMG activity during the MOV interval was biased in the opposite direction, *away* from the non-chosen target (**Figure. 6**). At first glance, these opposite directions of EMG recruitment in the SLR and MOV interval seem paradoxical. The forces consequent to the SLR are undoubtedly smaller than those developed closer to the time of reach initiation; in our task the duration of the SLR is brief, and the peak EMG magnitude during the SLR interval is smaller than that during the MOV interval. However, the SLR is not without a behavioral consequence, as it can induce small forces directed toward a stimulus in an anti-reach task (Gu et al., 2016). Here we show that forces arising from the averaged SLR bias the initial reach toward the non-chosen target. However, the earliest phase of the voluntary EMG response already compensates for the trial specific kinematic consequences of the averaging of the SLR. This suggests that voluntary control mechanisms very rapidly have information available about the averaged SLR responses and use this information for

feedforward adjustment of the voluntary wave of EMG activity. A similar fast mechanism has been reported for stretch reflexes (Pruszynski et al., 2009). If the background load to a muscle increases, the mono-synaptic short latency reflex increases, but adjustments in later phases, as quick as 45ms after perturbation onset, already compensate for the stronger adjustment in the first phase.

The similarities with saccadic averaging suggest a common neural substrate

Our task incorporated many task features used to elicit saccadic averaging (Chou et al., 1999; He and Kowler, 1989), including the requirement for an immediate response and equivalent sensory stimuli. Saccade kinematics offer a straightforward readout of the temporal evolution of decision-making, paralleling observations made for SLRs. For example, the temporal transition from an averaged to a goal-directed command we observed between the SLR and MOV epoch, resembles the observation that the greatest amount of saccadic averaging is seen for short-latency saccades, while more goal-directed saccades occur for longer-latency RTs (Chou et al., 1999; Walker et al., 1997). Further, we saw a systematic decrease in the extent of averaging with increased angular separation between targets, resembling that seen for saccadic averaging (Chou et al., 1999; Vokoun et al., 2014). Saccadic averaging has been related to the initial representation and subsequent resolution of competing saccade plans within the intermediate layers of the superior colliculus (Edelman and Keller, 1998; Port and Wurtz, 2003; Vokoun et al., 2014). Interestingly, the superior colliculus has also been implicated as a potential substrate for the SLR on upper limb muscles, which is delivered to the motor periphery via the tecto-reticulo-spinal pathway (Corneil and Munoz, 2014; Glover and Baker, 2019; Gu et al., 2016; Pruszynski et al., 2010; Contemori et al., 2021, Kozak and Corneil, 2021; Kozak et al.,

2019). Thus, circumstantial evidence suggests that the phenomena of saccadic averaging and the averaging of the SLR on upper limb muscles may be linked through a common collicular substrate. This subcortical substrate for the deliberation process would be in line with recent findings that M1 and PMd are mainly involved in the commitment to a choice (Derosiere et al., 2019; Thura and Cisek, 2020), but not the competition between alternatives. Unraveling the causal structure between weighted averaging of SLR signals and its relation to the commitment to a single goal-directed reach is a key direction for future neurophysiological experiments.

In summary, we examined neuromuscular activity during a free-choice reaching task to two targets. We found that, similar to saccadic averaging, the earliest motor command in the reaching system attests to a still-unresolved competition between multiple distinct motor plans. However, this competition is rapidly resolved and by the time of movement onset the motor system generates a goal directed reach movement that compensates for the averaging observed in the early trajectory.

AUTHOR CONTRIBUTIONS

Conceptualization – LPS, BDC, and WPM; Methodology – LPS; Investigation – LPS; Writing, Original Draft – LPS; Writing, Review and Editing – LPS, BDC and WPM; Funding Acquisition – WPM; Resources – LPS and WPM.

DECLARATION OF INTERESTS

The authors declare no competing interesting.

FIGURE LEGENDS

Figure 1: SLR from a representative participant. a. Individual (middle panel) and mean ± SEM (right) log-normalized EMG activity from the right PEC muscle during left-outward (yellow), straight outward (gray), and right-outward (green) *Single Target* reach trials (left panel). All EMG activity is aligned to the onset of the peripheral visual target (thick black vertical line). For individual trials, each row represents EMG activity with a single trial and trials were sorted based on reach RT (colored squares). Dashed white box and shaded area in the individual and mean EMG plots represent the SLR epoch (85-125 ms after stimulus onset). **b.** EMG activity for *Double Target* trials when matched for the same outward reach movement. The non-chosen target was either 60° CW (blue) or CCW (red) of the reach target. Same layout as **a**. **c.** EMG activity for 120° *Double Target* trials for the same visual target layout, but different. The trials were sorted based on the chosen target direction. Same layout as **a**. * $P < 0.05$.

Figure 2: Directional tuning of the SLR during *Single Target* trials. a. Cosine tuning of log-normalized SLR magnitude as a function of the target direction for *Single Target* trials from the representative participant in **Figure 1**. Dots indicate each trial, the solid line indicates the fit, and the arrow indicates the PD of the fit. **b.** The cosine tuning is maintained regardless of the ensuing reach RT, same data as **a**. but re-fitted for *Fast* (black) and *Slow RT* (gray) *Single Target* trials separately. For illustration purposes only, we have staggered the individual trial data to illustrate the difference between the two conditions. We did not stagger the cosine tuning curves. **c, d.** Group (n = 11) mean ± SEM for the PD (**c**) and amplitude (**d**) of the fits between the *Fast* and *Slow RT* trials. Each gray line indicates an individual participant and the darker line indicates the representative participant. * $P < 0.05$.

Figure 3: Systematic changes in directional tuning of the SLR during *Double Target* trials. **a.** Fits for 60°, 120°, and 180° conditions of the *Double Target* trials with all data aligned to the chosen target direction from the representative participant. For both the 60° and 120° conditions, the trials were sorted based on whether the non-chosen target was either CW (blue) or CCW (red) of the chosen target direction. Data in the shaded panel indicates the trials from **Figure 1b**. **b.** Group mean ± SEM shifts in PD (ΔPD) between the CW and CCW trials (left panel) and the normalized averaging ratio (right) for both 60° and 120° conditions across our participants. Dashed box indicates the predicted ΔPD if the SLR would be a complete average of the two targets (averaging ratio = 1 a.u.). **c.** Mean ± SEM amplitude of the fits for the three different *Double Target* conditions across our participants. The amplitudes were normalized to each participant's own amplitude fit from the *Single Target* trials. Each grey line indicates a different participant and the darker line indicates the representative participant from **a**. * $P < 0.05$.

Figure 4: Model predictions of the tuning curves during *Double Target* trials. a. The *winner-takes-all* model chooses one visual stimulus as the target and converts it into the final motor command. **b.** The *spatial averaging* model averages the two visual stimulus directions into an intermediate target direction and that target direction is converted into a motor command. **c.** The *motor averaging* model first converts the two visual stimuli into two separated motor commands. Then it averages the two motor commands into a single motor command. **d.** The *weighted motor averaging* model first converts the two visual stimuli into two separate motor commands, but the cosine tuning have different weights. Then it averages the two motor commands into a single

motor command. **e.** The predicted tuning curves for 120° *Double Target* trials from the representative participants in **Figures 1** and **2**.

Figure 5: Comparisons of model predictions and observed group data for *Double Target* trial fits. a, b. The model predictions (colored lines) overlaid over the observed mean ± SEM group data (open black bars) for EMG activity during the SLR epoch (85-125 ms after stimuli onset) for both the averaging ratio (**a**) and amplitude (**b**). **c.** The mean ± SEM group model fit errors for the four different models. **d-f.** Same analysis as **a-c.** but examining the EMG activity during the MOV epoch (-20-20 ms around reach RT). * $P < 0.0083$.

Figure 6: Systematic repulsion away from the non-chosen target direction at the time of reach RT. a. Histogram of reach error direction, relative to the chosen target direction, at the time of reach RT for the representative participant during the experiment. For *Double Target* trials, the location of the non-chosen target direction is shown as colored circles along the *x*-axis. Vertical lines represent the median reach errors. **b.** Mean ±SEM of difference in median reach error between CW and CCW during *Double Target* trials. Dashed boxes represent full averaging. **c.** Initial reach errors converge to the target direction while the reach unfolds.

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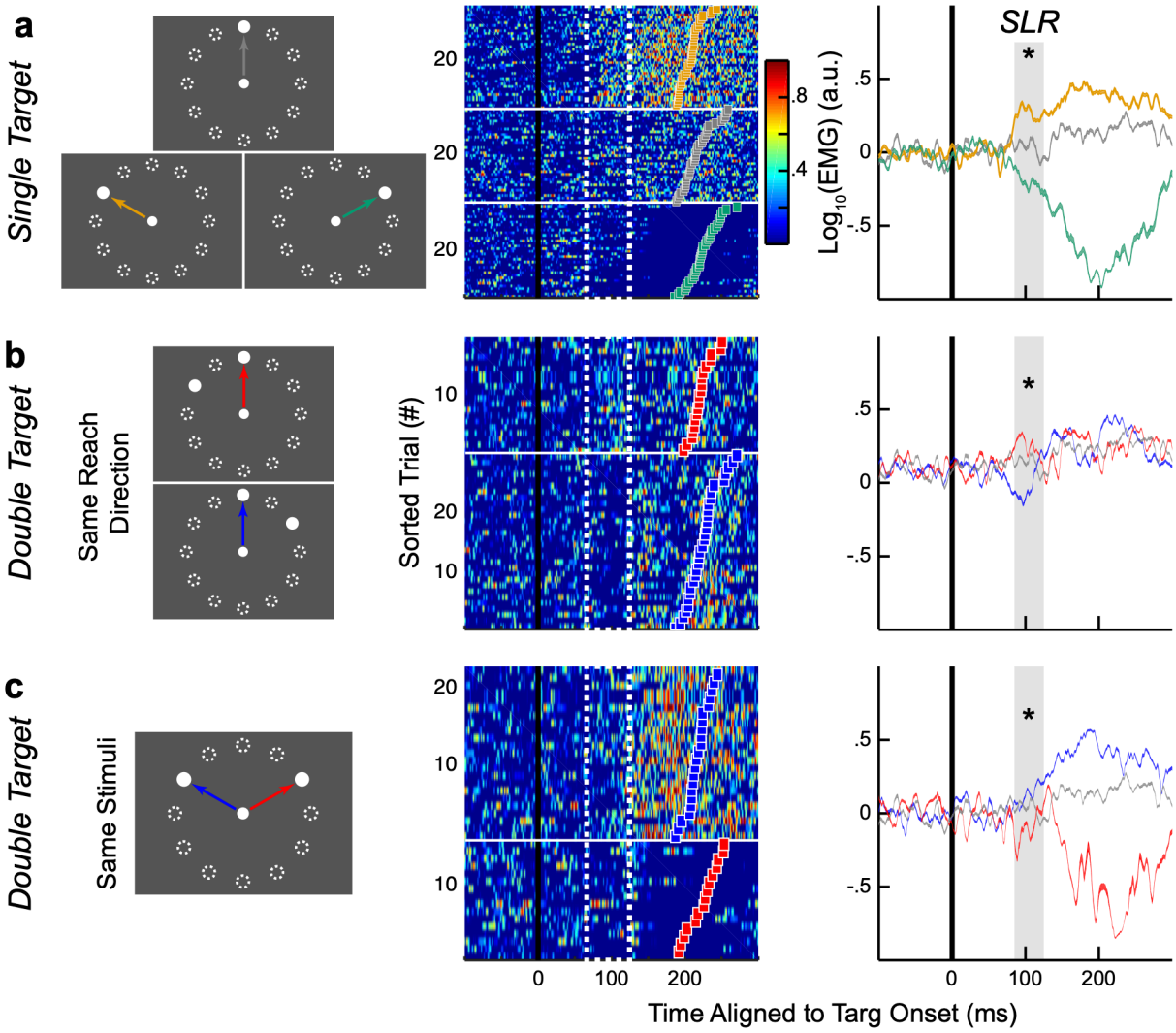

a
Single Target
b
Double Target
Same Reach Direction
c
Double Target
Same Stimuli
Sorted Trial (#)
SLR
Log10(EMG) (a.u.)
Time Aligned to Targ Onset (ms)

Figure 1

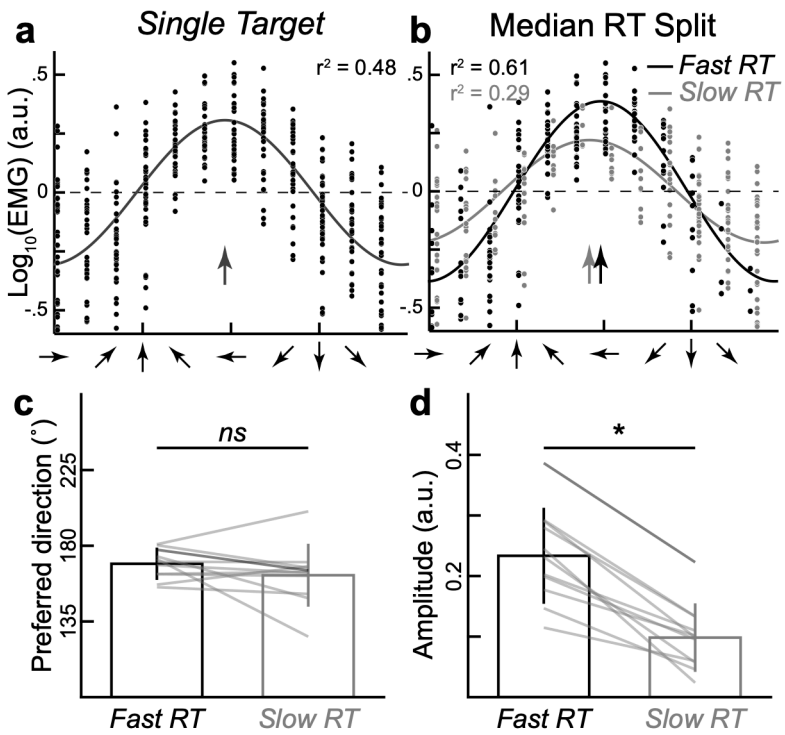
a
Single Target
b
Median RT Split
r² = 0.48
r² = 0.61
r² = 0.29
Fast RT
Slow RT
Log10(EMG) (a.u.)
.5
0
-.5
c
d
ns
*
Preferred direction (°)
225
180
135
Amplitude (a.u.)
0.4
0.2
Fast RT
Slow RT

Figure 2

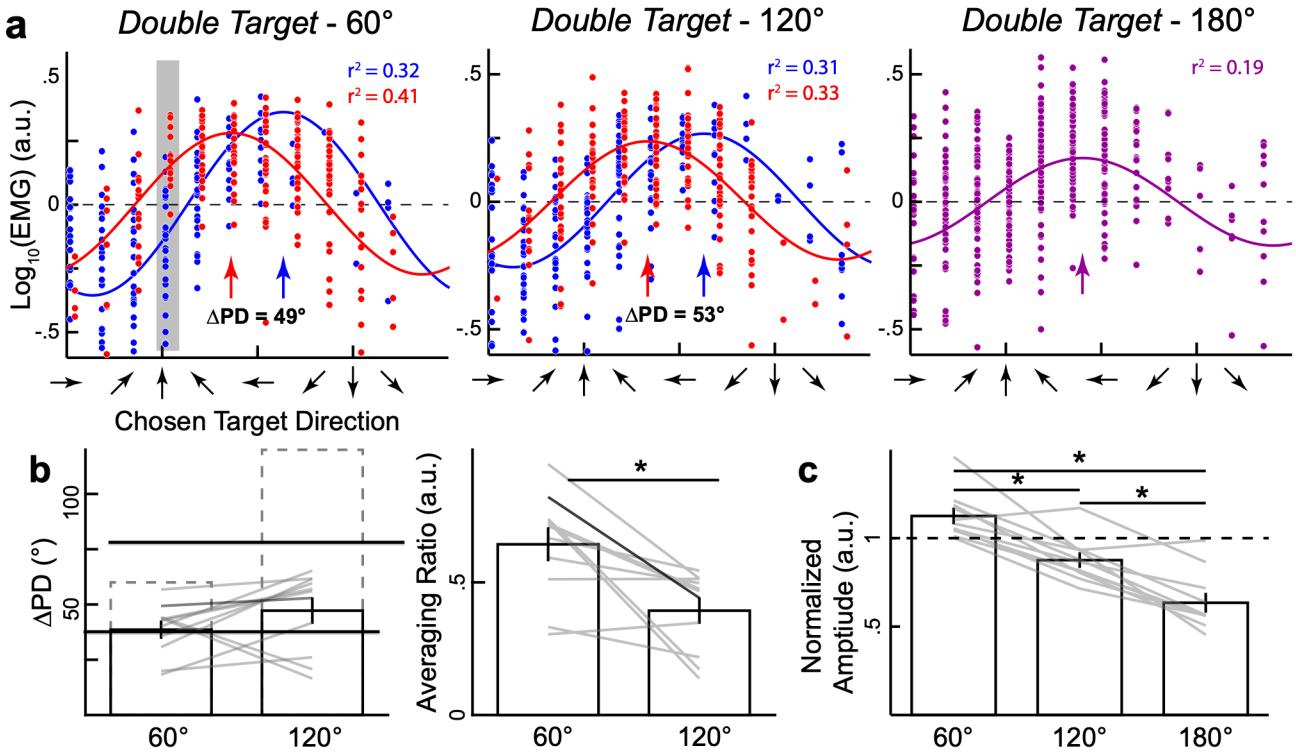
a
Double Target - 60°
Double Target - 120°
Double Target - 180°
r² = 0.32
r² = 0.41
r² = 0.31
r² = 0.33
r² = 0.19
ΔPD = 49°
ΔPD = 53°
Log10(EMG) (a.u.)
Chosen Target Direction
b
ΔPD (°)
Averaging Ratio (a.u.)
c
Normalized Amptiude (a.u.)
60°
120°
180°

Figure 3

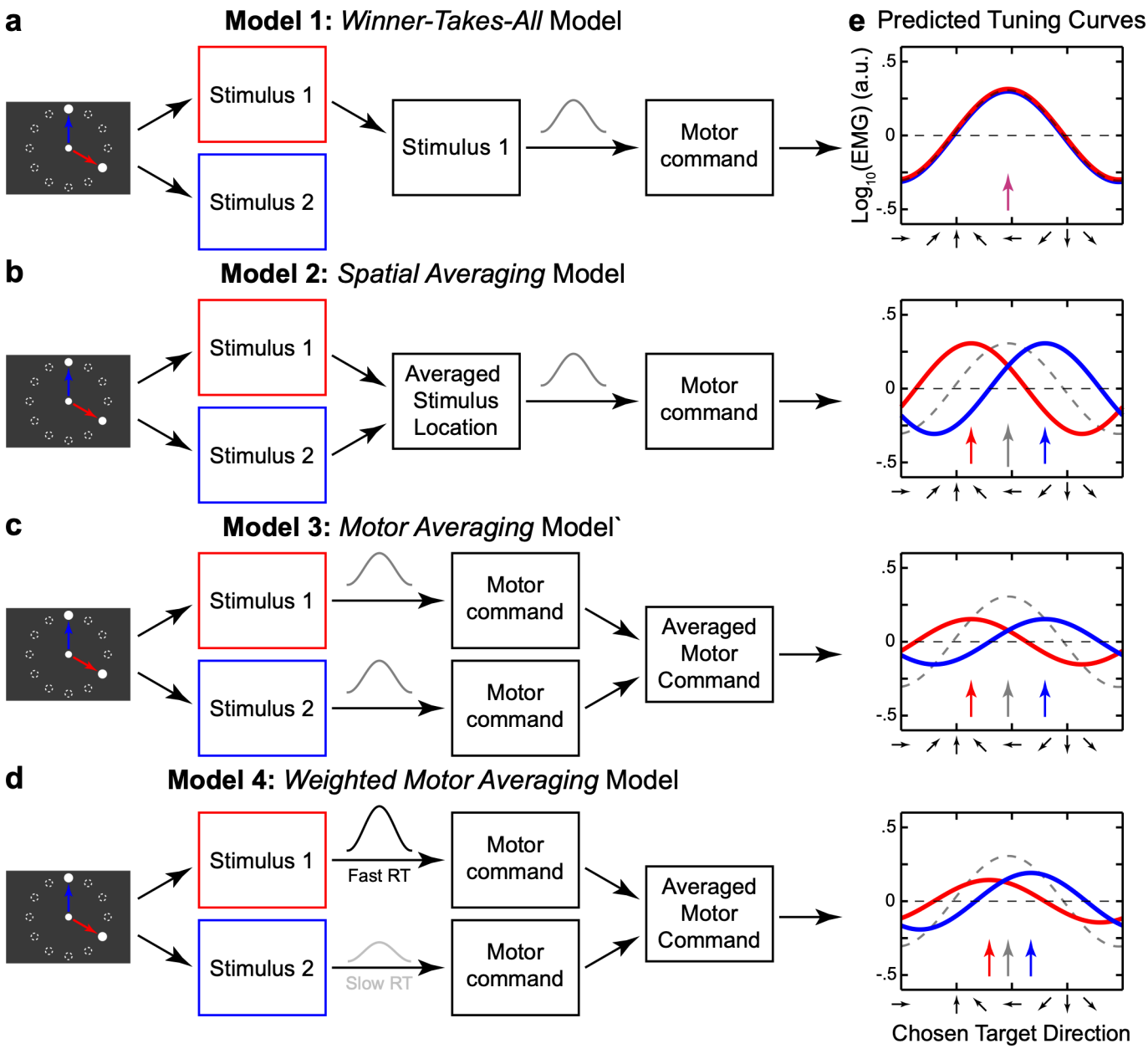
a
Model 1: Winner-Takes-All Model
e Predicted Tuning Curves
Stimulus 1
Stimulus 2
Stimulus 1
Motor command
Log10(EMG) (a.u.)
.5
0
-.5
b
Model 2: Spatial Averaging Model
Stimulus 1
Stimulus 2
Averaged Stimulus Location
Motor command
c
Model 3: Motor Averaging Model`
Stimulus 1
Stimulus 2
Motor command
Motor command
Averaged Motor Command
d
Model 4: Weighted Motor Averaging Model
Stimulus 1
Stimulus 2
Fast RT
Slow RT
Motor command
Motor command
Averaged Motor Command
Chosen Target Direction

Figure 4

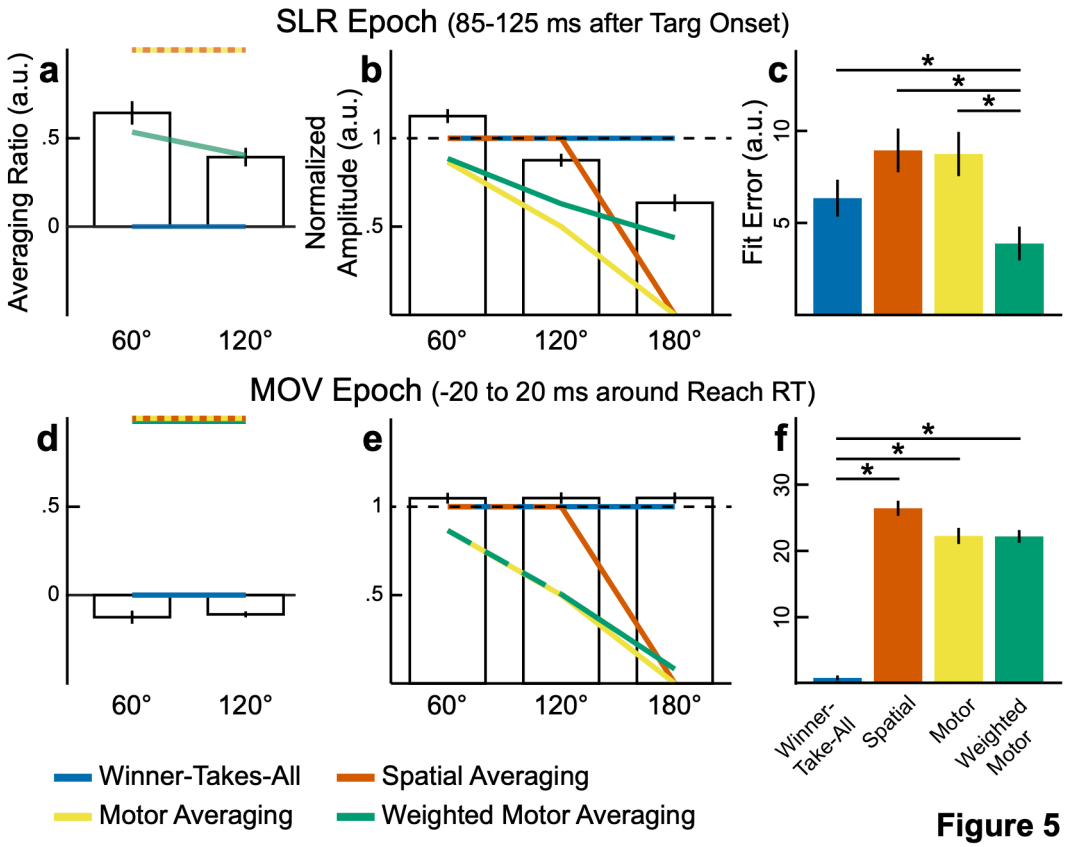
SLR Epoch (85-125 ms after Targ Onset)
a
Averaging Ratio (a.u.)
.5
0
60°
120°
b
Normalized Amplitude (a.u.)
1
.5
60°
120°
180°
c
Fit Error (a.u.)
10
5
*
*
*
MOV Epoch (-20 to 20 ms around Reach RT)
d
.5
0
60°
120°
e
1
.5
60°
120°
180°
f
30
20
10
*
*
*
Winner-Take-All
Spatial
Motor
Weighted Motor
Winner-Takes-All
Spatial Averaging
Motor Averaging
Weighted Motor Averaging

Figure 5

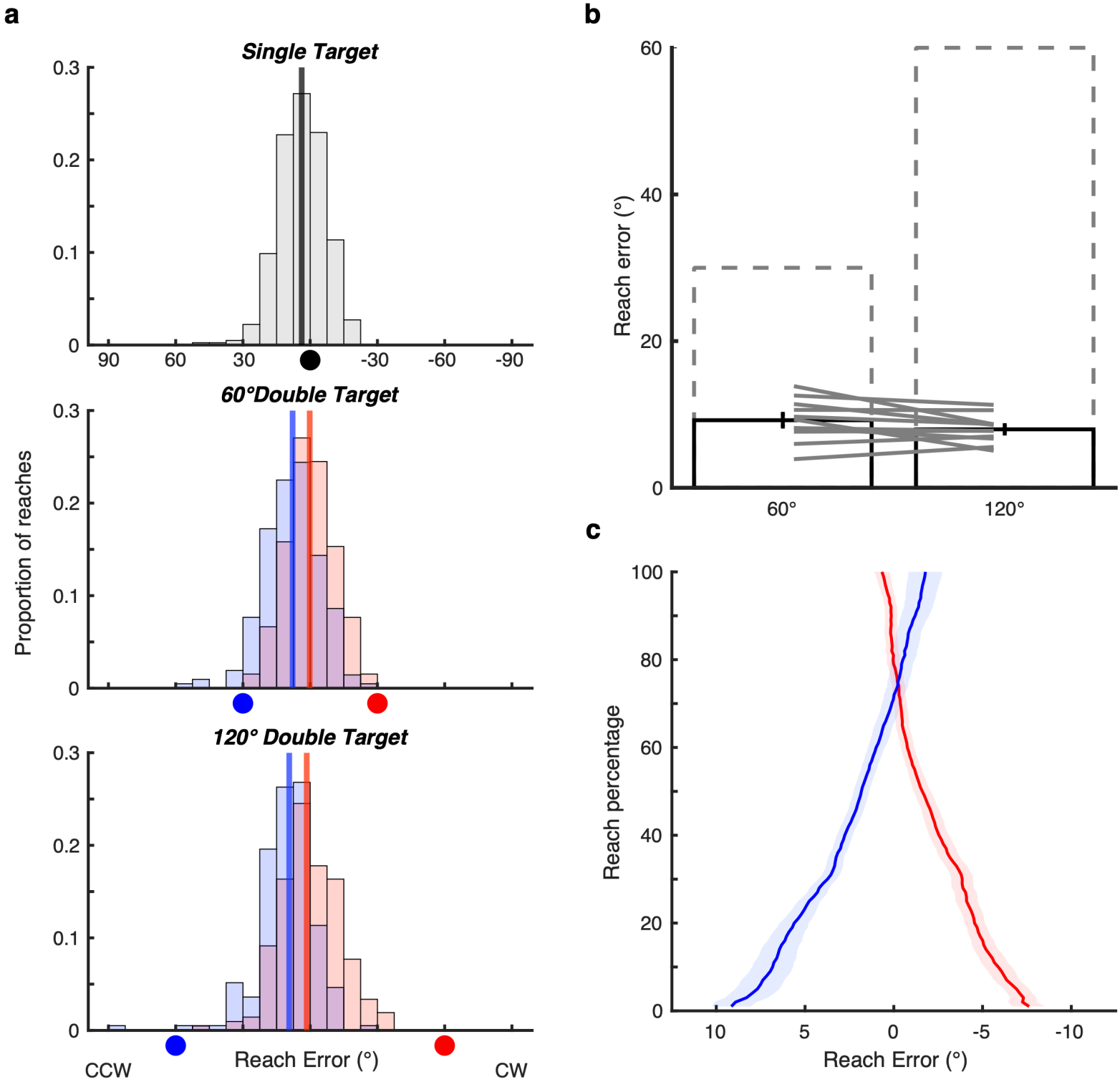
a
Single Target
60°Double Target
120° Double Target
Proportion of reaches
0.3
0.2
0.1
0
90
60
30
-30
-60
-90
CCW
Reach Error (°)
CW
b
Reach error (°)
60
40
20
0
60°
120°
c
Reach percentage
100
80
60
40
20
0
10
5
0
-5
-10
Reach Error (°)

Figure 6