From competing motor plans to a single action within a single trial on the human motor periphery

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ABSTRACT

Contemporary theories of motor control have suggested that multiple motor commands compete for action selection. While most of these competitions are completed prior to movement onset, averaged saccadic eye movements that land at an intermediate location between two visual targets are thought to arise when a movement is initiated prior to the resolution of the competition. In contrast, while averaged reach movements have been reported, there is still debate on whether averaged reach movements are the result of a resolved competition between two potential actions or a strategic behavior that optimally incorporates the current task demands. Here, we use a reach version of the paradigm that has previously shown to elicit saccadic averaging to examine whether similar averaging occurs based on neuromuscular activity of an upper limb muscle. On a single trial basis, we observed a temporal evolution of the two competing motor commands during a free-choice reach task to one of two visual targets. The initial wave of directionally-tuned muscle activity (~100 ms after target onset) was an averaged of the two motor commands which then transformed into a single goal-directed motor command at the onset of the voluntary reach (~200-300 ms after target onset). The transition from an early motor command to a single goal-direct command resembled the fact that saccadic averaging was most prominent for short-latency saccades. Further, the idiosyncratic choice made on a given trial was correlated with the biases in the averaged motor command.

INTRODUCTION

Our environment offers multiple potential motor actions, but ultimately only one action can be selected. So how does our brain decide between these potential motor actions? Classical theories of decision-making assume a two-stage process, in which the brain first selects an appropriate action and then plans the desired motor commands to execute the selection action (Donders, 1969; McClelland, 1979). However, neurophysiological studies have shown that multiple potential motor plans can be concurrently encoded within brain regions involved in eye (Bichot et al., 1996, 2001; Basso and Wurtz, 1997; McPeck and Keller, 2002) or reach movements (Cisek and Kalaska, 2005; Cui and Andersen, 2011; Klaes et al., 2011). Further, these potential motor plans are thought to compete for selection at the neurophysiological level (Schall, 2001; Cisek, 2007). There are behavioral indicators that are thought to arise from such competitions. For example, when participants are free to look to either one of two suddenly appearing visual targets (i.e. a free-choice task), they often generate an initial saccade that lands somewhere in between the two targets (Findlay, 1982; He and Kowler, 1989; Chou et al., 1999). The extent of this *saccadic averaging* is inversely correlated with saccadic reaction time (RT), where saccadic averaging is most prominent for short-latency RT trials (Ottes et al., 1984; Walker et al., 1997). The dependency of RT for saccadic averaging is thought to arise because the saccade is initiated prior to the competition between the two different motor plans being resolved.

While there is clear evidence for competition and averaging within the oculomotor system, it is less clear whether a similar competition between motor plans influences reaching behavior. Averaged reaching movements can be evoked in a ‘go-before-you-know’ task, where information about the true target is only provided after reach movement onset (Chapman et al., 2010; Stewart et al., 2014; Gallivan et al., 2017). However, these averaged reach movements can

be abolished by changes to either task instructions or constraints (Hudson et al., 2007; Chapman and Goodale, 2010), suggesting that the averaged movement may reflect an optimal task strategy rather than a competition between two motor plans (Wong and Haith, 2017). More fundamentally, the neurophysiological evidence for multiple potential reach plans has recently been questioned (Dekleva et al., 2018) in that the observed averaging may be an artifact caused by combining neural activity across multiple trials rather than examining activity on an individual trial-by-trial basis. Thus, it is still debated whether similar rules apply for saccades and reaches when the brain has to resolve multiple potential motor plans.

Our approach here is to use the same paradigm that has previously been shown to elicit saccadic averaging and look for signatures of averaging during visually-guided reaches. In this paradigm, participants are free to reach towards one of two visual targets that appear concurrently (**Fig. 1b, c**, *Free-Choice Task*). Unlike the ‘go-before-you-know’ task (Chapman et al., 2010), there is nothing to be gained by strategically aiming between the two potential locations (Wong and Haith, 2017) and thus any observed averaging can be attributed to an unresolved competition between two reach plans. By examining electromyographic (EMG) activity from an upper limb muscle during this free-choice task, we observed a transition from an initial averaged motor command (~100 ms after target onset) into a goal-directed reach movement towards a single selected target (~200-300 ms after target onset). Further, the participant’s idiosyncratic choices on a given trial correlated with the bias observed in the initial averaged motor command (Pastor-Bernier and Cisek, 2011). Thus, our results suggest that the initial wave of upper limb muscle recruitment is a readout of a still unresolved competition between the two reach movements, similar to that previously observed for averaged saccades.

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 $\pm$ SD = 24 $\pm$ 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 known motor impairments.

Reach Apparatus and Kinematic Acquisition

Participants were seated in a chair in front 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.

Experiment 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%). All peripheral targets were presented 10 cm away from the start position and at one of 12 equally spaced locations (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. The trial ended as soon as the cursor entered one of the peripheral targets. To ensure that the participants reached as fast as possible, the peripheral targeted turned red if the cursor had not moved out of the start

position within 500 ms after the onset of the peripheral target. Participants were not given any instructions of where to look and eye movements were not tracked during the experiment.

Each experiment consisted of eight blocks, with each block containing 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. Every possible single and double target configuration was presented five times in every block, resulting in 40 repetitions 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 (blue arrow). Thus, for all CW and CCW reach trials the non-chosen target direction was in the CCW and CW directions, respectively. Trials from the 180° *Double Target* condition cannot be sorted in this way, since the non-chosen target direction was always 180° away.

Reach onset detection and initial reach direction: Reach onset was identified as the first time-point after the onset of the peripheral targets at which the tangential hand velocity exceeded two cm/sec. Reach 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 connecting 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 chosen target.

EMG processing: 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 differences 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 waves of EMG activity: (1) The initial *stimulus-locked response (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 the onset of the reach movement. To prevent any overlap between these two different epochs, we excluded all trials with RTs less than 185 ms (~7% of all trials). We also excluded trials with RTs greater than 500 ms (<0.1% of all trials).

Receiver-Operating Characteristic Analysis: As done previously (Corneil et al., 2004; Pruszyński 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 directions between 120° to 240°) and rightward (-60° to 60°) *Single Target* trials. For each time-point from 100 ms before to 300 ms after stimulus 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 stimulus direction based solely on the distribution of EMG activity at that given time-point. A value of 0.5 indicates chance discrimination, whereas a value of 1 or 0 indicates perfectly 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 time after stimulus onset at which the ROC was above 0.6 and remained above that threshold for at least five out of the next 10 samples. 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 direction for both the SLR and MOV epochs:

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

in which x is the chosen target direction in degrees, starting CCW from straight right; $EMG(x)$ is the log-normalized EMG activity for the given target direction; 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 $0^\circ \leq \theta < 360^\circ$. The initial values of the parameters were $A = 1$ and $\theta = 180^\circ$. 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 stimuli into a motor command. Here to drive the predictions for the *Double Target* models, we used the *Single Target* data and assumed a non-linear cosine tuning between target direction and reach direction (**Fig. 2a**). Each model used parameters derived from each

participant's own *Single Target* data 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 direction 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 directions, respectively.

Model 2: The *spatial averaging model* (Fig. 4b) assumes that the two potential target directions are first spatially averaged into an intermediate target direction. Then that target direction 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 directions 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 directions are converted into their associated motor commands, but that they are differentially weighted into the final averaged motor command. A higher weight is assigned to the chosen target compared to the non-chosen target direction. To estimate these weights, we used each participant's own *Single Target* data.

Previous works 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 direction. Thus, we took the 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. We then used these parameters to compute the tuning curves for the *Double Target* trials. The

Fast RT tuning curve parameters were used for the chosen target direction and the *Slow RT* tuning curve parameters were used for the non-chosen target direction. 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, we calculated the mean squared error (MSE) between the predicted and observed PD and normalized amplitude for each participant. Due to the non-linear interaction between PD and normalized amplitude, we evaluated the total fit error. To do this, we took the sum of the MSE between the predicted and observed cosine tuning for each of the 12 different target reach directions (i.e. $x_1 = 0^\circ, 30^\circ, 60^\circ, \dots 330^\circ$).

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

Participants sat at a desk and used their right hand to interact with the handle of a robotic manipulandum (Howard et al., 2009) that controlled the position of a virtual cursor presented on a horizontal mirror reflecting a downward facing LCD screen. Participants performed a free-choice goal-directed right-handed reach movements in response to the onset of either one (**Fig. 1a**, *Single Target*) or two visual stimuli (**Fig. 1b** and **c**, *Double Target* trials) that appeared simultaneously. The visual target pseudo-randomly appeared at 12 different possible directions equally spaced around the start position. During *Double Target* trials, the two visual stimuli had

an angular separation of either 60°, 120°, or 180°. All conditions and target configurations were randomly interleaved. Throughout the experiment, we measured EMG activity from the PEC muscle.

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 panel) 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 in the right PEC muscle for left-outward and right-outward reach movements, respectively. Consistent with previous studies (Pruszynski et al., 2010; Wood et al., 2015), we observed a reliable difference in activity for the three different reach directions at two epochs of neuromuscular activity: the initial SLR-epoch that occurs ~100 ms after stimulus onset and the later MOV-epoch associated with reach RT (stochastically occurring ~200 ms after stimulus onset). Across our participants, the mean $\pm$ SEM discrimination time (see **Materials and Methods**) for the SLR was 87.7 ± 2.7 ms and the corresponding reach RT was 232.2 ± 3.3 ms. We calculated the SLR magnitude for a given trial as the mean log-normalized EMG activity during the SLR epoch as 85-125 ms after stimulus onset (Gu et al., 2018, 2019, indicated by the white dashed boxes and shaded panels in **Fig. 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 on *Double Target* trials

changed the SLR. For a direct comparison with **Fig. 1a**, we first examined trials with the same chosen (i.e. straight outward) target direction but with a different non-chosen target direction (60° CW, blue, or 60° CCW, red, from the target, **Fig. 1b**). If the non-chosen target direction has no influence (i.e. no averaging), we would predict that the SLR magnitude would resemble that observed during outward reach movements during *Single Target* trials, which we overlaid in gray in **Fig. 1b**. Despite the same chosen target direction, we observed an increase or decrease of EMG activity during the SLR epoch for the *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), if the non-chosen target lay in the left-outward or right-outward position, respectively. This result suggests that EMG activity during the SLR is systematically altered by the presence of the 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 chosen target 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 resemble that of an outward reach movement during *Single Target* trials (gray trace). However, even though the same two visual targets appeared, we observed a reliable difference in SLR magnitude depending on whether the participants chose either the left-outward or right-outward target direction (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 target 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 chosen target 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 well 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 the individual trial data (dots) and the cosine tuning fit (line) for the *Single Target* trials from the representative participant in **Fig. 1**. The PD of this fit was 173° CCW (arrow) from straight rightward, indicating that the largest SLR magnitude could be evoked by a visual stimulus presented straight leftward of the start position. Importantly, this cosine tuning between SLR magnitude and target direction was not simply due to movement-related EMG activity from trials with the shortest RTs: as this relationship was still presented when we performed a median RT split and re-fitted the data on either only *Fast RT* (**Fig. 2b**, dark line) or *Slow RT* trials (light), separately. Across our participants, we found no systematic differences in the PDs between *Fast* and *Slow RT* trials (**Fig. 2c**, group mean $\pm$ SEM: PD = 169° $\pm$ 3 and 162° $\pm$ 5°, respectively, paired *t*-test, $t_{(10)} = 1.30$, $P = 0.22$). We did find larger amplitude fits (i.e. larger SLR magnitude) for *Fast RT* compared to *Slow RT* trials (**Fig. 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). We will leverage this relationship later in the modeling portion of the

RESULTS.

We next fitted the SLR magnitude for the *Double Target* trials. Note, we chose to align the trials based on the participant's chosen target direction (**Fig. 1b**) rather than controlling for the visual target locations (**Fig. 1c**) to accentuate the effect of the non-chosen target direction. **Figure 3a** shows the fits for the three different angular separations for the representative participant. For both the 60° and 120° conditions, we generated separate fits for when the non-chosen target direction was either CW (red) or CCW (blue) relative to the chosen target direction. The highlighted data (shaded box in the left panel of **Fig. 3a**) corresponds to the same trials as shown in **Fig. 1b**. The rightmost panel of **Fig. 3a** shows the fit of SLR magnitude to the 180° *Double Target* condition. Despite the two targets being in diametrically opposite directions, the SLR tuning during the 180° condition was still reliably tuned towards the chosen target direction similar to that observed in the *Single Target* trials (paired *t*-test, $t_{(10)} = 1.92$, $P = 0.08$). However, we did find a systematic decrease in the amplitude of the fits (see below).

For the 60° and 120° conditions, since we aligned our data relative to the chosen target direction, the only difference between CW and CCW trials was the non-chosen target direction. If the EMG activity was the result of a perfect averaging between the two target directions, 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. $\Delta PD = 60^\circ$ 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 ($\Delta PD = 0^\circ$). Consistent with the individual trial data from **Fig. 1b**, we observed signs of averaging, albeit incomplete, for the representative participant for both the 60° and 120° conditions, with $\Delta PDs = 49.3^\circ$ and 53.0° , respectively (**Fig. 3a**).

We found similar results of partial averaging across our participants for both the 60° (**Fig. 3b**, left panel, mean $\pm$ SEM, $\Delta PD = 38.6^\circ \pm 3.5^\circ$, one sample *t*-test against zero, $t_{(10)} = 10.9$, $P <$

10⁻⁶) and 120° *Double Target* conditions ($\Delta PD = 47.2 \pm 5.4^\circ$, one sample *t*-test, $t_{(10)} = 8.7$, $P < 10^{-5}$). To directly compare the extent of averaging between the 60° and 120° conditions, we converted the ΔPD into an averaging ratio (**Fig. 3b**, right panel): where a value of 1 indicates complete averaging ($\Delta PD = 60^\circ$ and 120° , dashed line in **Fig. 3b**) and a value of 0 indicates no averaging ($\Delta PD = 0^\circ$). Overall, we found that the extent of averaging decreased 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 magnitude, we also quantified the changes in the amplitude of the fits 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 $t_{(10)} > 5.5$, $P < 10^{-3}$). These 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 visual information from the two targets may be integrated into a single motor command. These models make distinct predictions for how the PD and amplitude of the cosine tuning should change between *Single* and *Double Target* trials (see **MATERIALS AND METHODS** for exact details). **Figure 4e** shows the predicted cosine 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 participant shown in **Figs. 1** and **2**. **Model 1** is the *winner-takes-all model* (**Fig. 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 direction (Donders, 1969; McClelland, 1979). Effectively, there is no integration between the two targets direction 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* (**Fig. 4b**), which proposes that the two targets are first averaged into a single spatial representation, resulting in a motor command towards the intermediate spatial direction (Findlay, 1982; Glimcher and Sparks, 1993; Chou et al., 1999). **Model 3** is the *motor averaging model* (**Fig. 4c**), which proposes that the two targets are first converted into their own motor command (Edelman and Keller, 1996; Cisek and Kalaska, 2002; Port and Wurtz, 2003) 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* (**Fig. 4d**), which is a variation of the motor averaging model. Once again, the two targets are first converted into two separate and independent motor commands, but a stronger weighting is given towards the chosen compared to the non-chosen target direction (Kim and Basso, 2008, 2010; Pastor-Bernier and Cisek, 2011). The final motor command is an average of these two differentially weighted motor commands. This model can be conceptualized as a race between two independent accumulators (Schall, 2001), with the eventual chosen motor command accumulating at a faster rate compared to the non-chosen command. Instead of estimating the weights of the chosen and non-chosen target direction, we used the *Fast RT* and *Slow RT* cosine tuning fits from the *Single Target* trials, respectively. Previous studies (Gu et al., 2016, 2018) have linked SLR magnitude to the

‘readiness’ of the motor system towards a specific target direction. Here, we assumed that during *Double Target* trials the motor system chooses the more ‘ready’ target direction.

Figure 5a and b summarize the four different model predictions (color lines) for both the changes in ΔPD averaging ratio and 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 averaging* and *motor averaging models* predicted complete averaging (i.e. averaging ratio = 1 a.u.). The key difference between the two models was the predicted amplitude, where the *spatial averaging model* predicted no change (i.e. normalized amplitude = 1 a.u.), while the *motor averaging model* predicted an overall decrease (i.e. < 1 a.u.). Finally, the *weighted motor averaging model* predicted both a partial shift in PD (i.e. averaging ratio between 0 and 1) and an overall decrease in amplitude. The extent of these changes depended on each participant’s own *Fast RT* and *Slow RT* fits.

Figure 5a and b also shows our observed group data (white 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 both the averaging ratio and amplitude that was observed in the group data between the 60° and 120° *Double Target* conditions. 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** shows the mean $\pm$ 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 cosine tuning 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).

Systematic repulsion away from the non-chosen target direction during 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 how does the EMG activity associated with movement onset (MOV) change during *Double Target* trials? Previous behavioral studies have reported reach averaging by examining the initial reach direction to two potential visual targets (Chapman et al., 2010; Stewart et al., 2014; Gallivan et al., 2017). Here, we examined both EMG activity during the MOV epoch (i.e. mean EMG activity -20 to 20 ms around reach onset), as well as the initial reach direction error.

Figure 5d and e show both the averaging ratio and amplitude fits for the participants when we re-fitted cosine tuning fits for 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 best explanation for our data, we still observe an influence of the non-chosen target in our data, but with an averaging ratio shifting in the opposite direction, i.e. *away* from the non-chosen target direction (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**). Thus, unlike

previous reaching experiments using the ‘go-before-you-know’ paradigm, we did not observe reach averaging in the EMG activity during the MOV epoch.

This systematic repulsion away from the non-chosen target direction is also present in the reach kinematics. **Figure 6a** shows the representative participant’s initial reach error (i.e. the difference between the chosen target direction and the initial reach direction at the time of reach onset) for both *Single* and *Double Target* trials. We observed systematic shifts in median reach error (vertical lines) away from the non-chosen target direction (red and blue circles along the x-axis in **Fig. 6a**) for both the 60° and 120° *Double Target* conditions. **Figure 6b** shows the group differences of the median initial reach error direction between the CW and CCW reach trials (Δ Initial Reach Error = $-25.7^\circ \pm 21.7^\circ$ and $-23.0^\circ \pm 2.6^\circ$, paired *t*-test, $t_{(10)} = -9.6$ and -8.9 , both $P < 10^{-5}$, respectively). These reach error directions are consistent with the repulsion effect in Δ PD observed during the MOV epoch (Δ PD = -7.5 ± 1.8 and -13.1 ± 1.1 , for 60° and 120° *Double Target* trials, respectively, **Fig. 6c**). Note, this repulsion effect is abolished at the end of the reach movement (i.e. 10 cm away from the starting position, Δ Final Reach Error = $0.05^\circ \pm 0.15^\circ$ and $0.44^\circ \pm 0.19^\circ$, paired *t*-test, $t_{(10)} = 0.16$ and 3.8 , $P = 0.88$ and $P = 0.004$ in the opposite direction as the initial reach error).

DISCUSSION

Contemporary theories of decision-making have suggested that the multiple potential motor commands compete for action selection (Schall, 2001; Cisek, 2007). While there are clear behavioral indications of such competition during saccadic averaging (He and Kowler, 1989; Chou et al., 1999), where eye movements land in between two potential visual targets, there is an ongoing debate on whether averaging occurs for reach movements (Chapman et al., 2010;

Gallivan et al., 2017; Wong and Haith, 2017). Here, by measuring the earliest wave of visually evoked neuromuscular response (i.e. the *stimulus-locked response*) on an upper limb muscle during a free-choice reach task, we observed averaging of two motor commands associated with the two possible targets, similar to that observed previously for saccadic averaging. Further, consistent with current theories of decision-making in motor control (Gallivan et al., 2018), we observed a temporal transformation going from a competition between two different motor commands during the SLR epoch (~100 ms after target onset) into a single goal-directed motor command by the time of voluntary reach onset (~200-300 after target onset). Importantly, the initial averaged motor command was biased towards the participant's chosen target direction on a trial-by-trial basis.

We specifically chose to employ a free-choice reach task with an emphasis on short-latency reach RTs. This task design, which has been proven successful in eliciting saccadic averaging (see below for reach averaging paradigm), allowed a direct comparison between saccadic averaging and a possible counterpart for reach movements. The averaged motor response observed during the SLR epoch is reminiscent of the properties of saccadic averaging. First, the greatest amount of saccadic averaging is seen for short-latency saccades (i.e. saccadic RTs < 100 ms), while more goal-directed saccades occur for longer-latency RTs (Walker et al., 1997; Chou et al., 1999). Similarly, we only observed reach averaging during the SLR but not during the later MOV response. Second, in the saccadic system the extent of averaging decreases as the angular separation increases between the two visual targets (Chou et al., 1999; Vokoun et al., 2014). Again, we also observed larger reach averaging when the visual targets were 60° rather than 120° apart.

The temporal separation between the SLR and the voluntary MOV epochs (Wood et al., 2015) allowed us to examine how and at what potential stage of the sensorimotor transformation the motor system may be averaging the two different potential targets. Classic saccadic averaging studies have suggested that the brain first *spatially averages* the two visual stimuli and then generates a motor command towards the intermediate direction (Coren and Hoenig, 1972; Walker et al., 1997). In contrast, recent behavioral studies on reach averaging have suggested that the brain averages the two different motor commands that are competing for selection (Stewart et al., 2014; Gallivan et al., 2017), i.e. *motor averaging*. Due to the non-linear mapping between the visual stimulus direction and the corresponding motor command, we could directly test whether the averaging observed during the SLR epoch was the result of either spatial or motor averaging (**Fig. 4**). Note, that we tested two different motor averaging models: (1) the *motor averaging* model assumed that the two competing motor commands contributed equally to the final averaged command, regardless of the final chosen target direction. In contrast, (2) the *weighted motor averaging* model assumed that the initial competition between the two targets was biased (Kim and Basso, 2010; Pastor-Bernier and Cisek, 2011) towards the eventual chosen target, thus resulting in a larger weighting for the motor response corresponding to the chosen compared to the non-chosen target. To estimate the weighting of the chosen and non-chosen targets for each participant, we used the difference in SLR magnitude between fast and slow RT trials during the *Single Target* trials (see **MATERIALS AND METHODS**).

We found that the *weighted motor averaging model* explained the SLR magnitude better than any of the other models (**Fig. 5**). This result is consistent with contemporary theories of decision-making for multiple competing motor plans (Schall, 2001; Cisek, 2007). For example, previous neurophysiological studies have shown that experimentally manipulating the decision

variable through either target uncertainty (Basso and Wurtz, 1997; Dorris and Munoz, 1998), target expectation (Bichot et al., 1996; Basso and Wurtz, 1998), or reward expectation (Rezvani and Corneil, 2008; Pastor-Bernier and Cisek, 2011) modulates the neural presentation of the competing motor commands. Here, rather than experimentally manipulating biases 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 eventual chosen target direction *Double Target* trials. This suggests that random fluctuations along the sensorimotor pathway (Faisal et al., 2008) or idiosyncratic preferences based on earlier choices bias the competition process and thus influence the final decision.

Our results pertain to recent findings debating whether neural activity in dorsal premotor cortex represents two potential targets simultaneously (Cisek and Kalaska, 2005; Klaes et al., 2011) or whether such results arise from combining single-trial data representing either one of two locations across multiple trials (Dekleva et al., 2018). Our results clearly show an influence of a competition between both targets on the earliest wave of EMG activity on a trial-by-trial basis. Note that our results are based on the initial visual transient response, which previous neurophysiological studies have specifically excluded and only examined the delay activity for any potential motor actions.

While our SLR results are consistent with earlier kinematic results of reach averaging studies (Stewart et al., 2014; Gallivan et al., 2017), these studies have suggested that motor averaging should also leak out to the reach kinematics at the time of reach onset. However, in our study there was no indication of motor averaging in the reach kinematics. Instead, the error in the initial reach direction was systematically *away* from the non-chosen target direction, which was also supported by the observed shift in the PD of EMG activity at the time of reach onset

(**Fig. 6**). This repulsion effect disappeared when we examined the final reach error, thus suggesting that participants were actively generating curved reach movements away from the non-chosen target direction. While counterintuitive, this observation is in line with previous reach studies (Chapman and Goodale, 2008, 2010; de Haan et al., 2014) that reported curved movements away from a visual stimulus that was defined as an obstacle rather than a target. Our current results suggest that by the onset of reach initiation (~200-300 ms after stimuli onset) participants have already decided which target to reach towards and they have also incorporated a strategy to actively avoid the non-chosen target direction (Wong and Haith, 2017).

In summary, we examined neuromuscular activity during a reach version of free-choice task that has previously been shown to elicit saccadic averaging. We found that similar to saccadic averaging, the initial short-latency reach motor command (i.e. the SLR) is a behavioral indicator of an incomplete competition of two distinct motor plans. However, this competition is rapidly resolved and the motor system then generates a strategic motor plan that is optimal for the current task demands.

AUTHOR CONTRIBUTIONS

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

DECLARATION OF INTERESTS

The authors declare no competing interesting.

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661

FIGURE LEGENDS

Figure 1: SLR from a representative participant. **a.** Individual (middle panel) and mean $\pm$ 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. 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 (color squares). Dashed white box and shaded panel 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 with the same left-outward and right-outward visual targets. 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 reach direction for *Single Target* trials from the representative participant in **Fig. 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 $\pm$ 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 same trials from **Fig. 1b.** **b.** Group mean $\pm$ SEM shifts in PD (Δ PD) 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 Δ PD the SLR completely averaged the two targets (averaging ratio = 1 a.u.). **c.** Mean $\pm$ 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 **Figs. 1** and **2**.

Figure 5: Comparisons of model predictions and observed group data for *Double Target* trial fits. **a, b.** The model predictions (color lines) overlaid over the observed mean $\pm$ 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 $\pm$ 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 $\pm$ SEM of difference in median reach error between CW and CCW during *Double Target* trials. **c.** Mean $\pm$ SEM of Δ PD during the MOV epoch. Same layout as left panel in **Fig. 3b**.

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6