

RESEARCH ARTICLE | *Control of Movement*

Reaching movements are automatically redirected to nearby options during target split

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Kurtzer IL, Muraoka T, Singh T, Prasad M, Chauhan R, Adhami E. Reaching movements are automatically redirected to nearby options during target split. *J Neurophysiol* 124: 1013–1028, 2020. First published August 12, 2020; doi:10.1152/jn.00336.2020.—Motor behavior often occurs in environments with multiple goal options that can vary during the ongoing action. We explored this situation by requiring subjects to select between different target options during an ongoing reach. During split trials the original target was replaced with a left and a right flanking target, and participants had to select between them. This contrasted with the standard jump trials, where the original target would be replaced with a single flanking target, left or right. When participants were instructed to follow their natural tendency, they all tended to select the split target nearest the original. The near-target preference was more prominent with increased spatial disparity between the options and when participants could preview the potential options. Moreover, explicit instruction to obtain the “far” target during split trials resulted in many errors compared with a “near” instruction, ~50% vs. ~15%. Online reaction times to target change were delayed in split trials compared with jump trials, ~200 ms vs. ~150 ms, but also highly automatic. Trials in which the instructed far target was correctly obtained were delayed by a further ~50 ms, unlike those in which the near target was incorrectly obtained. We also observed nonspecific responses from arm muscles at the jump trial latency during split trials. Taken together, our results indicate that online selection of reach targets is automatically linked to the spatial distribution of the options, though at greater delays than redirecting to a single target.

NEW & NOTEWORTHY This work demonstrates that target selection during an ongoing reach is automatically linked to the option nearest a voided target. Online reaction times for two options are longer than redirection to a single option. Attempts to override the near-target tendency result in a high number of errors at the normal delay and further delays when the attempt is successful.

action selection; decision-making; visual feedback; visual processing; visuomotor

INTRODUCTION

Motor behavior often confronts an environment with multiple goal options that may change during action toward one. In the context of upper limb movements, this situation is exem-

plified by the game of “whack-a-mole.” A player attempts to strike fake garden moles (a burrowing pest) with a mallet as they pop out from their holes and then retreat back down. Sometimes, the player will have already initiated a mallet strike to one mole when it suddenly disappears and two of its peers pop up. Rapid redirection of the mallet is required in order to strike either mole, so what determines the online selection between two new options? Surprisingly, this basic question has received limited attention despite the extensive research on redirecting ongoing movements to a change in target location (Prablanc and Martin 1992; Soechting and Lacquaniti 1983) as well as research on selection between targets placed at different distances and locations before reach initiation (Cos et al. 2011, 2014; Diamond et al. 2017; Morel et al. 2017).

An intuitive expectation is that online target selection will tend to be directed to the option nearest to the original. However, this is complicated by the fact that online responses to a target change occur at different delays and that these express different capabilities (reviewed in Gaveau et al. 2014; Sarlegna and Mutha 2015). The earliest kinematic changes range from 120 to 200 ms (depending on the behavioral paradigm, stimuli, and detection method) and act to minimize the hand/effector’s distance to the displaced target (Franklin et al. 2016; Gritsenko et al. 2009; Prablanc and Martin 1992; Saunders and Knill 2003; Smeets and Brenner 1994; Soechting and Lacquaniti 1983). This spatial relation of target change and early corrective action is highly automatic and cannot be reversed (i.e., increase the hand-target distance) even with an explicit instruction (Day and Lyon 2000) or extensive training with a mirror mapping between the hand and cursor (Gritsenko and Kalaska 2010; Lillicrap et al. 2013). In contrast, responses which increase the distance between the hand and target can be enforced at will, but only at a later delay (150–300 ms). Later responses are considerably more integrative and include sensitivity to nonspatial information such as color (Cressman et al. 2006; Pisella et al. 2000; Veerman et al. 2008) and texture (Veerman et al. 2008) as well as potential obstacles to the movement (Aivar et al. 2008). In addition, early responses to target jumps can saturate with displacement amplitudes as small as 2 cm

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(Franklin et al. 2016), whereas later responses scale linearly with displacement magnitude.¹

The few previous studies examining fast selection between target options indicate that it can be quite versatile. When reaching to sequentially presented targets and instructed to maximize their acquisition, participants will select the easy or hard option (small and distant vs. large and close) depending on the relative onset of the two targets (Brenner and Smeets 2015). The easy option was selected for ~95% of trials during simultaneous presentation vs. ~40% of trials when the hard option was delayed by 150 ms, which appropriately matched their speed-accuracy behavior. Although the delay for target selection was not analyzed, it was visually estimated to be around 200 ms from the grand mean trajectories; note the combined reaction time and movement time was under 500 ms, on average. Another example is single reaches to two target options with an enforced initiation time (Cos et al. 2014). Participants select targets aligned with the minor axis of the arm's inertial resistance, rather than its major axis, based on ~200 ms of viewing time, indicating decisions can be rapidly influenced by the biomechanical costs of the options. In contrast, target selection in a continuous tracking task was relatively insensitive to biomechanics and occurred with a 500-ms delay when the two upcoming options were parallel vs. oblique to the ongoing action (Michalski et al. 2020). Still, target selection was highly sensitive to the size and placement of the options, since the oblique target was selected more frequently when it was increasingly large, increasingly near, and more aligned with the ongoing action.

Taken together, previous results suggest two contrasting possibilities for how the nervous system might handle target splits during reaching. Online reactions could occur at a short delay but with little or no accounting for displacement magnitude given the limited time to integrate spatial information, or target selection may be withheld until a longer delay and reflect an arbitrary criterion easily altered with instruction. To test between these possibilities and understand the basic organization of online target selection, we need to identify its pattern, delay, and modifiability with instruction. Note that the aforementioned studies on target selection, while insightful, are unable to resolve between the two possibilities. The online reaction time for selecting between two targets midflight was either not measured, not relevant, or not compared with that for a single target change, nor did those studies examine whether the selection patterns reflected an automatic process that was difficult to override or a strategic process that could be altered with instruction.

Our experiments yielded different results from the two possibilities described above. In brief, participants naturally express a tendency to select the target option nearest the original, the online reaction time (oRT) to two options is delayed compared with that for one option, and the process is highly automatic, e.g., error prone and further delayed when participants are instructed to perform opposite the natural

tendency. Two secondary results should also be highlighted: target selection was impacted by the ongoing hand motion, and arm muscles showed nonspecific responses during split trials at the jump oRT.

MATERIALS AND METHODS

Participants. The study followed procedures approved by the Institutional Review Board of New York Institute of Technology and required written informed consent by the participant. A total of 54 right-handed individuals contributed to three experiments, $n = 18$ participants for each experiment. Participants were young adults from the university [mean age = 23.8 yr (± 2.5 SD), 26 women and 28 men] and were compensated at \$15/h for a session lasting ~2 h.

Behavioral apparatus. We utilized a robotic exoskeleton (Kinarm, Kingston, ON, Canada) that supports the upper limb within the horizontal plane and permits flexion/extension of the shoulder and elbow. Joint angles were sensed by high-precision goniometers, acquired at 1,000 Hz, and then transformed into the hand's forward and lateral position. Although the device can apply joint-based loads to the arm, no additional loads were applied in the present experiment.

Visual targets and a hand-aligned cursor were projected by a video system (LG monitor, frame rate = 60 Hz) onto a tinted glass sheet placed ~15 cm above the arm. Given the same separation between the projector and the tinted glass, the images appeared to be in the same horizontal plane as the reaching arm; a direct view of the arm was blocked by a metal partition. A photodiode was secured to the left nearby corner of the screen and covered with an opaque sheet. This allowed us to measure when a small circle was illuminated while it remained unseen to the participant. A direct measure of illumination allowed us to account for delays in the video monitor and software. All trials were aligned to the onset of this illumination corresponding to target changes on perturbation trials or when a target change would have occurred on nonperturbation trials.

Electromyography apparatus. In *Experiment 1* we obtained surface electromyography (EMG) from four muscles of the reaching arm: posterior deltoid (a shoulder extensor), pectoralis major (a shoulder flexor), triceps lateral (an elbow extensor), and brachioradialis (an elbow flexor). Data collection followed procedures described in an earlier paper (Pruszynski et al. 2008). The skin surface overlying each muscle was lightly abraded with alcohol, and bipolar Ag-AgCl electrodes (#FT007; MVAP Medical, CA) were then affixed; the ground electrode was placed on the subject's acromion, also cleaned. EMG signals were routed and amplified using a Bortec AMT-8 system (Bortec Biomedical Ltd, Canada), which has -6 dB per octave from 10 to 1,000 Hz. The amplifier gain was set to 10,000, and its output signals were then digitally sampled at 1,000 Hz.

Experiment 1: Uncued target change paired with "natural" instruction. Eighteen participants reached with their right arm to circular targets. One participant's data were rejected for having movements that were highly curved and variable, approximately three times the average reaching angle and standard deviation of reaching angle measured at target onset. The start target (visual radius = 0.75 cm) and end target (visual radius = 1 cm) were placed 10 cm behind and 10 cm ahead of the hand when the arm adopted a midrange posture, 30° shoulder flexion, and 90° elbow flexion. These target positions obliged a forward hand movement of 20 cm roughly aligned with the right shoulder.

The experimental sequence is shown in Fig. 1, *A* and *B*. Targets were first presented as white unfilled circles. The start target disappeared upon hand entry, and 1–3 s later the end target filled white, which cued the participant to reach. Subject were verbally instructed to reach "a single natural movement." In two-thirds of trials, the end target remained at the same position throughout the reach. In one-third of trials, the hand's forward movement triggered a change in the end target's lateral position(s). Due to intrinsic limitations of the software and monitor, there was a delay

¹ Studies on cursor displacement have reported some similar results such as an automatic link between hand/cursor displacement and manual correction (Franklin and Wolpert 2008) and delayed integration of obstacle information (Cross et al. 2019). However, target and hand/cursor signals likely initially involve different streams of processing (Brenner and Smeets 2003; Franklin et al. 2016; Reichenbach et al. 2014; Sarlegna et al. 2003), cautioning us from generalizing from one domain to the other.

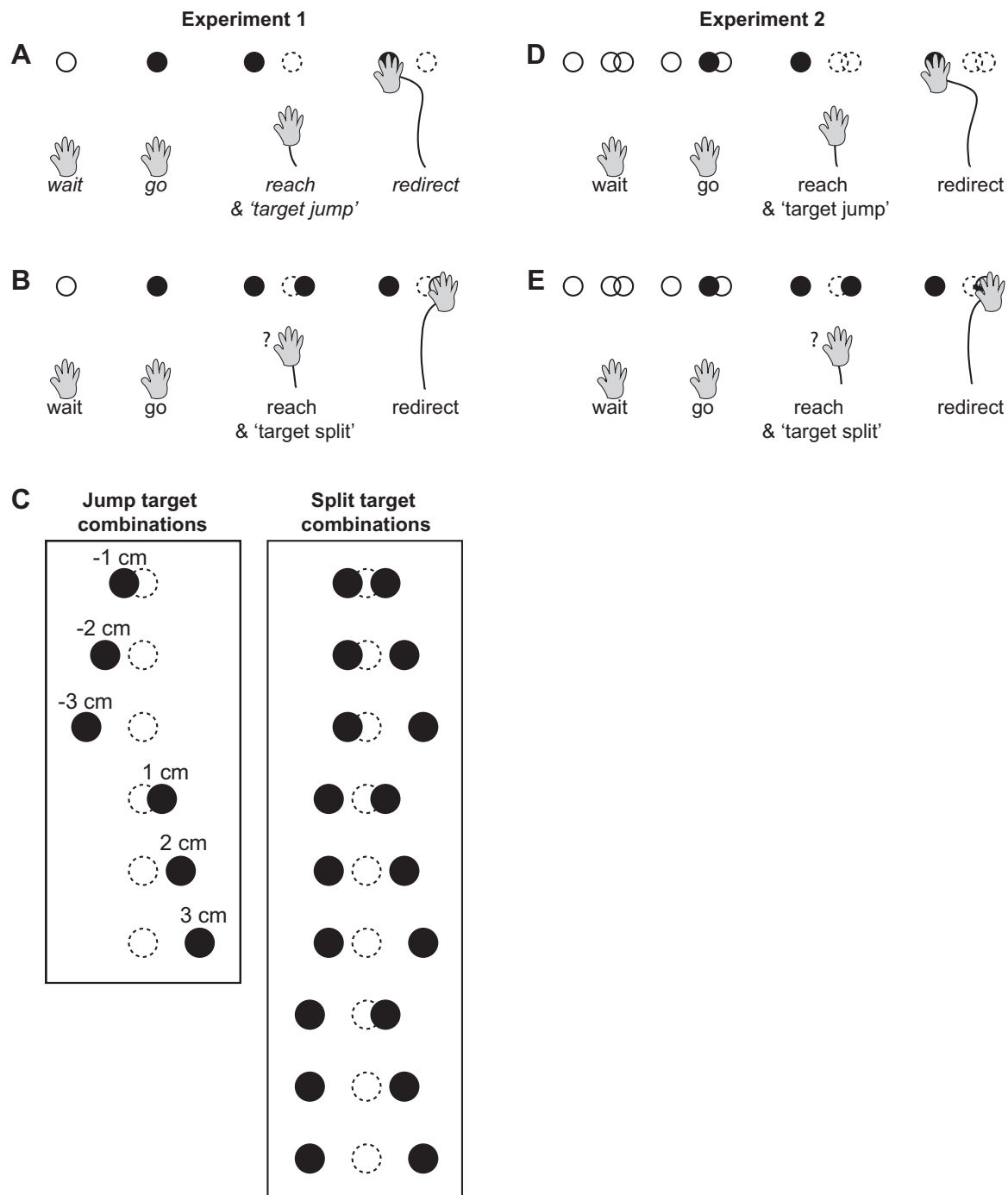


Fig. 1. Sequence for jump and split trials in *Experiments 1* and *2*. *A* and *B*: cartoon hand and trailing black traces indicate the evolving hand motion by an exemplar participant. In *Experiment 1* they viewed a single open circle during the wait period and reached to that circle when it filled. On a random subset of trials, the original target could be laterally shifted ("jump") or be replaced by 2 flanking targets ("split") once the hand moved a fixed distance ahead; the 2 conditions displayed are a leftward jump of 3 cm vs. a split of 3 cm left and 1 cm right. Participants redirected their hand to the only available target in jump trials (*A*), whereas participants could redirect their hand to either available target in split trials (*B*). *C*: all jump and split target combinations of *Experiments 1* and *2*. *D* and *E*: in *Experiment 2*, 3 targets were shown during the wait period: a central target and 2 flankers. In jump trials (*D*), the central target and one flanker disappeared and the other flanker was filled midflight. Participants redirected their hand to the only available target. In split trials (*E*), the central target disappeared and both flankers were filled midflight. Participants redirected their hand to either available target. Data are from a different exemplar participant.

of ~52 ms between the triggering event with the hand at 2.8 cm ahead and visible change of target with the hand at ~4.5 cm (~20% of the total distance to the end target).

Target changes included jump trials and split trials. During jump trials, one new target appeared to the left or right of the original target. During split trials, two targets appeared to the left and right of the

original (now removed) target. Three displacement magnitudes were utilized which yielded six jump conditions (-3, -2, -1, 1, 2, and 3 cm) and nine split conditions (-3 and 1, -3 and 2, -3 and 3, -2 and 1, -2 and 2, -2 and 3, -1 and 1, -1 and 2, and -1 and 3 cm). Negative and positive values indicate the left and right distance from the center target, respectively. All jump and split conditions are shown

in Fig. 1C. Each experimental block included 15 perturbed trials randomly intermixed with 30 unperturbed trials.

During nonperturbation trials, participants needed to exit the start target and obtain the end target within a movement time of 600–750 ms and also stay inside for 500 ms. Success was indicated by the target filling green. Slow movement times resulted in a blue fill and “too slow” text, whereas fast movement times resulted in a red fill and “too fast” text. There were no reaction time demands. In perturbation trials, participants only needed to obtain the target within a movement time of 2,000 ms; the selected target remained white after entry and the unselected flanker disappeared. Participants were verbally instructed to “not stop your movement or slow down for a conscious decision. Rather keep going to the target which is most natural.” The relatively open-ended time criterion avoided target selection based on inter-target temporal exigencies. Participants practiced the task and then completed 8 blocks, 360 trials total, such that each jump and split condition was repeated eight times.

Experiment 2: Cued target change paired with “natural” instruction. Experiment 2 largely employed the same design as Experiment 1, including the same jump and split combinations in Fig. 1C. The experimental sequence for these 18 participants is shown in Fig. 1, D and E. The critical difference involved the prereach target display. Rather than one open target being shown during the wait period, a central target and two flankers were shown. There were nine combinations of lateral positioning for the two flanking targets: –3 and 1, –3 and 2, –3 and 3, –2 and 1, –2 and 2, –2 and 3, –1 and 1, –1 and 2, and –1 and 3 cm. These are the same target positions used in the perturbation conditions of Experiment 1. Note that preview information only indicated the potential targets, not the particular condition. The trial could be unperturbed, jump, or split depending on which targets disappeared and which remained. The reveal occurred when the hand was ~4.5 cm ahead of the start target. During unperturbed trials, the two flankers disappeared and the central target remained filled. There were three perturbation possibilities: 1) the right target filling and the others disappearing (a rightward target jump), 2) the left target filling and the others disappearing (a leftward target jump), and 3) both the right and left target filling and the central target disappearing (a target split). Hence, unperturbed trials had 9 flanker combinations, jump conditions had 18 flanker combinations (3 positions for the opposing flanker which disappeared for each flanker position that was filled/6 jump displacements), and split conditions had 9 combinations. Unperturbed trials were again presented two-thirds of the time for a single block containing 135 trials: 18 jump trials, 27 split trials, and 90 unperturbed trials. Each block was randomized, and participants paused for a break at the midpoint of the block. Participants practiced the task and then completed 3 blocks for a total of 405 trials such that each jump condition was repeated three times and each split condition was repeated nine times.

Experiment 3: Uncued target changes paired with a “near” or “far” instruction. Experiment 3 employed the same design as Experiment 1 with a few critical differences. The 18 participants were exposed to two, not three, displacement magnitudes, leading to 4 jump conditions: –3, –1, 1, and 3 cm. Also, the flankers used for split trials always had an unequal magnitude, leading to two possible conditions: –3 and 1 and –1 and 3 cm. Last, participants were verbally instructed which target to obtain during split trials. The “Near” instruction was to “go to the one with the shortest distance to the original target which disappeared.” The “Far” instruction was to “go to the one further from the original target which disappeared.” Participants were also instructed “to not stop, mistakes are expected to happen.” The first and second halves of the experiment involved different instructions with the order counterbalanced across participants. Forty-eight trials occurred in each block: 32 unperturbed trials, 8 jump trials, and 8 split trials. Participants practiced and then completed 4 blocks with one instruction and 4 blocks with the other instruction, which yielded 384 trials total. Thereby, each jump condition (with a given instruction)

was repeated 8 times and each split condition (with a given instruction) was repeated 16 times.

Behavioral analysis. The hand’s position was low-pass filtered (Butterworth, 6th order, 25 Hz). For most analyses the signals were time-aligned to the photodiode signal of the unseen circle triggered by the hand’s forward motion. Perturbation trials were time-aligned to the visible target change, whereas unperturbed trials were time-aligned to when a target change would be visible. We rejected unperturbed trials if the forward or lateral position deviated more than three standard deviations from the grand mean in a window 300 ms before the (virtual) target change to when the hand acquired the target. Perturbed trials were rejected if the forward or lateral position was outside this range 300 ms before the target change to 90 ms afterward, i.e., before any corrective response. Approximately, 8% of unperturbed trials and 5% of perturbed trials were rejected. The lower rejection rate for the perturbed trials is due to sampling 90 ms after the target change rather than the entire time to target acquisition.

We used several measures to characterize the pattern of target selection during split trials starting with the most general and then becoming more specific. We first determined the frequency of selecting the right vs. left target for each flanker combination. The most general measure from this is the average selection frequency from all nine flanker combinations. This “selection bias” characterizes the overall tendency to the left or right of the central target. A selection bias of 1.0 indicates that the subject always selected right targets, 0.0 indicates they always selected left targets, and equal selection of left and right targets results in a selection bias of 0.5.

Sensitivity to the relative positions of the two targets from the center was first examined with a model-free measure we termed “selection contrast.” Selection contrast was the difference in average right-selection frequency when the right target’s position from the center was smaller than the left’s (3 conditions) vs. the average right-selection frequency when the left target’s position from the center was smaller than the right’s (3 conditions). A value of –1 indicates exclusive selection of the nearer option, 1 indicates exclusive selection of the further option, and 0 indicates no selection preference. A more detailed measure we termed “selection gradient” contrasted the different right-selection frequencies for the most unequal flanker combinations (–3 and 1 cm vs. –1 and 3 cm, $\Delta\text{Prob}_{\text{most unequal}}$ between –1 and 1) against the remaining unequal combinations (–2 and 1 and –3 and 2 cm vs. –1 and 2 and –2 and 3 cm, $\Delta\text{Prob}_{\text{less unequal}}$ between –1 and 1), $\Delta\text{Prob}_{\text{most unequal}} - \Delta\text{Prob}_{\text{less unequal}}$. A positive selection gradient (>0) would reflect a graded selection between right and left targets rather than a step function.

We also conducted a univariate logistic regression of the data [generalized linear model (GLM) with logit link and binomial error distribution; MATLAB function `glmfit`]:

$$\text{Prob}(\text{right selection}) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 \Delta x)}},$$

where $\Delta x = -\Delta 2$ cm (–3 and 1 cm), $-\Delta 1$ cm (–2 and 1, –3 and 2 cm), 0 cm (–1 and 1, –2 and 2, –3 and 3 cm), $\Delta 1$ cm (2 and –1, 3 and –2 cm), and $\Delta 2$ cm (–1 and 3 cm).

We conducted further analyses on factors which could impact a participants’ target selection aside from viewing the options. We first considered the impact of the hand’s lateral movement. Each participant’s trials were separated into those in which a left target vs. a right target was eventually obtained. At each time point a receiver operator curve (ROC) classified the data into two sets based on the collection of lateral hand velocities (Green and Swets 1966; Pruszyński et al. 2008). This was done separately for the jump and split conditions. Perfect misclassification, random classification, and perfect classification correspond to ROC values of –1, 0, and 1, respectively. Each participant’s ROC was then examined at the moment of target change, i.e., before the influence of visual processing on hand motion.

Another analysis considered whether target selection was influenced by the closest preceding jump trial. Congruence between target selection and the closest preceding jump trial was scored as 1 (both rightward or both leftward), whereas incongruence was scored as -1 (one rightward and the other leftward). The summed magnitude of all split-jump contrasts normalized by their total number could vary from -1 (indicating a perfect negative correlation) to 1 (indicating a perfect positive correlation); 0 indicates no correlation. Note that only unperturbed trials could separate a given split-jump pair; i.e., we only considered split trials whose closest preceding perturbation was a jump trial.

A wholly different set of analyses examined when the participant's lateral hand motion first exhibited a response to the lateral target change. We designate this delay between stimulus and response as the online reaction time (oRT). The analysis involved eight steps for each subject:

- 1) For every trial, the hand's lateral position was double-differentiated to obtain an acceleration profile. Note that the position signal was already filtered at 25 Hz.
- 2) In a 90-ms window starting from target onset, the summed squared difference of the lateral acceleration in a given perturbed trial versus every unperturbed trial was calculated. This time window immediately precedes any kinematic response to the visual stimulus and allowed us to tailor the baseline for each trial, i.e., how the hand would move in the absence of a perturbation. A similar approach of trial-specific templates was recently employed by Zhang et al. (2020).
- 3) The acceleration trajectories of the 10 unperturbed trials with the lowest summed squared difference from the perturbation trial were averaged.
- 4) The trajectory was adjusted by subtracting the trial-specific baseline acceleration trajectory from the perturbation trial's acceleration trajectory.
- 5) The adjusted right jump acceleration trajectories from all rightward target displacements were averaged, and then the same was done for the adjusted left jump trajectories, adjusted right split trajectories, and adjusted left split trajectories.
- 6) The leftward average trajectory was then subtracted from the rightward averaged trajectory.
- 7) The zero-crossing of this acceleration difference was considered to be the participant's online reaction time. It was estimated with a linear regression of the 10 ms preceding 25% of the peak difference. This approach is similar to the suggested method of Oostwoud Wijdenes et al. (2014).
- 8) If a participant evinced an apparent response faster than 110 ms in either the jump or split data sets (a potential false positive), then we adopted a larger threshold of 40% for both conditions. Fourteen of 53 participants required a larger threshold, and the modification yielded realistic data for 10 of them; the online reaction time of 4 participants was disregarded.

We also determined when the corrective responses were sensitive to the amplitude of target displacement, rather than the direction of target displacement. For this, we contrasted the left-right acceleration difference for the smallest target jump with the left-right acceleration difference for the largest target jump. The regression approach described above was applied to this contrast.

The number of trials available for all analyses varied with the particular subject and experiment owing to differences in their scheduled jump and split trials, particular selection patterns, and any rejected trials. The mean number of trials utilized for each condition is shown in Table 1.

Electromyography analysis. Muscle activity obtained in *Experiment 1* was band-pass filtered (25–250 Hz, 6th-order Butterworth, forward/backward pass to eliminate delays) and rectified. Each muscle's mean activity from the unperturbed trials (time-aligned to the change in the hidden target/photodiode) was used for normalization: 1) the grand mean EMG was obtained, 2) this grand mean was further filtered with a moving average of 50 ms, and 3) the difference between the maximum and minimum value at any time within the reach was used to normalize all trials. Signal quality (Q) of each muscle was scored as 2 (great), 1 (weak), or 0 (unacceptable). Data scored as 0 had clear artifacts and/or large noise and were not considered further. Suitable data were obtained from posterior deltoid (Q2 = 14, Q1 = 2, Q0 = 1), pectoralis major (Q2 = 6, Q1 = 8, Q0 = 3), and triceps lateral (Q2 = 10 and Q1 = 4, Q0 = 3). Brachioradialis activity was consistently weak or marred by artifact and so rejected (Q2 = 0, Q1 = 11, Q0 = 6). We focus on samples obtained from individuals whose split oRT was at least 30 ms later than their jump oRT to allow a disambiguation in the muscular events underlying the movement events.

Muscle activity was processed in parallel to the hand's lateral motion. The unperturbed trials which served as a kinematic baseline for a given perturbation trial were also used for its EMG baseline and subtracted away. This process should account for any preperturbation differences in the EMG which lead to differences in the acceleration. The perturbation data was combined as previously done for the kinematics (e.g., all the right jump trials averaged together). Importantly, we aligned each participant's EMG to their oRT to relate the muscular and movement events. Three alignments were considered: their jump trial data to their jump oRT, their split trial data to their split oRT, and their split trial data to their jump oRT. The first two alignments should reveal the reciprocal changes in EMG that create the estimated divergence of the lateral hand motion to left and right targets. Aligning the EMG from split trials to the participant's jump oRT could reveal EMG changes which precede the split oRT and did not create a divergence in lateral hand motion, because of either co-contraction or a fixed but biased response leading to similar hand deviation. We examined the mean EMG in a 30-ms window preceding the aligned oRT and in a baseline period of 80 ms after the target change. In addition, we realigned the lateral accelerations to the oRTs in the same manner as the EMG (jump trial data to the jump oRT, the split trial data to the split oRT, and the split trial data to the jump oRT) to examine the kinematics associated with the EMG. We examined the mean acceleration in a 30-ms window following the aligned oRT and in a baseline period of 10 ms prior. This kinematic analysis was also conducted for individuals in *Experiments 1* and *3* whose split oRT was at least 30 ms later than their jump oRT.

ANOVAs, *t* tests (paired and unpaired), and linear correlations were used for statistical evaluation. Statistical significance was set at $P < 0.05$ and involved two-sided tests, unless stated otherwise.

Estimating relative torque for different target directions. We estimated the torque requirement for obtaining the different targets with

Table 1. Number of participant trials averaged for determining the online reaction time

	Left Jump	Right Jump	Left Split	Right Split
<i>Experiment 1</i>	22.6 ± 1.6	22.8 ± 1.0	30.9 ± 9.9	37.1 ± 10.8
<i>Experiment 2</i>	25.3 ± 2.3	24.8 ± 3.2	39.3 ± 14.9	36.1 ± 14.2
<i>Experiment 3</i>				
Near instruction	15.8 ± 1.2	15.7 ± 1.3	13.8 ± 1.8*	13.3 ± 2.4*
Far instruction	15.2 ± 1.2	14.9 ± 1.1	6.8 ± 4.9*	7.7 ± 4.9*

Values are means ± SD of number of participant trials. *Correct trials.

a simple empirical model of the arm dynamics. For this we analyzed kinematic data from three co-authors (I.K., M.P., and R.C.) in response to known loads applied to the arm. Each individual brought their arm to a small target requiring 30° shoulder flexion and 90° elbow flexion which was equidistant from the start target and central end target and approximately where the arm began exerting corrective actions. Torque pulses of 100 ms in duration and 1 N·m in magnitude were applied to the arm in nine equally spaced directions of torque space: equal extension at both joints (225°), elbow extension only (270°), equal elbow extension and shoulder flexion (315°), shoulder flexion only (0°), equal elbow flexion and shoulder extension (45°), and the four directions between them (22.5°, 247.5°, 292.5°, and 337.5°). These loads resulted in the arm being displaced between pure elbow flexion (backward and leftward in hand space) to pure elbow extension (forward and rightwards in hand space). The piecewise change in hand-displacement magnitude versus the change in hand-displacement direction (measured 50 ms following the perturbation) allowed us to estimate the torque necessary to displace the hand directly toward the default end target and those positioned to its left and right. We then normalized the torque magnitude associated with these lateral targets by the torque associated with the default target. This allowed a simple empirical approach to the inverse dynamics rather than simulating a complex trajectory and solutions with complex equations.

RESULTS

General patterns of reaching movements. During unperturbed trials in all three experiments, participants made mildly curved hand movements to the target placed 20 cm ahead. The initial portion deviated an average of 4.6° (± 1.7 SD) from the end target. These deviations were leftward for some subjects and rightward for others with minimal overall bias. Unperturbed reaches had a peak forward velocity of 40.8 cm/s (± 3.2 SD) and overall movement time of 691 ms (± 34 SD). The average movement time of most participants (49/53) was within the prescribed limits of 600–750 ms, although there was considerable trial-to-trial variability: overall mean correct = 58% (± 14 SD), slow = 24% (± 11 SD), and fast = 18% (± 11 SD).

Change(s) to the end target's lateral position(s) required participants to redirect their ongoing movement. Redirections leftward and rightward obviously required the participant to exert different patterns of torque but also different magnitudes of torque owing to the arm's inertial anisotropy. The participants passed through the forward midpoint at an average of 142 ms from the target change, which is generally when the first corrective responses began (see *Online reaction times in Experiments 1 and 2* and *Target selection and online reaction times in Experiment 3*). Data from three individuals (all authors) indicated that 22% (± 4 SD) more torque was needed to accelerate the hand directly toward the leftmost target from this position compared with the central target directly ahead of the hand; 25% (± 4 SD) less torque was needed to accelerate the hand directly toward the rightmost target compared with the central target. This direction dependency resulted from the leftward targets having greater alignment with the major axis of the arm's inertial ellipse (parallel to the forearm) than rightward targets (Gordon et al. 1994; Graham et al. 2003; Mussa-Ivaldi et al. 1985). The overall torque magnitudes will certainly vary with different arm sizes and trajectories, but the general pattern should be consistent: less torque required to accelerate the hand by a fixed amount toward leftward targets

than rightward targets. Notably, when participants were obliged to redirect during jump trials, they took an average of 27 ms (± 61 SD) longer to acquire the farthest left target than the farthest right target [$t(52) = 3.3$, $P = 0.002$], which is consistent with incomplete compensation of the arm's inertial anisotropy.

Target selection in Experiments 1 and 2. During the split conditions, participants sometimes reached to left targets and sometimes to right targets. No participant exclusively reached to one or the other. Data from two exemplar participants in *Experiments 1* and *2* are shown in stem plots (Fig. 2A). The vertical height of the gray stems indicates the frequency of participants selecting the right target, and the stem placement corresponds to the particular split combination of left and right target positions from the center target. Frequency of selecting the right target systematically varied across conditions. A rightward target at 1 cm and leftward target at -3 cm led to a high frequency of selecting the right option. A rightward target at 3 cm and leftward target at -1 cm led to a low frequency of selecting the right option. Split conditions in between these two extremes tended to have selection frequencies in between. Accordingly, the exemplar participants more frequently selected the target whose position was nearest to the original target.

This general pattern is apparent when data from all the participants are examined (Fig. 2B). The group average is depicted by black dots, and individual data are depicted by gray dots. *Experiment 1* included some individuals with a modest preference for leftward targets and others with a modest preference for rightward targets, while other had preferences up to approximately four times greater, i.e., ~ 0.2 and ~ 0.8 selection bias, but overall, the group did not exhibit a selection bias to either side [mean = 0.54 (± 0.15 SD), $t(16) = 1.1$, $P = 0.28$]. A similar pattern of individual diversity and unbiased group behavior was present in *Experiment 2* [mean = 0.48 (± 0.18 SD), $t(17) = -0.5$, $P = 0.62$].

The selection contrast (Fig. 2D) also showed a degree of variation across participants, but all participants tended to select targets with the smaller displacement [*Experiment 1*: mean = 0.51 (± 0.12 SD), $t(16) = 17.8$, $P < 0.0001$; *Experiment 2*: mean = 0.69 (± 0.16 SD), $t(17) = 18.7$, $P < 0.0001$]. To be clear, the near-target selection pattern was never an absolute but rather a tendency. On average, participants were $\sim 50\%$ and $\sim 70\%$ more likely to select the target with the smaller displacement in *Experiments 1* and *2*, respectively. Comparison of the data between groups indicates that the selection contrast was greater for the group with preview information [$t(33) = 3.8$, $P = 0.0006$].

The overall sensitivity to relative displacement showed a gradation of selection frequency with increasing difference between the target options. This was evident by comparing the change in right-selection frequency between the two most extreme conditions (1 and -3 cm and -3 and 1 cm) versus the change between less extreme (but still unequal) conditions (e.g., 2 and -3 cm and -3 and 2 cm). This selection gradient was positive in 33/35 cases [*Experiment 1*: mean = 0.38 (± 0.22 SD), $t(16) = 7.1$, $P < 0.0001$; *Experiment 2*: mean = 0.26 (± 0.16 SD), $t(17) = 6.7$, $P < 0.0001$]. Moreover, the overall pattern of target selection was well characterized by a logistic fit of right-selection frequency versus the relative distance of the two options to the center [*Experiment 1*:

mean $R^2 = 0.75$ (± 0.12 SD); *Experiment 2*: mean $R^2 = 0.85$ (± 0.14 SD)]. This indicates that the selection tendency of individual subjects was well described by a simple contrast of the magnitude of two options.

The most detailed analysis of the spatial structure of online target selection was motivated by the long-established fact that perceptual discrimination is yoked to the relative size of two signals (Gescheider 2013). Accordingly, the tendency to select the nearer target would be expected to decrease with the absolute size of the options which have a fixed difference, although this is may be very subtle for the small changes in target position we considered. Right target selection should be less pronounced for the -3 and 2 -cm split than the -2 and

1 -cm split, whereas left target selection should be less pronounced for the -2 and 3 -cm split than the -1 and 2 -cm split. We found that the summed difference of these contrasts was typically greater than zero in *Experiment 2* [mean = 0.13 (± 0.21 SD)], though not every individual exhibited the trend [$t(17) = 2.7$, $P = 0.016$]. The trend in *Experiment 1* was positive but more variable and so did not reach statistical significance [mean = 0.15 (± 0.36 SD), $t(16) = 1.7$, $P = 0.11$].

A related factor which may have impacted target selection is the hand's trajectory before viewing target options, as this codetermines the hand's distance to the two options. We first conducted an ROC analysis on the likelihood of identifying the left-right selection at each point in time based on the two sets of lateral hand velocity. The individual and group ROC trajectories are presented in Fig. 3 and show positive trends for the split conditions (i.e., toward the selected target). In *Experiment 1*, the mean ROC at target change was 0.60 classification accuracy [$(\pm 0.09$ SD), $t(16) = 4.3$, $P = 0.0005$]; note that 0.5 indicates chance level and 1.0 is perfect classification. In *Experiment 2*, the mean ROC was 0.59 classification accuracy (± 0.09 SD) [$t(17) = 4.0$, $P = 0.001$]. This indicates that target selection to a given side was considerably more likely when the hand was already closer to that side. As an internal control, the same analysis was conducted on the jump data and indicated no significant trends (mean classification accuracy < 0.51 , $P > 0.5$) for either experiment. Note that viewed targets in *Experiment 2* had no apparent impact on the initial direction of hand motion, i.e., before target change. The grand mean reach angle differed by $< 1^\circ$ across the nine target configurations.

Finally, we considered whether the preceding jump trial influenced selection for the subsequent split trial. A positive effect would have a correlation of 1 (redirecting rightward for both and leftward for both), whereas a negative correlation would have a correlation of -1 (redirecting leftward for one and rightward for the other). We found no systematic impact of the previous jump history on target selection for either experiment [*Experiment 1*: mean = -0.03 (± 0.18 SD); *Experiment 2*: mean ~ 0.00 (± 0.16 SD), $P > 0.5$].

Online reaction times in Experiments 1 and 2. A second set of analyses examined when participants redirected their reaching movements to a new target, i.e., the online reaction time (oRT). Note that our approach matched each perturbation trial to its own baseline from the unperturbed trials based on their

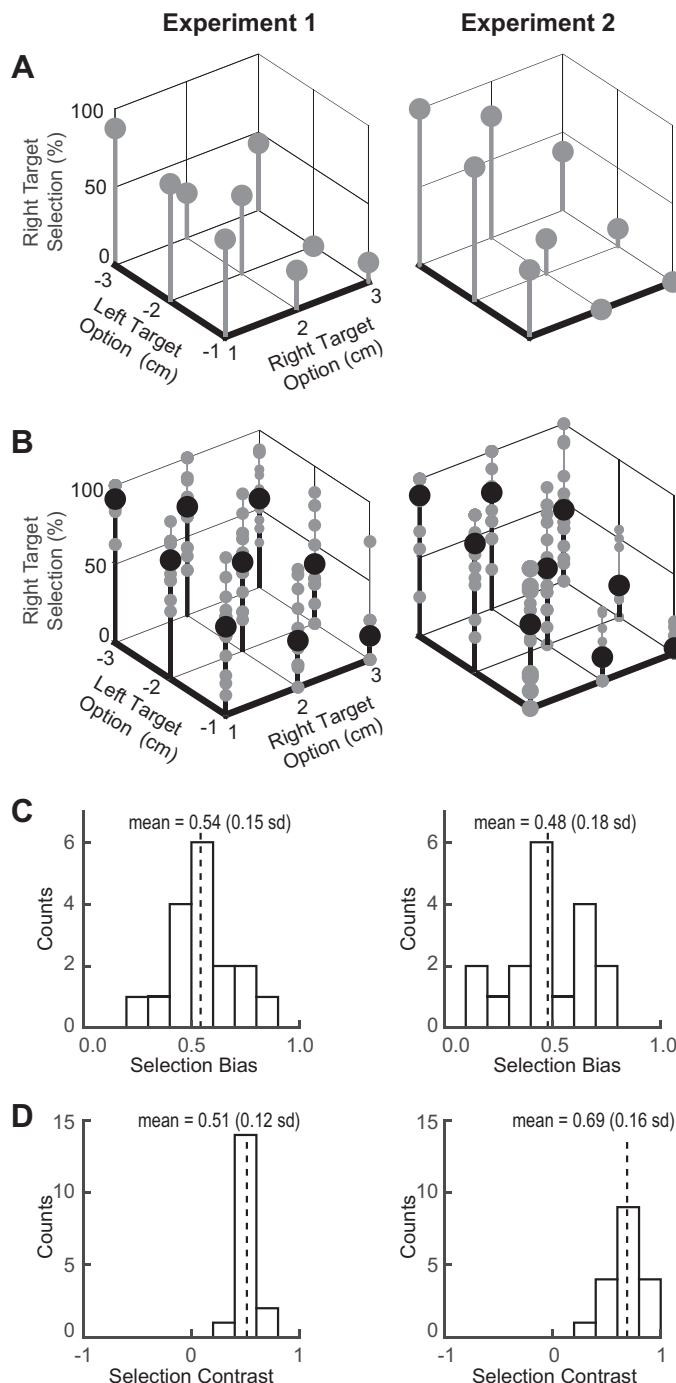


Fig. 2. Pattern of online target selection in *Experiments 1* and *2*. *A*: data from 2 exemplar participants. The 9 stems represent data during the 9 split conditions with the 3 right targets arranged on the x -axis and 3 left targets arranged on the y -axis. The height of each stem reflects the percentage of trials in which the participant selected the right target, ranging between 0 and 100% ; note that limited repeats translated to step sizes of $\sim 12\%$. The exemplar participants selected the right target more often during split combinations with a smaller right than left target displacement and less often with a smaller left than right target displacement. *B*: individual data for all participants in the 2 experiments (*Exp. 1*: $n = 17$ participants; *Exp. 2*: $n = 18$ participants) are shown with small gray circles, and the group means are shown in large black circles. *C*: selection bias could vary from always left (0), equal left and right (0.5), and always right (1). Individual participants exhibited a range of biases, but there was no apparent group bias to the left or right in either experiment. *D*: selection contrast could vary from always selecting the target with the largest displacement (-1), no impact of relative displacement amplitude (0), and always selecting the target with the smallest displacement (1). All participants in both experiments tended to select the target with the smallest displacement amplitude (selection contrast > 0).

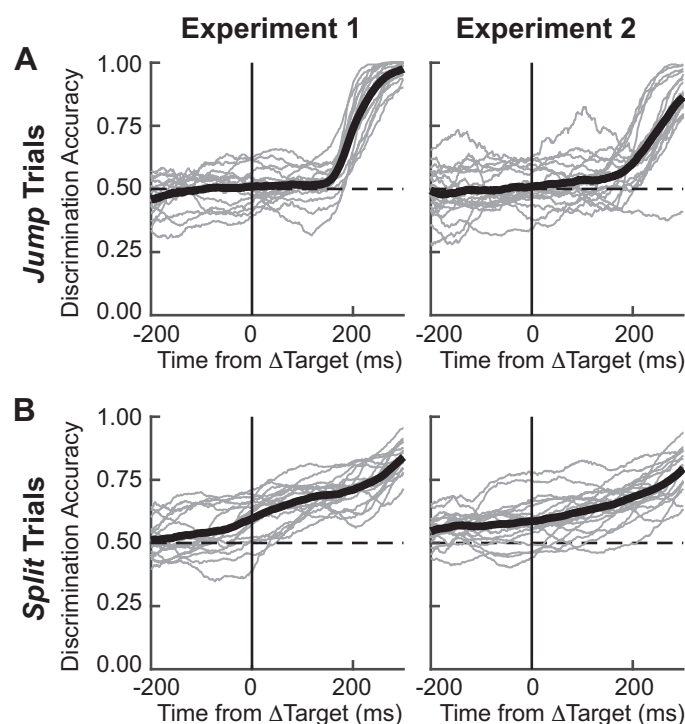


Fig. 3. Influence of lateral hand velocity on target selection in *Experiments 1* and *2*. *A*: instantaneous ability of an ideal observer to discriminate between trials that selected the right vs. left target during all jump trials. A value of 1.0 indicates perfect discrimination, 0.5 indicates random discrimination (horizontal dashed line), and 0.0 indicates always wrong discrimination. Data in *Experiment 1* ($n = 17$ participants) and *Experiment 2* ($n = 18$ participants) is aligned to the onset of the target change (Δ Target). Thin gray traces and thick black traces show individual participants and the group average, respectively. *B*: instantaneous ability of an ideal observer to discriminate between trials that selected the right vs. left target selection during all split trials. Same format as in *A*.

similar acceleration immediately after the target change. This helped account for the differences in pretarget hand motion for right vs. left target selection (see ROC analysis described in *Behavioral analysis*) as well as maximize the ability to detect a reaction to the visual target. Figure 4, *A* and *B*, presents the adjusted lateral acceleration by all participants in *Experiments 1* and *2*; note that each participant's trace is the average of several trials across several conditions (see MATERIALS AND METHODS and Table 1 for details). Following the target change, the hand movements were directed to the leftward targets (black traces) or rightward targets (negative sign). In *Experiment 1*, the mean oRT was 142 ms (± 9 SD) after target jump and 189 ms (± 37 SD) after target split, and the mean difference in oRT (47 ms) was statistically significant [$t(16) = 5.5$, $P < 0.0001$]. In *Experiment 2*, the mean oRT for the jump and split conditions was 167 ms (± 25 SD) and 202 ms (± 40 SD), respectively, and their mean difference (35 ms) was statistically significant [$t(15) = 4.5$, $P = 0.0004$]. Hence, online selection between two target options was slower than redirecting to a single viable option, and this slowing occurred whether or not the potential targets were previewed and despite the greater near-target tendency during preview (Fig. 4C). Note that statistical contrasts between the two experiments indicate that the oRT for jump targets was longer during *Experiment 2* [$t(31) = 3.9$, $P = 0.005$], but there was no difference for split targets [$t(31) = 0.9$, $P = 0.36$].

Two additional analysis of the oRT in *Experiments 1* and *2* are relevant. Response scaling to jump target magnitude tended to be later than the split oRT, estimated from the acceleration pattern for 3-cm target displacements vs. 1-cm target displacements. The difference was significant in *Experiment 2* [mean difference = 29 ms (± 43 SD), $t(14) = 2.6$, $P = 0.02$] but not in *Experiment 1* [mean difference = 21 ms (± 44 SD), $t(15) = 1.9$, $P = 0.07$]. Also, intrasubject correlation of oRT during jump and split trials was not significant in either experiment [*Experiment 1*: $R = 0.22$, $P = 0.39$; *Experiment 2*: $R = 0.62$, $P = 0.1$], although limitations in our detection algorithm may obscure their linkage.

Target selection and online reaction times in Experiments 3. *Experiment 3* examined whether the selection patterns and online reaction times were impacted by explicitly instructing participants which target to obtain during split trials. When instructed to obtain the Near target, participants consistently acquired the target displaced by 1 cm rather than the target displaced by 3 cm [mean error rate = 13.1% (± 9.2 SD)].

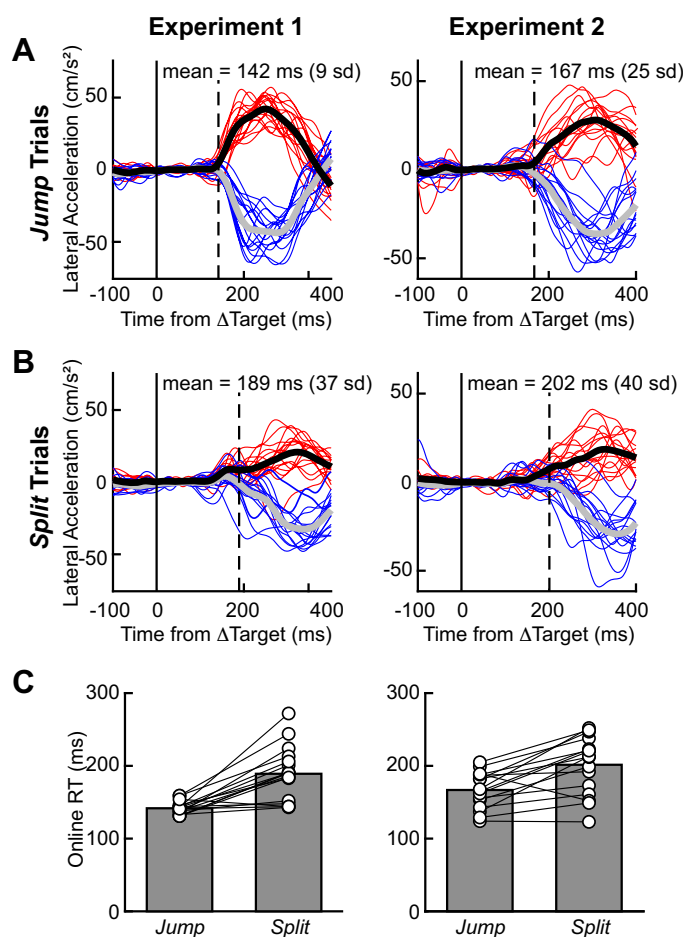


Fig. 4. Online reaction times in *Experiments 1* and *2*. *A*: change in the hand's lateral acceleration from baseline in response to a target jump. All data are aligned to the onset of target change. Average trajectories for each participant to the left and right target are depicted with thin blue and red lines, respectively; see Table 1 for average number of trials in *Experiment 1* ($n = 17$ participants) and *Experiment 2* ($n = 16$ participants). Group averages are depicted with thick black and gray lines. Dashed vertical lines indicate the average online reaction time with the mean and SD shown at top. *B*: similar format for responses during split trials. *C*: online reaction time (RT) during jump and split conditions is shown for individual subjects (white circles connected by thin black lines) and group data (gray bars).

Participants invariably performed worse with the Far instruction (Fig. 5A). In roughly half the trials they went to the wrong/near target [mean error rate = 52.2% (± 23.2 SD)]. This was a statistically significant increase in error rate from the Near instruction [$t(17) = 7.4$, $P < 0.0001$].

The oRT results are shown in Fig. 5B. The average oRT in jump trials was 139 ms (± 9 SD) and 145 ms (± 12 SD) with the Near and Far instruction, respectively (see Fig. 4B). Target split resulted in an average oRT of 169 ms (± 22 SD) with the Near instruction and 253 ms (± 81 SD) with the Far instruction. Note that this only describes the correct trials where the participant obtained the near target during the Near instruction and the far target during the Far instruction. A repeated measures ANOVA identified a main effect of instruction [$F(1,15) = 16.3$], target type [$F(1,15) = 43.2$], and instruction \times target interaction [$F(1,15) = 12.8$]. Specific contrasts among the four oRTs revealed a significant difference between jump and split trials for the Near instruction [$t(15) = 4.9$, $P = 0.0002$] and Far instruction [$t(15) = 5.3$, $P = 0.0001$] like in *Experiments 1* and *2*. The instruction did not significantly alter oRTs for jump trials [$t(15) = 1.7$, $P = 0.10$], whereas oRTs in the split condition were significantly greater with the Far instruction than with the Near instruction [$t(15) = 3.9$, $P = 0.0016$].

Possibly, the oRTs during the Far instruction were falsely inflated owing to the lower number of correct trials (see Table 1). To control for this, we ran a bootstrap analysis that randomly sampled a subset of the participant's correct trials during the Near instruction and recalculated the group average ($n = 1,000$ trials); in no case was the resampled bootstrap mean equal to or greater than the mean oRT with the Far instruction. Further, the median resampled mean was 196 ms, which is 27 ms higher than the estimation when all the trials were used, but adding this fixed amount to the Near oRTs did not alter our conclusion. The Far oRT and shifted Near oRT were significantly different [$t(15) = 2.6$, $P = 0.0196$].

Our final oRT analysis examined the oRTs of incorrect trials during the Far instruction, i.e., the oRTs of trials where the participant obtained the near target (Fig. 5B, light gray bar). The mean oRT of incorrect Far trials was 178 ms (± 32 SD),

which was significantly lower than that occurring for the correct Far trials [$t(11) = -3.5$, $P = 0.0005$] and not different from the oRTs with the Near instruction [$t(11) = 1.1$, $P = 0.3$]. That is, there was a systematic shift in the oRT in the Far instruction depending on the target selection: delayed from the Near oRT when movements were correctly directed to the far target, and similar to the Near oRT when movements were incorrectly directed to the near target.

In each of the above analyses for *Experiments 1–3*, we examined the entire group of participants. We also conducted a series of post hoc analyses to examine any potential differences between the two sexes in their selection bias, selection gradient, and online reaction time. No significant statistically differences were found for any of the measures we considered ($P > 0.05$).

Muscle activity in Experiment 1 and reexamination of hand motion in Experiments 1–3. The activities of three arm muscles, posterior deltoid (PD), triceps lateral (Tlat), and pectoralis major (PM), were examined in *Experiment 1* (see Fig. 6). Maintaining the arm at the starting position required tonic activity in the shoulder extensor which was released concurrent with a burst in the shoulder flexor muscle to accelerate the hand forward (Fig. 6, A, C, and D). The PD then increased its activity to a peak ~ 100 ms after the potential target change to help decelerate the limb. The PM agonist burst peaked ~ 200 ms before the potential target change, and then the muscle showed a smaller and slower increase in activity during the terminal portion of the reach. The elbow extensor exhibited a complex pattern which partially resembled the PD and PM: multiphasic activity in the first half of the movement followed by large terminal increase in the second half of the movement (Fig. 6B). It is most likely that other arm muscles (particularly anterior deltoid and biceps brachii) were engaged, but they were not recorded.

The PD and Tlat activity aligned to the participant's jump oRT (Fig. 6, A and B, second column) exhibited large reciprocal changes in the 30-ms period preceding the corrective action. The two extensors decreased their activity when redirecting to leftward targets [PD mean $\Delta = -0.30$ au (± 0.18 SD); Tlat mean $\Delta = -0.33$ au (± 0.20 SD)] and increased their activity when redirecting to rightward targets [PD mean $\Delta = 0.82$ au (± 0.4 SD); Tlat mean $\Delta = 0.59$ au (± 0.39 SD)]. Such changes in activity were appropriate to move the hand leftward and rightward according to the muscle's mechanical action and the arm placement (Fig. 6E, second column). In both muscles, the change of activity between targets was significant [PD: $t(10) = 8.2$, $P < 0.0001$; Tlat: $t(9) = 6.2$, $P = 0.0002$], whereas changes in PM were very small (< 0.10) and did not reach significance [$t(9) = -1.1$, $P = 0.32$; Fig. 6C, second column).

The PD and Tlat activity immediately preceding redirection in the split trials (Fig. 6, A and B, third column) showed decreases in activity with the leftward target [PD mean $\Delta = -0.31$ au (± 0.17 SD); Tlat mean $\Delta = -0.23$ au (± 0.23 SD)] though little change from baseline for the rightward direction [PD mean $\Delta = -0.04$ au (± 0.23 SD); Tlat mean $\Delta = 0.00$ au (± 0.20 SD)]. The difference between targets was significant [PD: $t(10) = 4.4$, $P = 0.002$; Tlat: $t(9) = 2.3$, $P = 0.047$]. The PM again showed very small changes (< 0.10) which did not statistically differ [$t(9) = 1.3$, $P = 0.22$].

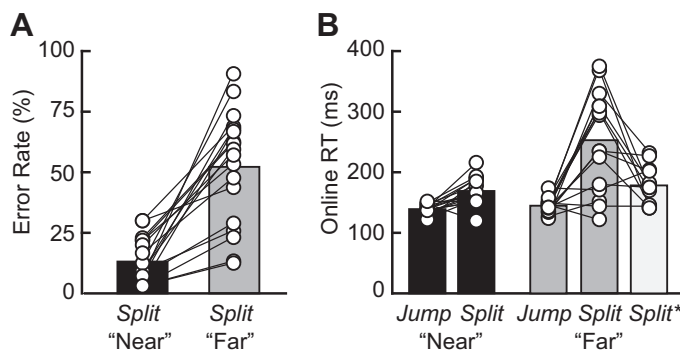


Fig. 5. Accuracy and timing of target selection in *Experiment 3*. A: black bar and white circles depict group average and individual rates for incorrectly obtaining the far target during the “Near” instruction. Gray bar and white circles show the group average and individual rates for incorrectly obtaining the near target during the “Far” instruction. Lines connect data from individual subjects (*Experiment 3*: $n = 18$ participants). B: black bars and white circles depict group average and individual online reaction times (RT). Data for the correct trials with the Near and Far instructions are shown by the black and dark gray bars ($n = 16$ participants); data for the incorrect trials with the Far instruction are shown with the light gray bar ($n = 12$ participants).

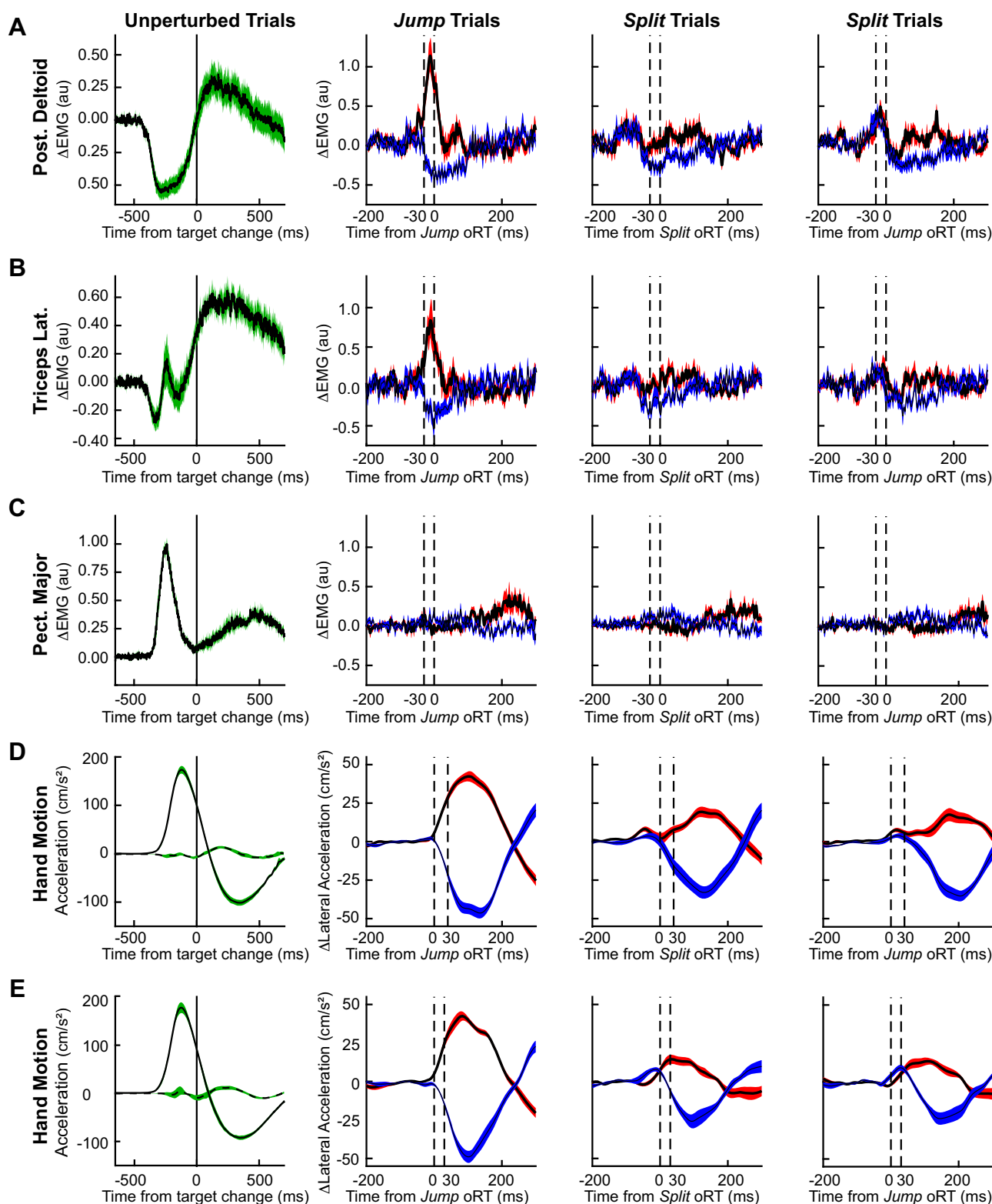


Fig. 6. Muscle activity and lateral hand motion in *Experiment 1* aligned to online reaction time (oRT). *A*: group average of posterior deltoid activity (Post. deltoid; $n = 11$ participants) is shown with mean and SE. Green traces depict unperturbed trials, while blue and red traces depict perturbed trials to the left and right targets, respectively. Muscle activity in the unperturbed trials is aligned to when the target change would occur. Data in the “Jump Trials” column results from aligning each participant’s target-evoked muscle activity in the jump trials to their jump oRT. Data in the first “Split Trials” column results from aligning each participant’s target-evoked muscle activity in the split trials to their split oRT. Data in the second “Split Trials” column results from aligning each participant’s target-evoked muscle activity in the split trials to their jump oRT. *B* and *C*: data for the triceps lateral (Triceps Lat.; $n = 10$ participants) and pectoralis major (Pect. Major; $n = 10$ participants) using the same format and color code as in *A*. *D*: hand motion examined using the same approach of aligning data to the jump or split oRT ($n = 11$ participants); same color code as in *A*–*C*. Leftmost column shows the forward hand acceleration with a solid line and the lateral hand acceleration with a dashed line; the remaining columns show the change in lateral hand acceleration from baseline. *E*: hand motion in *Experiment 3* (Near instruction) examined in the same manner as in *D* ($n = 8$ participants).

The patterns described above generally follow our expectations. An outstanding issue is whether the muscles expressed a response in the split trials before the split oRT. That is, did the muscles show some reliable response at the jump oRT that did not result in the limb moving in separable directions either because it was very small, a co-contraction, or nonspecific? To test this we aligned the data obtained during split trials to each participant's jump oRT (Fig. 6, fourth column). Both extensor muscles showed an increase in activity immediately before the jump oRT whether they would subsequently redirect leftward or rightward [PD mean $\Delta = 0.22$ au (± 0.17 SD) leftward and $\Delta = 0.29$ au (± 0.23 SD) rightward; Tlat mean $\Delta = 0.09$ au (± 0.17 SD) leftward and $\Delta = 0.18$ au (± 0.16 SD) rightward]. In both cases, the difference between conditions was not statistically significant [PD: $t(10) = 1.7$, $P = 0.1$; Tlat: $t(9) = 1.8$, $P = 0.1$].

Since PM showed little evoked activity, it could be that similar extensor responses led to a nonspecific movement in the split trials which went undetected by our approach based on the difference in lateral hand acceleration for trials destined to the right and left targets. In fact, realigning the lateral hand motion data in the split trials to the jump oRT revealed a small rightward deflection in the subsequent 30 ms (Fig. 6D and Table 2). Rightward accelerations occurred for trajectories eventually acquiring left targets [1.4 cm/s^2 (± 2.7 SD)] as well as those eventually acquiring right targets [2.6 cm/s^2 (± 2.9 SD)]. These motions were not statistically different [$t(10) = 1.4$, $P = 0.2$]. In contrast, jump trials aligned to jump oRT had subsequent reciprocal accelerations [-7.0 cm/s^2 (± 2.7 SD) and 10.1 cm/s^2 (± 4.0 SD)] as did split trials aligned to the split oRT [-6.3 cm/s^2 (± 4.7 SD) and 1.2 cm/s^2 (± 2.9 SD)]. For both these alignments, the left and right trials were significantly different [$t(10) = 9.9$, $P < 0.001$ and $t(10) = 5.1$, $P < 0.001$, respectively].

This pattern was repeated in *Experiment 3* (Near instruction; Fig. 6E and Table 2). Participants showed rightward deviations following the jump oRT for split trajectories destined to the left and right target, and these congruent rightward deviations were not significantly different [$t(7) = -0.1$, $P = 0.88$]. Participants also showed reciprocal accelerations for the jump trials aligned to jump oRT [$t(7) = 6.5$, $P < 0.0003$] and split trials aligned to split oRT [$t(7) = 4.6$, $P = 0.003$].

Experiment 2 differed from *Experiments 1* and *3* in that split trials aligned to jump oRT had subsequent deviations which were small, reciprocal, and not significantly different [$t(8) = 1.0$, $P = 0.34$; Table 2]. But like the other two experiments, the participants showed reciprocal accelerations for jump trials aligned to jump oRT [$t(8) = 4.7$, $P = 0.0015$] and split trials aligned to split oRT [$t(8) = 2.6$, $P = 0.03$].

DISCUSSION

Healthy adults reached to a visual target which would occasionally jump sideways or split into two left-right options during the course of the forward movement. Such target changes always required an online reaction to achieve task success but differed in having one option versus two. The principle results of three experiments using this straightforward manipulation are that participants tend to select the option nearest the original when confronted with split targets, the near-target tendency is automatic, and the online reaction time of split trials is longer than that of jump trials.

Factors impacting the selection pattern. It should be emphasized that the near-target tendency was not an absolute with participants always selecting the nearest of the two options. Rather they showed a tendency that depended on several identified factors. Foremost, the likelihood of selecting the nearest option grew with its contrast. The overall selection pattern appeared as a difference-dependent gradient well-described by a logistic regression as is commonly used in perceptual estimation (Gescheider 2013) and decision-making (Glimcher and Fehr 2013). Visibility of the options was most apparent in *Experiment 2* and resulted in a near-target selection of 70% greater than random selection compared with 40% greater than random in *Experiment 1*; maximum near-target selection is 100% and random is 0%. This indicates a powerful but incomplete role of visible contrast.

The other factor demonstrated to impact online target selection is the participant's hand motion before viewing the options. An ROC analysis of each participant's trial-to-trial variation in lateral hand velocity showed positive trends to left-right discrimination before viewing the options. This finding complements the near-target tendency since the left-right hand motion impacts left-right selection. It could even be considered to be the same factor since target displacement and hand motion co-determine the distance to the target options, though target and hand/cursor signals likely initially involve different streams of processing (Brenner and Smeets 2003; Franklin et al. 2016; Reichenbach et al. 2014; Sarlegna et al. 2003). In either case, our results complement two previous reports of hand motion on target selection. The sequential reach study described in the INTRODUCTION (Brenner and Smeets 2015) found that the grand mean hand trajectories to easy and hard targets differ before the selection time; the ones eventually headed to the easy target were generally closer at the target presentation, although this was not quantified. Nashed et al. (2014) also found that hand motion impacted target selection in a paradigm involving mechanical perturbations which move the reaching hand to imminent collision with an obstacle, discussed further below.

Table 2. Mean acceleration 0-30 ms from alignment to the online reaction time

	Left Jump Aligned to Jump oRT	Right Jump Aligned to Jump oRT	Left Split Aligned to Split oRT	Right Split Aligned to Split oRT	Left Split Aligned to Jump oRT	Right Split Aligned to Jump oRT
<i>Experiment 1</i>	-7.0 ± 2.7	10.1 ± 4.0	-6.3 ± 4.7	1.2 ± 2.9	1.4 ± 2.7	2.6 ± 2.9
<i>Experiment 2</i>	-4.4 ± 3.6	6.0 ± 5.4	-6.5 ± 9.5	2.0 ± 2.6	0.5 ± 3.6	-0.8 ± 2.2
<i>Experiment 3</i> (Near instruction)	-5.1 ± 4.0	10.7 ± 5.5	-6.2 ± 2.7	5.8 ± 5.6	3.8 ± 5.9	4.2 ± 5.2

Values are means \pm SD of mean acceleration (cm/s^2).

The last extravisual factor we examined was the history of jump trials and whether a preceding target jump to the left(right) resulted in an increased likelihood of selecting a left(right) target on the subsequent split trial, or vice versa. We did not find an influence of jump history, though this could reasonably change with different condition statistics than our approach with two-thirds unperturbed trials and symmetrical perturbations.

Several other factors could reasonably impact online target selection but are speculative. These include sensitivity to limb biomechanics, perceptual anchors, and gaze direction. Previous studies have convincingly shown that decision-making for self-initiated actions is sensitive to limb biomechanics (Cos et al. 2011, 2014; Diamond et al. 2017; Morel et al. 2017). As mentioned in the INTRODUCTION, this requires just 200 ms of target view time before movement initiation, which indicates fast processing and comparison of the biomechanical costs (Cos et al. 2014). In our experiment, rightward targets (approached from the midrange posture of 30° shoulder angle and 90° elbow angle) are closer aligned to the arm's inertial minor axis and so require less joint torque to obtain than leftward targets. The mechanical imbalance would be expected to result in an overall bias to the right, and, in fact, some participants showed a rightward bias, but others showed a leftward bias, and overall there was no bias. Biomechanics may be a general factor with other target arrangements and effective for participants who exhibited rightward biases, but this also implies the potency of an opposing factor leading to leftward biases in other participants. One possibility is a perceptual anchor of the body's midline which is left of the target distribution ahead of the right shoulder. Body midline is the midpoint of our bimanual workspace as mechanically defined and statistically observed (Howard et al. 2009). It is also a cardinal landmark based on the brain's lateralized representations of space. Accordingly, parietal lobe damage commonly leads to unilateral spatial neglect (Gammeri et al. 2020), and various percepts are yoked to the body midline such as a bias in estimating the hand's mediolateral position (Qureshi et al. 2019) and block of the "rubber hand" illusion (misattribution of a felt touch to a viewed dummy hand) when either hand crosses the midline (Cadieux et al. 2011). It is possible that participants with a leftward tendency were biased by this perceptual anchor.

A final (speculative) factor impacting target selection is gaze direction. Gaze is intimately related to the guidance of action (Land and Hayhoe 2001), and aligning gaze to the movement direction results in shorter delays and more vigorous corrections to a jump in a viewed hand/cursor (de Brouwer et al. 2018), though this may differ for target jumps (see above). Our participants may be expected to foveate the central target; however, their gaze direction was not controlled (nor measured), and so left-right differences in gaze could have led to different left-right biases while trial-to-trial changes in gaze would blunt the near-selection tendency.

Future work will need to test these speculative factors. Regardless, it is clear that the near-target tendency for online target is typical, being expressed by every subject examined in *Experiments 1* and *2* with a "natural" instruction. *Experiment 3* demonstrated that it is also a highly automatic tendency. Participants explicitly instructed to obtain the near target (1 vs. 3 cm) incorrectly obtained the far target on ~15% of trials. In

contrast, when instructed to obtain the far target, participants incorrectly obtained the near target on ~50% of trials.

Pattern of online reaction times. The pattern of online reaction times revealed key facts about how target changes are handled during an evolving action. Online reaction times in the standard jump conditions of *Experiments 1* and *3* showed a similar timing to previous reports of ~140 ms. Previewing the target options in *Experiment 2* led to a reliable increase in its jump oRT, ~165 ms, though still within the range of previous studies (reviewed in Gaveau et al. 2014; Sarlegna and Mutha 2015). The increased oRT could reflect a lowered saliency of the jump target from an open to a filled circle compared with transitioning from a blank background (Veerman et al. 2008), and/or it could reflect competitive inhibition from the other potential targets (discussed further below).

We found that split trials led to mean oRTs of ~170–200 ms in the three experiments. This timing overlaps with the ~200-ms selection time enforced in Cos et al. (2014) and visually estimated in Brenner and Smeets (2015) (see INTRODUCTION). Both these studies involved rapid point-to-point actions, whereas Michalski et al. (2020) examined slower tracking movements (steady 6 cm/s versus our peak of ~40 cm/s) and found notably slower oRT of ~500 ms. Is it unclear whether this difference reflects the slower movements or if the tracking task involves a slower control process.

Critically, the split oRT was elevated from jump trials in all three experiments: mean increase ~30–50 ms. Note that previewing the target options in *Experiment 2* did not lead to a reliable decrease in its split oRT from *Experiment 1*, which suggests that there are significant time constraints on the selection process. The overall elevation in split oRT from jump oRT coupled with the automaticity of near-target selection is inconsistent with the two general hypotheses we considered based on previous data: nonselective and automatic reactions with fast oRTs vs. selective and arbitrary reactions with delayed oRTs. In addition, the fact that split oRTs preceded or were indistinguishable from the amplitude effect on jump oRTs suggests that split oRTs could automatically incorporate stimulus features, such as color, which do not induce fast and automatic responses with switched targets (Cressman et al. 2006; Veerman et al. 2008).

The delayed oRTs and automatic selection during split trials are complemented by several other oRT results. Foremost, oRTs when participants correctly obtained the "far" target (during the Far instruction) were further elevated by ~50 ms than when they correctly obtained the "near" target (during the Near instruction). The delayed and error-prone behavior is unequivocal evidence that participants recruit more neural resources to act counter their natural tendency. This also appears to be a specific restraint on near-target reactions, not a global restraint on all reactions, since oRTs with the Far instruction were bimodal—normally delayed oRTs when the near target was incorrectly obtained and further delayed oRTs when the far target was obtained. It should be noted that the variability of the oRT during split trials was consistently greater than during jump trials. This likely reflects the imperfections in detecting oRTs given the influence of hand motions on target selection, a more variable underlying process for selecting between targets, and variability from small rightward motions observed at the jump oRT due to nonspecific extensor activity (see below).

Before addressing the conceptual frameworks and neural networks relevant to our results, we will discuss the electromyographic data collected in *Experiment 1*. Muscle activity can reveal neural processing not readily evident in kinematics, since there is more redundancy for muscles than joints and greater temporal precision in muscle than motion signals owing to the delays for integrating activity to force. Furthermore, our oRT procedure is based on the peak difference in left-right acceleration and would overlook transient kinematic differences from transient activity differences, parallel changes in motion from nonspecific in burst muscle activity, and unchanged motions from balanced co-contraction. Given the intersubject jitter in oRTs, we aligned each participant's muscle activity and hand motion to their own oRT. Not surprisingly, jump trial data aligned to jump oRTs involved reciprocal changes of muscle activity in the preceding 30 ms and reciprocal changes of hand motion in the subsequent 30 ms, i.e., increases and decreases in extensor activity resulted in rightward and leftward hand motion. A similar expected pattern was present when muscle activity during split trials was aligned to the split oRTs. The critical unknown was whether target split evoked muscle activity at latencies earlier than indicated from the split oRTs. Aligning the split trial data to the jump oRTs revealed a preceding increase in extensor activity for both directions of target selection. That is, the extensor muscles expressed a nonspecific increase at a jump oRT before the split oRT linked to target selection. Note that the shoulder flexor showed poor modulation to the target changes, the elbow flexor had poor baseline signals and was not further analyzed, and no attempts were made in collecting other flexors. The possibility of undetected co-contraction left it uncertain whether aligned hand motion would be indistinguishable from baseline or whether unbalanced extensor activity would result in rightward hand motion. We observed rightward hand motion consistent with unbalanced extensor activity. A similar pattern was present in *Experiment 3* but not in *Experiment 2*. We suspect that *Experiment 2* did not follow this pattern due to the same factors leading to its delayed jump oRTs.

Conceptual schemes and neural substrates for online target selection. The observed results are in broad concordance with the known neurophysiology of visually guided action and suggest several avenues to explore. The posterior parietal cortex (PPC) is a key player. Its most relevant portions are situated above the intraparietal sulcus and incorporate visual and proprioceptive information along a caudal-rostral gradient (Andersen and Cui 2009; Gallivan and Goodale 2018; Medendorp and Heed 2019). During reaching tasks, the PPC encodes the positions of the arm and intended target with a tight link to gaze direction. Understandably then, PPC damage is marked by deficits in updating manual actions to shifts in target location relative to the hand or eye: online reactions to target jumps are no longer fast and automatic (Gréa et al. 2002; Pisella et al. 2000); pointing to a target in peripheral vision is highly variable and drawn toward the gaze position (Khan et al. 2005), and pointing to a new target is strongly influenced by a previously viewed but voided target (Khan et al. 2005). Similar changes can also be induced by focal application of muscimol (Battaglia-Mayer et al. 2013; Hwang et al. 2012) and transcranial magnetic stimulation (Ciavarro et al. 2013; Desmurget et al. 1999).

Several authors have described portions of PPC as a part of a network of priority maps which integrates top-down signals for task goals and bottom-up signals for stimulus saliency within a spatially organized neural network (for review see Bisley and Goldberg 2010; Fecteau and Munoz 2006; Ptak and Fellrath 2013). In addition, there are intrinsic competitive mechanisms which shape target selection. In this framework, jump targets result in a fast and focused drive through parietal cortex owing to the lack of other viable targets and accompanying competition. These signals would be then relayed to premotor cortex and from there to primary motor cortex, which create descending motor commands via their own integrative processes.

We found that split targets create several bursts of muscular activity in the reaching arm. The first burst occurs just before the online reaction to jump targets but is nonspecific, i.e., similar increase whether the participant eventually heads to the left option or the right option. These nonspecific bursts occurred in muscles whose activity was already increasing during unperturbed trials, suggesting that multiple signals from parietal cortex briefly engage the most active "nodes" within motor cortex. This is reminiscent of the findings of Stavisky et al. (2017) with target jumps during reaching evoking an initial burst of activity within primary motor cortex that is constrained to a "null space" followed by a larger and sustained burst in "potent dimensions"; the former burst does not impact the hand's motion, whereas the later burst drives the hand one way or another.

The second burst of muscle activity during split trials is directionally specific. A time-consuming and obligatory process of redirecting to one or another target may reflect target competition within PPC and its intrinsic connections which gives higher priority to targets nearer the original. Additional factors that impact online target selection, such as the ongoing hand movement and possibly gaze, biomechanics, and perceptual anchors, would also be expected to modulate the priority map as instances of bottom-up and top-down signals; projections from superior colliculus to PPC likely play an important role in prioritization since muscimol injection results in ignoring targets in that visual field (Song et al. 2011). Testing for spatially organized connections within PPC and potential efficacy of various factors will require a paradigm similar to ours: two target options revealed during the movement and placed at different proximity to the voided target.

The near-target tendency could be partially overridden. In the described framework of a priority map, this requires the active suppression of the PPC's intrinsic connections and exerted prioritization of targets further away the original. Attempts to redirect the far target are error prone owing to the PPC's high degree of spatial organization and further delayed owing to the suppression of fast selection processes—incorrect redirection to the near target are as fast as normal consistent with a normal response escaping from top-down inhibition. Prefrontal cortex is the best candidate for this role given its centrality to executive function and task selection (for review see Miller and Cohen 2001). More specifically, various regions within prefrontal cortex are critical to quickly inhibit an impending action (stop signal paradigm; Rubia et al. 2003) and inhibit a default action (go/no-go paradigm, paradigm; Krämer et al. 2013; Rubia et al. 2003; Siegel et al. 2015). Damage to these regions leads these inappropriate actions and, presum-

ably, would further degrade the ability to override the near-target tendency inherent to PPC.

The preceding material focused on PPC as a principle site for a putative priority map and site for target competition. Another body of research is concerned with end-stage competition between simultaneously considered motor plans within premotor cortex and the formation of averaged motor plans (Christopoulos et al. 2015; Cisek and Kalaska 2005, 2010; Gallivan et al. 2017; Stewart et al. 2014). Recent studies suggest that appearance of parallel motor plans and averaged behavior result from averaging between plan-specific trials (Dekleva et al. 2018) and task conditions that are best handled by midway motor plans (Haith et al. 2015; Wong et al. 2017). However, this ongoing controversy is not resolved, and its continued clarification will inform our understanding of online reactions to altered targets.

The general scheme we have described should also be present for reactions initiated from a postural hold, though not necessarily with the same prominence of various factors. This is important for how we relate these different behaviors and, specifically, how previous studies have reported slower reaction times to a visual target which can change location across trials compared with online responses to visual target changing location within a trial (for review see Smeets et al. 2016). Various arguments for such differences include switching from a postural to movement control (Cluff and Scott 2016), time for retrieving a feedback law versus utilizing the current one (Franklin 2016), as well as differences in target competition (Wyble and Rosenbaum 2016), neural circuits (Chua et al. 2016; Sainburg and Mutha 2016) decision criteria (Reichenbach 2016), evoking a decision (Haith et al. 2016), need for target detection (Smeets et al. 2016), and temporal overlap of planning and execution processes (Ames et al. 2019). These are not mutually exclusive explanations, and they will require more efforts to sort out. Before moving on, we wish to highlight a finding which we find particularly compelling: reaction times to a unpredictable visual target can be in the range of reported oRTs if participants are forced to initiate their movements at a particular time after target viewing (Haith et al. 2016); also see (Yang et al. 2011) for a related paradigm showing task-dependent reflexes to a mechanical perturbation (~75-ms delay) with short view times of the target (~70 ms). This indicates that the difference between the response times is not essential, but rather situational. One of our primary findings is the complement: slowed oRTs with split trials indicate the obligatory nature of competition during an ongoing reach even when the near target is consistently selected.

Relation to other paradigms. From a broad vantage, we can contrast the paradigm we adopted to others used by various researchers in addition to those treated in the INTRODUCTION. Sudden changes in target redundancy has been examined by changing the target geometry during the reach. Increasing the target size is equivalent to presenting many overlapping targets, and participants quickly take advantage of the options in their online response (Knill et al. 2011). A critical difference from our paradigm is that selecting a new target is mandatory during target split, and these options can be hidden beforehand. Two other paradigms examine movement updating under ambiguous conditions. In one set, the visual noise associated with a single target (Izawa and Shadmehr 2008) or hand position (Körding and Wolpert 2004) was systematically altered. In the

other set, participants had to “go-before-they-know” which target option was correct (Gallivan et al. 2016; Hudson et al. 2007; Resulaj et al. 2009; Wong and Haith 2017). In both cases, participants integrated the visual information in a near-optimal manner for task success either by modulating the magnitude of their adjustment or the initial heading direction. Here, participants reach to a default target that is voided midflight and must select among the revealed options, both of which are acceptable. The strong tendency is consistent with a spatial “cost” being minimized, but we did not consider how well the participant’s behavior can be accounted by an optimal controller and defer that comparison to another time [for review of optimal control see Cluff et al. (2015), Diedrichsen et al. (2010), and Wolpert and Landy (2012), and for examples of suboptimality see Hudson et al. (2010), Ota et al. (2015), Wolpert and Landy (2012), and Zhang et al. (2013)].

The final relevant paper is by Nashed et al. (2014), which we briefly described above. Unexpected perturbations moved the reaching hand to imminent collision with an obstacle and evoked fast veering responses to one side or the other. The fast veering reaction is the result of reflex activity starting ~60 ms after the perturbation and is linked to the ongoing movement: leftward (rightward) responses for leftward (rightward) trajectories. The context-dependent selections are impressively fast and were argued to reflect the readiness of multiple action plans, although recent evidence indicates that premotor cortex does not support parallel plans (Dekleva et al. 2018). Possibly, the somatosensory volley leads to a fast shift of target prioritization similar to multisensory estimates following limb perturbation being initially dominated by proprioception (Crevecoeur et al. 2016). Neurophysiological studies will help clarify this issue and others that were discussed.

Summary. The past two decades have witnessed a burgeoning interest in sophisticated online control of visuomanual actions and an expansion of the relevant paradigms. The current study adds important information on how we achieve successful behavior in rich and dynamic environments (slower online reactions which are automatically linked to relative distance of the options) and a possible tool to reveal its neural underpinnings.

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No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

I.L.K. and T.M. conceived and designed research; M.P., R.C., and E.A. performed experiments; I.L.K. analyzed data; I.L.K., T.M., and T.S. interpreted results of experiments; I.L.K. prepared figures; I.L.K. drafted manuscript; I.L.K. and T.S. edited and revised manuscript; I.L.K. approved final version of manuscript.

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