

## RESEARCH ARTICLE

## Control of Movement

## The influence of temporal predictability on express visuomotor responses

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## Abstract

Humans are able to generate target-directed visuomotor responses in less than 100 ms after stimulus onset. These “express” responses have been termed stimulus-locked responses (SLRs) and are proposed to be modulated by visuomotor transformations performed subcortically via the superior colliculus. Unfortunately, these responses have proven difficult to detect consistently across individuals. The recent report of an effective paradigm for generating SLRs in 100% of participants appears to change this. The task required the interception of a target moving at a constant velocity that emerged from behind a barrier. Here, we aimed to reproduce the efficacy of this paradigm for eliciting SLRs and to test the hypothesis that its effectiveness derives from the predictability of target onset time as opposed to target motion per se. In one experiment, we recorded surface electromyogram (EMG) from shoulder muscles as participants made reaches to intercept temporally predictable or unpredictable targets. Consistent with our hypothesis, predictably timed targets produced more frequent and stronger SLRs than unpredictably timed targets. In a second experiment, we compared different temporally predictable stimuli and observed that transiently presented targets produced larger and earlier SLRs than sustained moving targets. Our results suggest that target motion is not critical for facilitating the SLR expression and that timing predictability does not rely on extrapolation of a physically plausible motion trajectory. These findings provide support for a mechanism whereby an internal timer, probably located in cerebral cortex, primes the processing of both visual input and motor output within the superior colliculus to produce SLRs.

**NEW & NOTEWORTHY** Express stimulus-driven responses in humans have been proposed to be originated subcortically via the superior colliculus. These short-latency responses are facilitated by the presentation of dynamic visual stimuli. Here, we show that this facilitation is related to the predictable target timing, regardless of its kinematic attributes. We propose that the superior colliculus can be primed to generate express stimulus-driven motor responses via cortical top-down projection.

*moving target; rapid visuomotor responses; stimulus-timing prediction; transient visual stimulus; visually guided reaching*

## INTRODUCTION

Sudden events demand rapid motor responses, for example, to catch an object accidentally knocked from a table, to react to an opponent in sporting context, or for self-defense to an unexpected physical threat. Often, the surrounding contextual features provide information to anticipate the timing of the event but not its exact location. For instance, when observing a child moving in an unstable way, it is possible to predict if and when a threatening event will happen to be prepared to react rapidly (e.g., intercepting an object knocked by the child before it hits the ground; grasping the

child’s hand before it gets in contact with dangerous surfaces or objects).

Rapid visuomotor reactions have been studied in oculomotor responses (1), neck muscles (2), arm muscles (3), and leg muscles (4). The term “express” was originally adopted by Fischer and Boch (5) to describe the extreme short latency at which monkeys can produce stimulus-driven saccades (i.e., less than 110–120 ms from stimulus onset time; 1, 5, 6). Akin to the express saccade latency, the target-directed electromyogram (EMG) activity in neck and proximal arm muscles can encode the target location within ~100 ms from the stimulus presentation (3, 7, 8). Our intention in using the

term “express visuomotor responses” in the title of the paper is to draw a parallel between express saccades and the most rapid visuomotor responses that can be generated in other body parts, potentially through a common retino-tecto-reticular pathway. We hope that the use of such terminology will contribute to more widespread consideration of the implications of subcortical visuomotor transformations for theories on human motor control and behavior.

Two different acronyms have been coined for these short-latency responses in neck and arm muscles: 1) stimulus-locked responses (SLRs) and 2) rapid visual responses (RVR). The term RVR was adopted by Glover and Baker (9) as indicative of the type of stimulus (i.e., visual) that was used to elicit the response. The term SLR is descriptive of a characteristic attribute of these EMG responses, which are consistently more time locked (within ~100 ms) to the stimulus onset time than to reaction time, defined as initiation of the reaching movement (2, 3, 7, 8, 10–14). In this paper, we will use the “SLR” acronym because it describes how we define and quantify the response (see MATERIALS AND METHODS), while noting that it may be misleading as to functionality and mechanism.

The latencies of express saccades and SLRs are consistent with the minimum time that is needed to accomplish the sensorimotor transformation of visual information (15). These responses invariably reflect the stimulus location rather than the volitional movement that is ultimately produced, when these are dissociated in the antisaccade (reviewed by 16) and antireach tasks (17). The general idea is that antitasks require longer cortical pathways to compute the desired direction, whereas express outputs are mediated at the subcortical level via the midbrain superior colliculus, whose outputs are driven directly by the stimulus location itself. For SLRs, outputs from the superior colliculus have been proposed to be delivered to spinal interneurons and motoneurons via the tecto-reticulo-spinal pathway (18).

Previous work showed that SLRs are not detected consistently in all individuals. Pruszynski et al. (3) failed to detect SLRs from surface EMG recordings and detected positive SLRs in only seven out of 16 participants (~44% prevalence rate) using intramuscular electrodes. Recently, Kozak et al. (19) obtained a 100% SLR detection rate with the use of surface EMG electrodes among a sample of five individuals by adopting an emerging target paradigm, which was motivated by earlier oculomotor studies (for review, see 20). This suggests that the circuit responsible for SLRs can be biased according to task conditions. A better understanding of the efficacy of behavioral tasks and stimuli to generate SLRs would improve both the design of experiments and the identification of the likely pathways and mechanisms that mediate and modulate them.

In the emerging target paradigm, the stimulus initially fell toward a visual barrier and re-emerged beneath it at a time that was specified by the target velocity. This made the target presentation time predictable via extrapolation of the target trajectory behind the barrier (19). Previous studies showed that the collicular response to visual stimuli is more vigorous with moving than static stimuli (21, 22), raising the possibility that target motion facilitates SLRs because it provides a higher sensory salience in the superior colliculus itself. However, temporal predictability of a stimulus itself

facilitates express motor outputs and could be computed outside of the superior colliculus. Both express saccades and SLRs are facilitated by the insertion of a constant and predictable time gap between a warning stimulus (e.g., offset of the fixation) and the imperative stimulus (e.g., target presentation) to move, such as in the gap task paradigm (3, 5, 9, 10). We hypothesized that the SLR-facilitation effect of the emerging target paradigm is attributable, at least in part, to the temporal predictability of the stimulus, rather than to target motion per se.

In *experiment 1*, we used a constant velocity moving target paradigm, akin to that used by Kozak et al. (19), thus making the stimulus onset time predictable from the extrapolation of a physically plausible target trajectory behind the barrier (20, 23, 24). In the second experiment, we kept the target onset time constant but varied the location at which it emerged beneath the barrier. This allowed us to test the effects of target location on the expression of SLRs, as well as whether a physically plausible motion trajectory helps facilitate SLRs. Furthermore, we used either sustained moving or transient flashing static targets to determine how the SLR is modulated by the temporal attributes of the visual stimuli.

We found that the presentation of predictable and transient stimuli facilitated the expression of SLRs, regardless of where the target appeared. Our findings suggest that the emerging target paradigm promotes SLRs by allowing the precise initiation of an internal timer for a learned duration, rather than by extrapolating a plausible target motion trajectory. This would be consistent with a priming effect of temporal expectations transmitted to the SLR circuit, potentially through known cortical projections to the superior colliculus (15). Furthermore, our results suggest that the SLR circuit is sensitive to the temporal attributes of the visual stimulus and not to the vertical location of the target within a hemifield, at least within the range of vertical visual angles explored in this experiment.

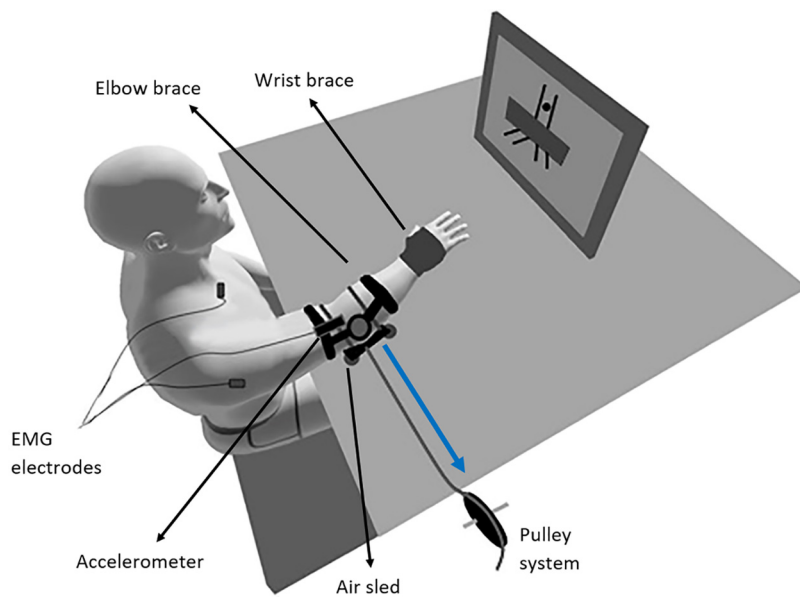
## MATERIALS AND METHODS

### Participants

Seventeen adults were recruited for this study. Fifteen subjects (11 males, 4 females; mean age: 29.0 years, SD: 5.8) participated in the first experiment. Nine of these people also participated in the second experiment, as part of a full sample of 11 adults (8 males, 3 females; mean age: 29.3 years, SD: 9.7). All participants were right handed, had normal or corrected-to-normal vision, and reported no current neurological or musculoskeletal disorders. All participants provided informed consent and were free to withdraw from the experiment at any time. All procedures were approved by the University of Queensland Medical Research Ethics Committee (Brisbane, Australia) and conformed to the Declaration of Helsinki.

### Apparatus

Participants were seated with the right elbow and forearm resting on a custom-built air sled that moved with limited friction on a table. The height of the chair was adjusted to allow reaching movements by the shoulder in the transverse plane centered at ~90° of flexion (Fig. 1). Both wrist and elbow mobility were restricted by orthopedic braces. The



**Figure 1.** Experimental setup. Participants sat in the experimental apparatus with their hand aligned with the fixation spot (cross bars beneath the barrier) and moved it toward the target that appeared beneath the barrier, either at the right or left of the fixation spot. The fingertip was close to the screen so that hand position corresponded closely to fixation point. Participants' fingertips never made contact with the screen. The eye-to-monitor distance was  $\sim 57$  cm, so 1 cm on the screen corresponded to  $\sim 1$  degree of visual angle. Head position was stabilized by chin and forehead rests (not shown here). EMG, electromyogram.

head was stabilized by a chin and forehead rest. A constant lateral load of  $\sim 5$  N was applied in the direction of shoulder transverse extension via a weight and pulley, thus increasing the baseline activity of shoulder transverse flexor muscles, including the clavicular head of the pectoralis major muscle (17). All stimuli were created in Matlab using the Psychophysics toolbox (25, 26) and were displayed on a LCD monitor with a 120-Hz frame rate positioned in front of the subject. The eye-to-monitor distance was  $\sim 57$  cm, so 1 cm on the screen corresponded to  $\sim 1$  degree of visual angle (dva). The target was a filled black circle (dimension:  $\sim 2$  dva in diameter; luminance:  $\sim 0.3$  cd/m<sup>2</sup>) presented against a gray background ( $\sim 170.4$  cd/m<sup>2</sup>). The aim was to create a salient and high-contrast target that has been shown to evoke short-latency and high-frequency collicular responses (27) and facilitate the expression of SLRs (10). The luminance of the background and target was measured with a colorimeter (Cambridge Research System ColorCAL MKII). A photodiode was attached to the left bottom corner of the monitor to detect a secondary light that was presented coincidentally with the time of appearance of the real target. This allowed us to index the time point at which the stimulus was physically displayed on the screen, thus avoiding uncertainties in software execution and raster scanning of the monitor.

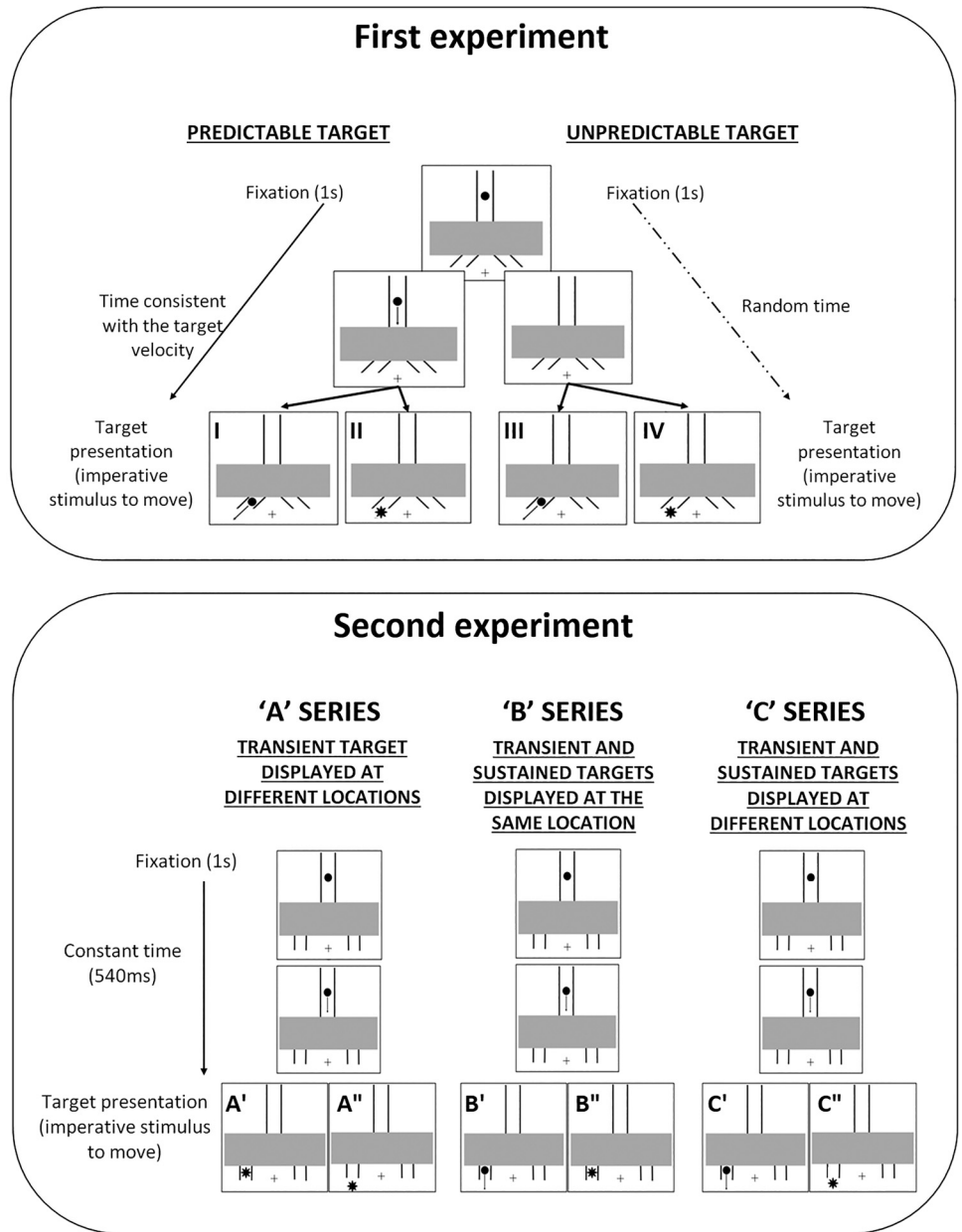
## Experimental Design

### **Experiment 1: predictable versus unpredictable stimulus onset time.**

In the first experiment, we used targets that randomly appeared at a predictable or unpredictable time from trial start. This allowed us to elucidate whether the effectiveness of the emerging target paradigm in eliciting SLRs relies on temporal predictability of the stimulus onset time. The participants performed visually guided reaches, always starting from a constant and static upper limb position and moving

as rapidly as possible toward visual targets that appeared randomly either to the right (extensor-ward) or to the left (flexor-ward) of the fixation spot, where the gaze and hand started for each trial. There were four task conditions in which the target onset time could be either predictable or unpredictable. In predictable tasks, the target was constrained to fall within an inverted y-shaped track, and a visual barrier occluded the junction point where targets could deviate left or right (Fig. 2, top). Predictable targets dropped at constant velocity of  $\sim 35$  dva/s until they gradually disappeared (sunset targets) behind the barrier, before (I) reappearing either just beneath the barrier (7 dva of fixation-target eccentricity) and continuing toward the interception point, or (II) suddenly flashing (one single flash of  $\sim 8$  ms of duration) at the interception point (10 dva of fixation-target eccentricity) at a time consistent with the target speed. In condition I, the target appeared just underneath the barrier at  $\sim 540$  ms from the trial start (onset time of target drop) and was occluded for  $\sim 380$  ms. In condition II, the target appeared transiently at the interception point at  $\sim 720$  ms from the trial initiation and remained invisible for  $\sim 560$  ms. Unpredictable targets disappeared from the origin and suddenly reappeared at a random time underneath the barrier, either (III) just beneath the barrier, whereupon they continued to the interception point at the constant velocity described for the predictable targets, or (IV) at the interception point, where they flashed transiently. The time at which the unpredictable targets appeared beneath the barrier was made random by adding a jitter time (0–300 ms) to the temporal delays of the predictable target conditions:  $540 + \text{jitter time}$  for condition III;  $720 + \text{jitter time}$  for condition IV. In unpredictable target conditions, the target onset times corresponded to the time during which the target was not visible. There was a distinction between the “predictable” and “unpredictable” conditions that participants could therefore infer from the initial context of each single trial. Specifically, if the target dropped toward the barrier, it always reappeared just beneath the barrier at the specified time (consistent with

**Figure 2.** First experiment: timeline of the predictable and unpredictable targets. In the predictable target conditions, the stimuli dropped from the stem of the track at constant velocity of  $\sim 35$  dva/s until it passed behind the barrier and reappeared either just beneath the barrier and continuing toward the interception point (I) or suddenly flashed at the interception point (II) at a time consistent with the target speed (i.e.  $\sim 540$  ms for condition I;  $\sim 720$  ms for condition II). In the unpredictable target conditions, the stimuli disappeared from the stem of the track and suddenly reappeared at a random time underneath the barrier (III), or at the interception point (IV), as described for the predictable targets. The onset time of the unpredictable targets was made random by adding a jitter time (0–300 ms) to the temporal delays of the predictable target conditions (i.e.  $\sim 540 + \text{jitter time}$  for condition III;  $\sim 720 + \text{jitter time}$  for condition IV). Second experiment: timeline of the transient and sustained targets. In all target conditions, the stimuli dropped from the stem of the track at constant velocity of  $\sim 35$  dva/s until they passed behind the barrier and reappeared underneath the barrier at  $\sim 540$  ms from the start of the trial. In A series, the target appeared transiently just beneath the barrier (A') or at the interception point (A''); in B series, the target appeared transiently just beneath the barrier (B') or appeared just beneath the barrier and continued moving toward the interception point (B''); in C series, the target appeared transiently at the interception point (C') or appeared just beneath the barrier and continued moving toward the interception point (C''). In both of the two experiments, the transient targets appeared by making one single flash of  $\sim 8$  ms of duration. dva, degree of visual angle.



target velocity), and then continued falling to reach the interception point, or suddenly flashed at the interception point at a specified time later. By contrast, if the target simply disappeared (without any motion) from the origin, then the subjects knew that the target onset time could not be predicted with certainty because of the inserted random delays. In each target condition, the participants had to initiate the movement as soon as they saw the target reappearing underneath the barrier.

The interception point was defined as the target trajectory point at which the hand could virtually reach the target, using only flexion/extension transverse plane movements of the shoulder. The participants could not bring the hand exactly to the physical target locations; hence, veridical target interception was not achieved. The target always

appeared as a full filled circle, thus avoiding a gradual emergence of the target from behind the barrier (rising moon stimulus), which would produce a high spatial frequency stimulus that has been reported to impair the SLR expression (14). The participants were instructed to react as quickly as possible to the stimulus presentation, by moving the hand toward the virtual point of interception with the target. That is, they had to bring the hand to the interception point as soon as they saw the target, even when it appeared just beneath the barrier (i.e., conditions I and III; Fig. 2).

To start the trial, participants were required to align the hand with the gaze fixation spot and to hold fixation for 1s. They were instructed to stay relaxed as much as possible before the target appearance and not to break fixation until the target reappeared underneath the barrier to the left or

right of the fixation point. On each trial, gaze-on-fixation was checked online with an EyeLink 1000 plus tower-mounted eye tracker device (SR Research Ltd., Ontario, Canada), at a sampling rate of 1,000 Hz. If the fixation requirement was not respected, participants received an error message and the trial was repeated.

For this experiment, participants performed 10 blocks of 48 reaches each (480 total reaches). The trial-list design of each block was 2 (predictable or unpredictable target)  $\times$  2 (transient static or moving target upon reappearance)  $\times$  2 (left or right target location), so eight unique trials types that were intermixed randomly in each block. As there were 10 blocks total, we obtained 60 repeats of every unique trial type.

### Experiment 2: sustained versus transient stimulus.

This experiment was designed to investigate whether the SLR facilitation in the emerging target paradigm occurs via a prediction of the stimulus onset time from implied target motion behind the barrier. To this end, we made the appearance time of the target consistent with its disappearance time and independent from its appearance location underneath the barrier. Therefore, the target onset time was predictable but inconsistent with extrapolation of a physically plausible target trajectory. Further, we used both transient flashing targets and sustained moving targets to test the sensitivity of the SLR circuitry to the temporal attributes of visual stimuli.

Experiment 2 was completed by 11 participants, nine of whom also participated in the first experiment and exhibited an SLR in at least one of the predictable target conditions of the first experiment (see RESULTS). They performed visually guided reaches toward temporally predictable targets, following the same task rules described for *experiment 1*. In this experiment, the target was constrained to move within a track that was shaped as an inverted diapacon, and it always started moving at a constant velocity before disappearing behind the barrier (Fig. 2, bottom).

The participants performed reaches toward three different target types, which were compared pairwise in three separate series of four trial blocks with 60 reaches per block (12 total blocks with 60 reaches per block = 720 total reaches). The order of the three series was randomized across participants, and the task comparisons in each series were between:

- target appearing transiently just beneath the barrier, or target appearing transiently at the interception point (A series, Fig. 2 bottom);
- target appearing transiently just beneath the barrier, or target appearing just beneath the barrier and continuing toward the interception point (B series, Fig. 2 bottom);
- target appearing transiently at the interception point, or target appearing just beneath the barrier and continuing toward the interception point (C series, Fig. 2 bottom).

All targets dropped at constant velocity of  $\sim$ 35 dva/s until they gradually disappeared behind the barrier and constantly emerged (“go” cue for movement initiation) from behind the barrier at  $\sim$ 540 ms from the start of the trial (onset time of target drop). In each target condition, the total disappearance time was  $\sim$ 380 ms. The eccentricity from the fixation spot was 10 dva for both of the two target locations.

The vertical distance between the “just beneath the barrier” and “interception point” spots was  $\sim$ 6 dva. The target always appeared below the barrier as a full, filled circle. In the transient target conditions, the stimulus appeared with one flash of  $\sim$ 8 ms of duration.

### Data Recording

Surface EMG (sEMG) activity was recorded from the clavicular head of the right pectoralis muscle (PMch), and from the posterior head of the right deltoid muscle (PD), with double-differential surface electrodes (Delsys Inc. Bagnoli-8 system, Boston, MA). The quality of the signal was checked, using an oscilloscope, before starting the recording session. The sEMG signals were amplified by 1,000, filtered with a 20–450 Hz bandwidth filter by the “Delsys Bagnoli-8 Main Amplifier Unit,” and full-wave rectified after digitization without further filtering.

Arm motion was monitored by a three-axis accelerometer (Dytran Instruments, Chatsworth, CA) positioned flat on the lateral aspect of the right upper arm, in line with the right humerus, just proximal to the lateral humeral epicondyle. The sEMG and kinematic data were sampled at 2 kHz and stored on a computer using a 16-bit analog-digital converter (USB-6343-BNC DAQ device, National Instruments, Austin, TX). Data synchronization was guaranteed by starting the recording of the entire data set at the frame at which the target started moving (predictable conditions), or disappeared from the screen (unpredictable conditions).

The accelerometer enabled the determination of the point in time, relative to the stimulus presentation, at which the force produced by the muscle was enough to overcome the upper limb inertia and initiate direct arm movement; herein after this will be called reaction time (RT). Movement onset was discriminated with the use of the cumulative sum method (28). More precisely, we defined the RT as the point in time at which the cumulative sum trace exceeded more than five standard deviations beyond the mean accelerometer signal, which was obtained by averaging the acceleration values recorded in the 100 ms before target onset time. We excluded trials with RT < 130 ms ( $\sim$ 5% of the trials) as indicative of anticipation, as well as those with RTs > 500 ms as indicative of inattentiveness. We decided to use a 130-ms RT cutoff because it is more conservative than the 100 ms adopted by Pruszynski et al. (3) to remove anticipatory responses in a gap-task paradigm. Furthermore, a recent work has provided evidence that humans can prepare accurate target-directed movements in  $\sim$ 130 ms from target presentation (29).

### Data Analysis

#### Detection of SLRs.

In line with previous approaches to quantify the SLR (3, 7), we used a time-series ROC (receiver operator characteristic) analysis to identify the presence of an SLR. The ROC analysis indicates the probability that an ideal observer could discriminate the side of the stimulus location based solely on sEMG activity. Here, we used the ROC analysis to detect the point in time at which the location of the target can be discriminated (discrimination time, DT) from the sEMG trace. The DT provides the earliest available indication that the target

location has been discriminated by some neural circuit in the brain, and that the motor command encoding this location has been delivered to the muscle. All analyses were aligned to the diode signal that detected the onset time of a secondary light displayed coincidentally with the real target (see APPARATUS description).

For every muscle sample and tested condition, we separated the sEMG activity for all correct reaches (~95% of the trials) based on visual stimulus location and sorted the trials according to RT. We then checked for an absence of voluntary muscle pretarget activation. For each individual trial, we computed the average voltage amplitude of the full-wave digitally rectified sEMG signal enclosed in a 50-ms time window before the target presentation. We then ran a correlation analysis between the individual sEMG values and the corresponding RTs. If a significant negative correlation was found, then we concluded that the muscle was preactivated to react faster, thus potentially biasing the sEMG activity between the stimulus onset and the movement initiation, including the SLR epoch. In this case, no further analysis was conducted on the sEMG data (3.17% of the recordings were discarded due to muscle pretarget activation). For recordings not showing muscle pretarget activation, we down-sampled the sEMG traces to 1 kHz. We then compared the sEMG activity for the target requiring muscle activation (left target for the pectoralis; right target for the posterior deltoid) and the target requiring muscle inhibition (e.g., right target for the pectoralis; left target for the posterior deltoid). Muscle activity for the two targets was split into two equally sized groups based on RT, subdividing the fastest 50% of the trials (fast trial set) and the slowest 50% (slow trial set). We then conducted separate ROC analyses on both trial sets. We ran the ROC analysis on every data sample obtained between 100 ms before to 300 ms after the visual stimulus onset, and we calculated the area under the ROC curve (AUC). The AUC values range from 0 to 1, where 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 thresholds for discrimination at 0.65; this criterion exceeds the 95% confidence intervals of data randomly shuffled with a bootstrap procedure. The time of earliest discrimination was defined as the time after stimulus onset at which the AUC overcame the defined threshold and remained above that threshold level for at least 15 ms. In accordance with the literature, the candidate SLR was considered only if the discrimination time of fast and slow trial sets was between 80 and 120 ms after visual stimulus onset (17).

To determine whether the short-latency muscle response was consistently time-locked to the visual stimulus onset, or covaried with the RT, we compared the two DTs (fast trials DT; slow trials DT) for the average RT in the slow and fast trial sets by fitting a line to the data (10). If the slope of the line is 45°, then the discrimination time covaries with RT, and so the initial sEMG is time-locked with the RT. Conversely, if the slope of the line is infinite (90°), then the DT remains the same irrespective of the RT, and the onset of sEMG is consistently linked to the appearance of the peripheral target. We classified an SLR observation as positive (+ SLR) if the slope of the line was >67.5° (halfway between 45° and 90°). If the SLR was positively detected, then we ran

a time-series ROC on all trials to determine the point in time at which the target location could be discriminated solely from the sEMG trace.

The DT variable that we extracted from the time-series ROC analysis is sensitive to the amplitude of the difference between the excitatory and inhibitory stimulus-driven responses relative to the background sEMG trace, including the signal noise. More precisely, the ROC analysis would return earlier discrimination times for large activation/inhibition responses deviating from low-variance background signals than small muscle responses diverging from high-variance background traces, even if both muscle responses deviate from background at the same time from the stimulus presentation. This is because the vigor of the muscular response to the visual stimuli directly influences how sharply the ROC curve rises toward the threshold defined for the discrimination time. In our experiment, this means that even if the ROC curves of two different target types (e.g., predictable, unpredictable) start diverging from chance (i.e., 0.5) at the same time after target onset, the location of the target eliciting the stronger responses can be discriminated earlier than the other one. This may mislead interpretation of the muscle response latency in the different task conditions. To provide a more sensitive determination of the visuomotor response onset time, we ran an analysis that searches for the inflection point at which the time-series ROC curve begins to deviate from chance toward the discrimination threshold (i.e., 0.65). To do this, we fit a DogLeg regression (30, 31) to the ROC curve for each millisecond spanning from 50 ms before target presentation up to the DT. The divergence time was then determined by taking the later time point between two possible candidates as the onset time of the response: 1) the point that minimizes the squared errors between the ROC curve and the DogLeg regression; 2) the last local minimum in the ROC curve before the DT. This analysis allowed us to reduce the influence of the visuomotor response size on the indexing of the time point at which the muscles started responding to the target.

#### **Correlation of visual SLR magnitude with reaction time.**

The relationship between SLRs and voluntary RT was tested to help disentangle the potential contribution of these express visuomotor response to the mechanical onset of target-directed reaches. Therefore, we correlated RT with the magnitude of the EMG activity in the SLR time window on a trial-by-trial basis (3, 17). More specifically, we defined the SLR magnitude as the mean sEMG activity recorded in the 10 ms subsequent to the DT of the slow trial sets (see ROC METHOD). We used this method to index the muscle activity in a time window restricted to a brief period consistent with the earliest time that the SLR-related EMG was present for both the fast and slow halves of the RT distributions. The aim was to minimize the potential for the index of SLR magnitude to be contaminated by EMG activity associated with the subsequent EMG burst that is time-locked to limb motion. Nonetheless, we also tested different methods to define the time window over which to quantify the SLR, including simple measurements of the peak and average activity within the nominal SLR time window (80–120 ms after stimulus presentation). Similar results were obtained irrespective of

the specific method employed (i.e., negative correlation between the SLR magnitude and the RT; see RESULTS).

**Statistical analysis.**

Statistical analyses were performed in SPSS (IBMSPSS Statistics for Windows, v. 25, SPSS Inc., Chicago, IL). Results were analyzed with one-sample and paired-sample *t* tests as the normality of the distributions was verified by the Shapiro–Wilk test. The chi-squared test was used to analyze changes in SLR prevalence across predictable and unpredictable conditions. For all tests, the statistical significance was designated at *P* < 0.05. Furthermore, we conducted single-subject statistical analyses to verify that the ROC outcomes can be relied upon for comparisons between the different target conditions (Supplemental Materials and Methods; all Supplemental Material is available at [https://osf.io/eans8s/?view\\_only=1790fec27e874d2caa2207d44b14d4fb](https://osf.io/eans8s/?view_only=1790fec27e874d2caa2207d44b14d4fb); <https://doi.org/10.17605/OSF.IO/EAN8S>).

**RESULTS**

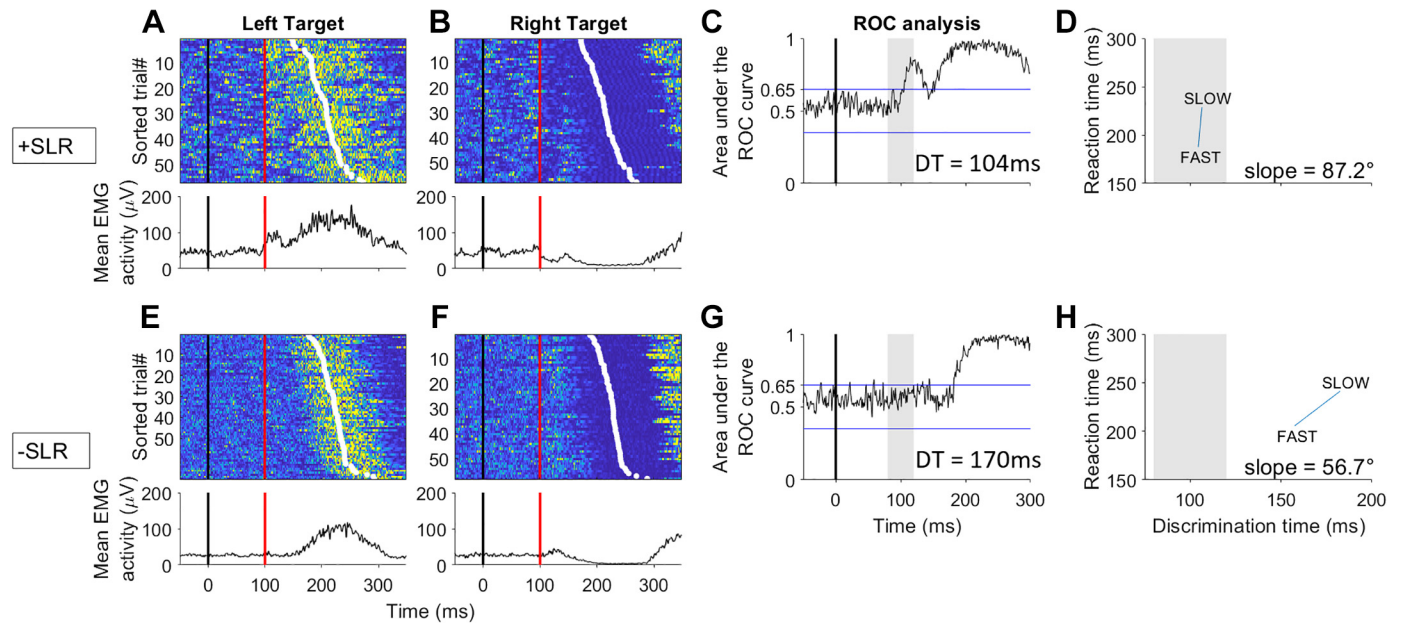
In the raster plots that are shown in Fig. 3, A and B, SLRs appear as a vertical band of either muscle activation (A) or

inhibition (B) that is time locked ~100 ms to the stimulus onset time, and which only slightly covaries with the voluntary RT. The consistency of the time-locking of the DT to the stimulus presentation was tested by running the ROC analysis over both fast and slow trial sets and fitting a line connecting the two DTs with the average RT of the slow and fast sets (see MATERIALS AND METHODS). When a +SLR was observed, the line slope exceeded 67.5°, meaning that the visuomotor response was more time-locked to the stimulus onset than to the RT (Fig. 3D). By contrast, for the –SLR example, the DT covaried with the RT rather than being driven by the stimulus (Fig. 3H).

**Experiment 1 Results**

**Predictable targets lead to more prevalent SLRs.**

In the first experiment, we investigated whether the effectiveness of the emerging target paradigm in eliciting SLRs relies on the predictability of the stimulus onset time. Trial-by-trial, the stimulus onset time was either predictable or unpredictable and, for each of the two predictability conditions, the target could appear either just beneath the barrier or at the interception point (see MATERIALS AND METHODS).



**Figure 3.** Surface EMG activity from the clavicular head of the pectoralis major muscle of an exemplar +SLR producer (subject 12, Table 1) and an exemplar –SLR producer (subject 5, Table 1) who participated in the first experiment. For both participants, the data are taken from to the trials in which the target appeared at a predictable time just beneath the barrier (condition I, Fig. 2). The muscle acts as agonist and antagonist for the left and right targets, respectively. For both subjects, rasters of rectified surface sEMG activity from individual trials are shown (darker yellow colors indicate greater sEMG activity; A, B, E, and F), as are the traces of the mean sEMG activity. Data are aligned on visual target presentation (solid black vertical line at time 0) and sorted according to reaction time (white dots within the rasters). The solid red line indicates the expected initiation time of the SLR (~100 ms from target onset). The +SLR subject shows a column of either rapid muscle activation (A) or inhibition (B) time-locked to the stimulus onset regardless of the time of voluntary movement initiation. By contrast, for the –SLR subject, the muscle activity at 100 ms from target presentation does not differ from the background level (E and F). The ROC analysis panels show the point in time [discrimination time (DT)] at which the location of the target can be discriminated by the muscle activity. The DT is identified by the first time frame at which the area under the ROC curve surpasses the value of 0.65 and remains over this threshold for 15 ms. For the +SLR subject, the discrimination time falls inside the SLR epoch highlighted by the gray patch (C), whereas the discrimination time of the –SLR producer exceeded the SLR time window (G). D and H show a line connecting the discrimination time identified by running the ROC analysis over the fast and slow trials. The two discrimination times are plotted for the slowest and fastest half of voluntary reaction times, and the line slope is showed. For the +SLR subject (D), both the early and late discrimination times are inside the SLR epoch evidenced by the gray patch, and the line slope exceeds 67.5°, thus indicating the presence of a visuomotor response that is more time-locked to the stimulus onset than to the reaction time. On the contrary, for the –SLR subject (H), the rapid visuomotor response is not observed, and the line slope indicates that the onset of the movement-related sEMG response covaries with the reaction time. EMG, electromyogram; ROC, receiver operator characteristic; sEMG, surface electromyogram; SLR, stimulus-locked response.

**Table 1.** Occurrences of positive SLRs in the clavicular head of the pectoralis major muscle and the posterior deltoid across participants in all four targets conditions tested in experiment 1

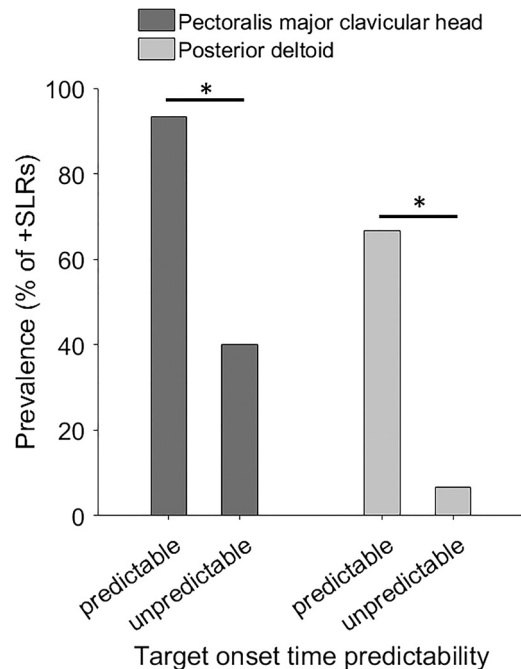
Subject	Predictable Target Conditions				Unpredictable Target Conditions			
	Target Appearing Just Beneath the Barrier		Target Appearing at the Interception point		Target Appearing Just Beneath the Barrier		Target Appearing at the Interception Point	
	PMch	PD	PMch	PD	PMch	PD	PMch	PD
1	x		x	+				
2	x		x		x		x	
3	x		x	+				
4	x		x	+				
5								
6			x					
7			x	+				
8			x	+				
9			x	+			x	
10	x		x					
11	x		x	+	x	+	x	+
12	x		x	+	x		x	
13	x	+	x	+			x	
14	x		x				x	
15			x	+				
Total +SLRs	9	1	14	10	3	1	6	1

PD, posterior deltoid; PMch, clavicular head of the pectoralis major muscle; SLR, stimulus-locked response.

Table 1 reports whether or not SLRs were detected among all the subjects and conditions tested in the *experiment 1*. The table shows that SLRs were much more frequent for the trials in which the subject knew exactly when the target would appear compared with those in which the subject was cued that the timing would be random. For the PMch, SLRs were elicited in all but one subject when the predictably timed target appeared at the interception point, and in nine of 15 subjects when the target appeared just beneath the barrier. For the PD, 10 subjects exhibited an SLR when the predictably timed target appeared at the interception point, but only one subject expressed an SLR when the predictably timed target appeared just beneath the barrier. SLRs were less prevalent but not entirely absent for the unpredictable timing condition. For the PMch, six subjects produced SLRs for targets at the interception point and three of them also exhibited an SLR when the predictable target appeared just beneath the barrier. For the PD, only one subject exhibited an SLR in both of the two unpredictably timed target conditions. Three subjects produced SLRs in the PMch under all four conditions. One subject produced no SLRs for any muscle or condition. The difference in SLR prevalence between the two muscle samples is likely due to the loading force, which led to increased baseline activity of the PMch while leaving unloaded the PD.

To determine the influence of temporal target predictability on the prevalence of SLR expression, we pooled the +SLR observations by selecting the participants who exhibited a +SLR with at least one of the two target locations beneath the barrier. For the PMch, 14 out of 15 participants expressed +SLRs with at least one of the two predictable target conditions, and six out of 15 participants exhibited +SLRs with at least one of the two unpredictable target conditions. These observations resulted in significantly higher prevalence of +SLR for predictable than unpredictable target conditions (chi-squared test;  $P = 0.002$ , chi-squared = 9.6,

$df = 1$ ; Fig. 4). For the PD, we identified +SLRs in 10 out of 15 participants for the predictable target conditions, and one out of 15 participants for the unpredictable target conditions, again resulting in significantly higher prevalence of +SLR for predictable than unpredictable conditions (chi-squared test;  $P < 0.001$ , chi-squared = 12.9,  $df = 1$ ; Fig. 4).



**Figure 4.** Dependence of +SLR prevalence on target onset time predictability. Significant differences between the predictable and unpredictable target conditions:  $*P < 0.01$ . SLR, stimulus-locked response.



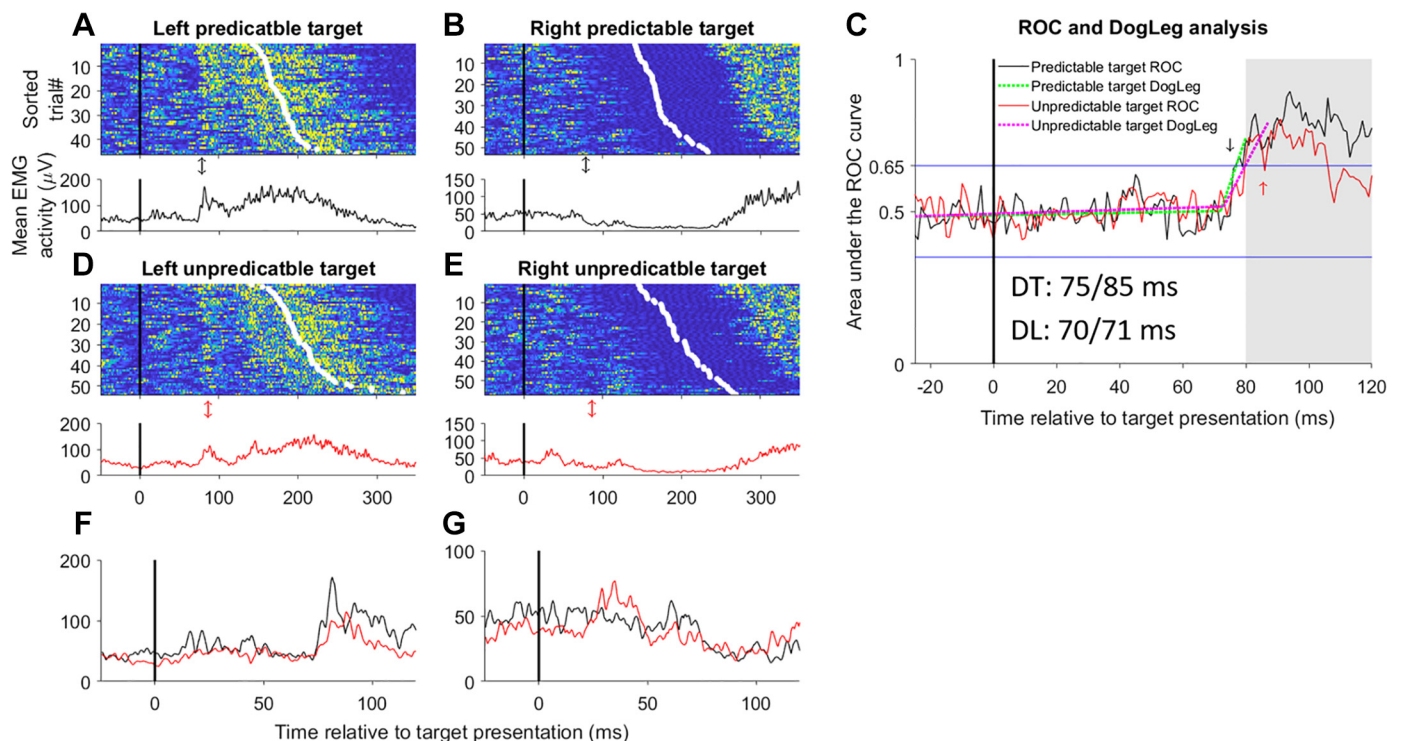
**Predictable targets facilitate SLRs.**

To elucidate the effect of temporal predictability on the magnitude and timing of the SLR, we selected the participants who produced a +SLR under both predictably and unpredictably timed target conditions. For each participant meeting this criterion, if the SLR was detected with all the tested conditions (*subjects 2, 11, and 12; Table 1*), we took the mean response onset time (DogLeg regression analysis), DT (ROC threshold analysis), and magnitude values (i.e., mean of the two predictable target conditions; mean of the two unpredictable target conditions). By contrast, if the number of +SLR observations mismatched between the temporal predictability conditions (*subjects 13 and 14; Table 1*), we considered the values of the +SLR that was expressed to the same presentation spot for both predictable and unpredictable timed targets (i.e., interception point for *subjects 13 and 14*).

For the PMch, six out of 15 participants exhibited +SLRs with both predictable and unpredictable target conditions, whereas only one participant had +SLRs in both target predictability conditions for the PD. Given the low number of +SLR observations for the PD, we considered only data

from the PMch sample to evaluate the effect of target onset predictability on the SLR.

Figure 5 shows the PMch activity for reaching movements toward predictable and unpredictable target conditions of an exemplar subject who participated in the first experiment and who exhibited +SLRs to both predictable and unpredictable timed targets (*subject 12; Table 1*). The SLR magnitude was larger for the predictable than the unpredictable target condition (predictable target: 111  $\mu$ V; unpredictable target: 92  $\mu$ V). The ROC threshold analysis revealed that the target direction could be first reliably discriminated from the sEMG at 75 ms for the predictable target (Fig. 5C) and at 85 ms for the unpredictable target (Fig. 5C). However, the DogLeg regression analysis showed that the ROC curve began to deviate from chance at  $\sim$ 70 ms for both of the two predictability target conditions (Fig. 5C). For this subject, the single-subject statistical analysis returned significant differences between the different target predictability conditions (Supplemental Fig. S1), and these results were consistent with those of the six participants who exhibited an SLR with both predictable and unpredictable targets (Supplemental



**Figure 5.** Surface EMG activity of the clavicular head of the pectoralis major muscle of an exemplar subject exhibiting +SLRs in both predictable and unpredictable target conditions. The data are from *subject 12* (*Table 1*) in trials in which the target appeared transiently (1 flash of  $\sim$ 8 ms of duration) at the interception point. For both predictable and unpredictable targets, rasters of rectified surface sEMG activity from individual trials are shown (*A, B, D, and E*; same format as *Fig. 3*), as is the trace of the mean sEMG activity. *F* and *G* offer a zoomed view of the mean sEMG traces and show how the SLR is larger with the predictable timed target (*F*, black trace) than the unpredictable timed target (*F*, red trace). However, the divergence onset time of the sEMG traces from baseline overlaps across the two temporal predictability conditions. *C* shows the results of the ROC analysis to identify the point in time [discrimination time (DT)] at which the location of the target can be discriminated from the sEMG, and the results of the DogLeg (DL) regression to determine the onset time of the visuomotor response (see MATERIALS AND METHODS). The DT of the predictable target condition is displayed as black arrows, whereas the DT of the unpredictable target condition is shown with red arrows. The ROC analysis reveals that the discrimination of the target location was earlier in predictable (75 ms) than unpredictable (85 ms) target conditions. However, the starting point of the ROC curve rising trend differs of just 1 ms between the two temporal predictability conditions (predictably timed target, DL = 70 ms; unpredictably timed target, DL = 71 ms). That is, the difference in discrimination time between the predictably and unpredictably timed targets is not evident from the earliest initiation of the response to the stimulus and is likely relative to the different magnitude of the short-latency response to temporal predictable and unpredictable targets. EMG, electromyogram; ROC, receiver operator characteristic; SLR, stimulus-locked response.

Table S1). Noteworthy, this gives us confidence on the reliability of ROC and DogLeg analyses to compare different stimulus conditions.

The temporal predictability effects on SLR timings and magnitude were consistent across the six participants exhibiting an SLR to at least one target location for both predictable and unpredictable timing. Specifically, the time at which the ROC curve started deviating from chance (DogLeg regression analysis) was not significantly different between temporal predictability conditions (Fig. 6A), thus suggesting that the short-latency response to the target was initiated at the same time irrespective of target onset time predictability. By contrast, the discrimination time variable extrapolated from the ROC analysis showed that the location of the predictable target was discriminated significantly earlier in predictable than unpredictable target conditions (paired *t* test;  $t = -2.31$ ,  $P = 0.034$ ; Fig. 6B). Further, we observed significantly stronger SLRs for predictable than unpredictable targets (paired *t* test;  $t = 4.39$ ,  $P = 0.003$ ; Fig. 6C).

Eight subjects generated +SLRs only in predictable target conditions (see Table 1). In those subjects, the target location could not be discriminated from the sEMG until ~135 ms after unpredictable stimulus presentation (solid red lines in Fig. 6B), well after the boundary defining the end of the SLR epoch (i.e., 120 ms). Further, the magnitude of the SLR to predictable targets (defined as the mean sEMG activity recorded in the 10 ms subsequent to the DT of the slow trial sets; see MATERIALS AND METHODS) was much higher than the mean sEMG activity recorded from 80 to 120 ms after unpredictable target presentation (Fig. 6C, solid red lines; +SLR mean magnitude ~70  $\mu$ V, -SLR mean magnitude ~30  $\mu$ V; paired *t* test;  $t = 4.43$ ,  $P = 0.001$ ).

### Experiment 2 Results: Transient Flashing Targets Facilitate Fast and Strong SLRs

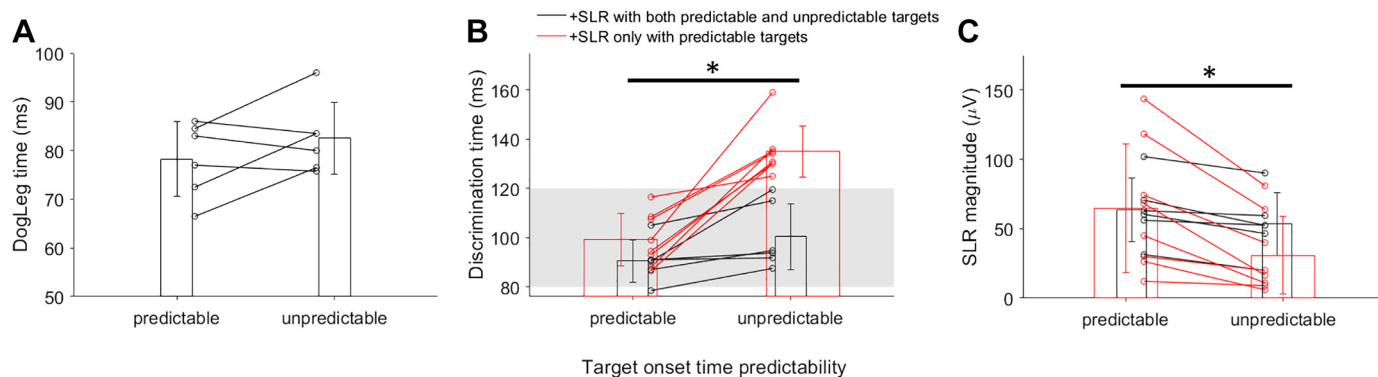
In the second experiment, we investigated whether the location or temporal attributes (transient flash vs. sustained

motion) of the target influence the SLR when stimulus eccentricity and appearance time are matched. Nine of the 11 subjects who participated in this experiment also participated in the first experiment and expressed an SLR with at least one of the two predictably timed targets (i.e., subject 1, 2, 3, 6, 9, 10, 11, 12, and 13 of the first experiment; Table 1).

As is consistent with *experiment 1*, the emerging target paradigm facilitated the expression of SLRs. Indeed, all of the 11 subject exhibited an SLR on the PMch with at least one of the conditions tested in *experiment 2* (Table 2). Again, SLRs were observed more frequently for the PMch than for the PD. For both muscle samples, the frequency of +SLRs was similar between the target conditions that were compared pairwise in each of the three series. Consistently, we did not observe any significant difference in +SLR prevalence between the target conditions tested in the second experiment (chi-squared test; PMch, A series  $P = 1$ , B series  $P = 0.138$ , C series  $P = 0.062$ ; PD, A series  $P = 1$ , B series  $P = 0.269$ , C series  $P = 0.338$ ). However, it is important to note that the outcome of the statistical test of differences in SLR prevalence between the transient and sustained targets is marginal, and it is possible that the effect might have been statistically significant with a larger sample size, such as that used in the first experiment.

For each of the three series of pairwise comparisons (A, B, and C series), we selected those participants who exhibited +SLRs for both of the two target conditions and compared the timings (DT, DogLeg) and magnitude of the SLRs. Again, a sufficient number of +SLRs to permit comparison was observed only for the PMch: A series, eight and three subjects met this criterion for PMch and PD, respectively; B series, nine and one subjects met this criterion for PMch and PD, respectively; C series, eight and two subjects met this criterion for PMch and PD, respectively (Table 2).

Figure 7 shows the PMch activity of an exemplar participant (subject 9; Table 2) who participated in the second experiment. The ROC analysis revealed similar DT for the transient flashing target presented at the two different



**Figure 6.** Latencies and magnitudes of the visuomotor responses on the PMch to stimulus presentation. *A* shows when the area under the ROC curve started to deviate from chance, which indexed the onset time of the visuomotor response to the target, via running a DogLeg regression analysis on the ROC trace (see MATERIALS AND METHODS). *B* shows when the area under the ROC curve exceeded the 0.65 threshold (see MATERIALS AND METHODS) that identifies the point in time at which the location of the target can be discriminated from the muscle activity. Each black line represents one of the six subjects with +SLRs on both predictable and unpredictable targets, whereas each red line represents one of the eight subjects exhibiting +SLRs only on predictable conditions. The ROC analysis (*B*) revealed that the location of predictable targets could be discriminated according to our threshold significantly earlier ( $*P < 0.05$ ) than that of unpredictable targets. However, the divergence time at which the area under the ROC curve deviated from chance (*A*) was not significantly different across the temporal predictability conditions. *C* shows the magnitude of the SLR encoding the location of the target that appeared to the left of the fixation spot, thus requiring the activation of the PMch. The predictable targets lead to significantly stronger ( $*P < 0.01$ ) SLRs than unpredictable targets. PMch, clavicular head of the right pectoralis muscle; ROC, receiver operator characteristic; SLR, stimulus-locked response.

**Table 2.** Occurrences of positive SLRs on the clavicular head of the pectoralis major muscle and the posterior deltoid for each target condition tested in experiment 2

Subject	A Series				B Series				C Series			
	PMch		PD		PMch		PD		PMch		PD	
	A'	A''	A'	A''	B'	B''	B'	B''	C'	C''	C'	C''
1	x	x			x				x			
2	x				x	x			x	x		
3	x	x	+	+	x	x	+		x	x	+	+
4	x	x			x	x			x	x		
5	x	x			x	x			x	x		
6		x	+	+	x	x			x			
7	x	x			x	x			x			
8	x	x	+	+	x				x	x	+	
9	x	x			x	x	+	+	x	x	+	+
10	x	x			x	x			x	x	+	
11					x	x	+		x	x		
Total + SLRs	9	9	3	3	11	9	3	1	11	8	4	2

PD, posterior deltoid; PMch, clavicular head of the pectoralis major muscle; SLR, stimulus-locked response. A series: comparison between the target that appeared transiently just beneath the barrier (A') and the target that appeared transiently at the interception point (A''); B series: comparison between the target that appeared transiently just beneath the barrier (B') and the sustained moving target that appeared just beneath the barrier and continued to the interception point (B''); C series: comparison between the target that appeared transiently at the interception point (C') and the sustained moving target that appeared just beneath the barrier and continued to the interception point (C''). Subjects 1–9 correspond to subjects 6, 2, 11, 9, 3, 10, 1, 13, and 12 in Table 1.

locations beneath the barrier (A series). The time at which the ROC curve started to diverge from chance, as calculated by DogLeg regression, was also similar (A series, right). The magnitudes were also similar: 59 μV for the target that appeared transiently just beneath the barrier; 63 μV for the target that appeared transiently at the interception point. By contrast, SLR timing and magnitude differed between the sustained moving target and the transient target conditions, regardless of the location of the transient stimulus. More precisely, SLRs to the transient target could be discriminated above threshold at ~20 ms before the SLR to the sustained target (B and C series), and DogLeg regression showed that the ROC curve of the transient target started to deviate from chance more than 10 ms before the ROC curve of the sustained target (right of B and C series). The sustained target SLR magnitude was also ~25 μV smaller than the SLR recorded with transient targets. Again, these results were consistent with those obtained by running the single-subject statistical analysis on the exemplar subject's data (Supplemental Results). Specifically, no significant difference was found between the two transient targets presented at different locations below the barrier (Supplemental Fig. S2). By contrast, the DT and DogLeg time were significantly shorter and the SLR magnitude significantly larger for the transient targets than the sustained moving targets, regardless of the location of the transient target relative to the barrier (Supplemental Fig. S2). Furthermore, the outcomes of the single-subject bootstrap analysis for the exemplar subject were consistent with those from the other subjects who produced an SLR to both target conditions tested in the different

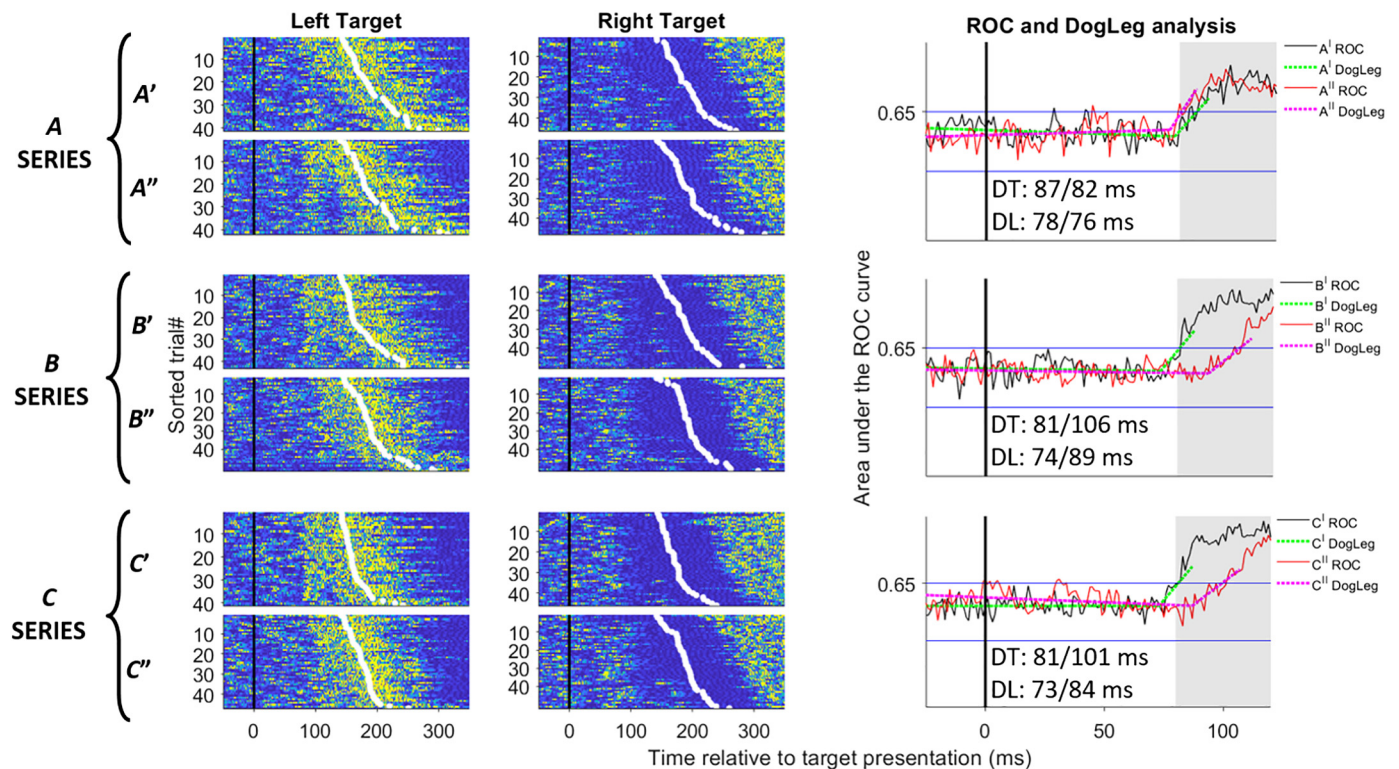
series of pairwise comparisons (Supplemental Table S2). Importantly, these results confirm that the ROC and DogLeg analyses can be relied upon to compare different stimulus conditions, consistent with the first experiment.

We observed similar trends across all participants of the second experiment. There were no statistically significant differences in the onset time of the visuomotor response (DogLeg time), discrimination time (DT), or SLR magnitude between the two transient targets that appeared at different distances from the bottom of the barrier (Fig. 8, A series). Conversely, the SLR to transient stimuli started significantly earlier than to the sustained moving target (DogLeg time: paired *t* test, B series, *t* = 3.36, *P* = 0.005; C series, *t* = 4.22, *P* = 0.002; Fig. 8) and also exceeded the discrimination threshold significantly earlier (discrimination time: paired *t* test, B series, *t* = 16.99, *P* < 0.001; C series, *t* = 7.8, *P* < 0.001; Fig. 8). Further, the transient stimuli led to significantly stronger SLRs than sustained moving targets, regardless of transient stimulus location (paired *t* test, B series, *t* = -2.25, *P* = 0.027; C series, *t* = -2.97, *P* = 0.01; Fig. 8).

### SLR Magnitude Correlates with the Latency of the Voluntary Movement Initiation

To test the SLR contribution to voluntary movement initiation, we ran a correlation analysis between the trial-by-trial SLR magnitudes and the corresponding RTs. For the first experiment, we selected all participants who produced a +SLR with at least one of the two predictable target conditions (14 subjects; Table 1) and all those who exhibited the SLR with at least one of the two unpredictable target conditions (6 subjects; Table 1). For both predictability target conditions, if a subject produced an SLR with both the sustained target presented just beneath the barrier and the transient target appearing at the interception point (e.g., subject 1 for predictable target conditions and subject 2 for unpredictable target conditions; Table 1), we then took the mean correlation coefficient. For the second experiment, we selected all the participants who produced a +SLR with at least one of the three target conditions across the three pairwise comparisons (11 subjects for the two transient targets, 10 subjects for the sustained target; Table 2). If a subject produced an SLR for the same target condition in more than one pairwise comparison (e.g., subject 2 for the transient target appearing just below the barrier; Table 2), we took the mean correlation coefficient.

In both experiments, the SLR magnitude correlated with RT. The relationship for a single exemplar subject and correlation coefficients across all subjects are illustrated in Fig. 9. In the first experiment, the SLR was negatively correlated with RT for both the predictable and unpredictable targets (one-sample *t* test; predictable targets, *t* = -9.95, *P* < 0.001; unpredictable targets, *t* = -7.4, *P* < 0.001). In the second experiment, the SLR magnitude was negatively correlated with RT for all three target presentation conditions (one-sample *t* test; transient target just beneath the barrier, *t* = -6.86, *P* < 0.001; transient target at the interception point, *t* = -6.81, *P* < 0.001; sustained target, *t* = -5.52, *P* < 0.001). That is, the latency of the RT tends to become longer as the magnitude of the SLR decreases, and vice versa.



**Figure 7.** Surface EMG activity of the clavicular head of the pectoralis major muscle of an exemplar subject (9, Table 2) who participated in the second experiment. The panels show the three pairwise comparisons, as consistent with the design of the second experiment (see MATERIALS AND METHODS and Fig. 2). For each target type, rasters of rectified surface sEMG activity from individual trials are shown (same format as Figs. 3 and 5). The ROC analysis reveals that the target location could be discriminated above threshold earlier for transient than sustained targets (*right* of B and C series). The different latencies of the visuomotor response to transient and sustained targets is also noticeable in that the column of the short-latency sEMG response is delayed in the rasters of the sustained target, with respect to the rasters of the transient targets. This accounts for the delayed initial deviation of the ROC curve from chance toward the discrimination threshold with the sustained targets, with respect to the transient targets (*right* of B and C series). EMG, electromyogram; ROC, receiver operator characteristic; sEMG, surface electromyogram.

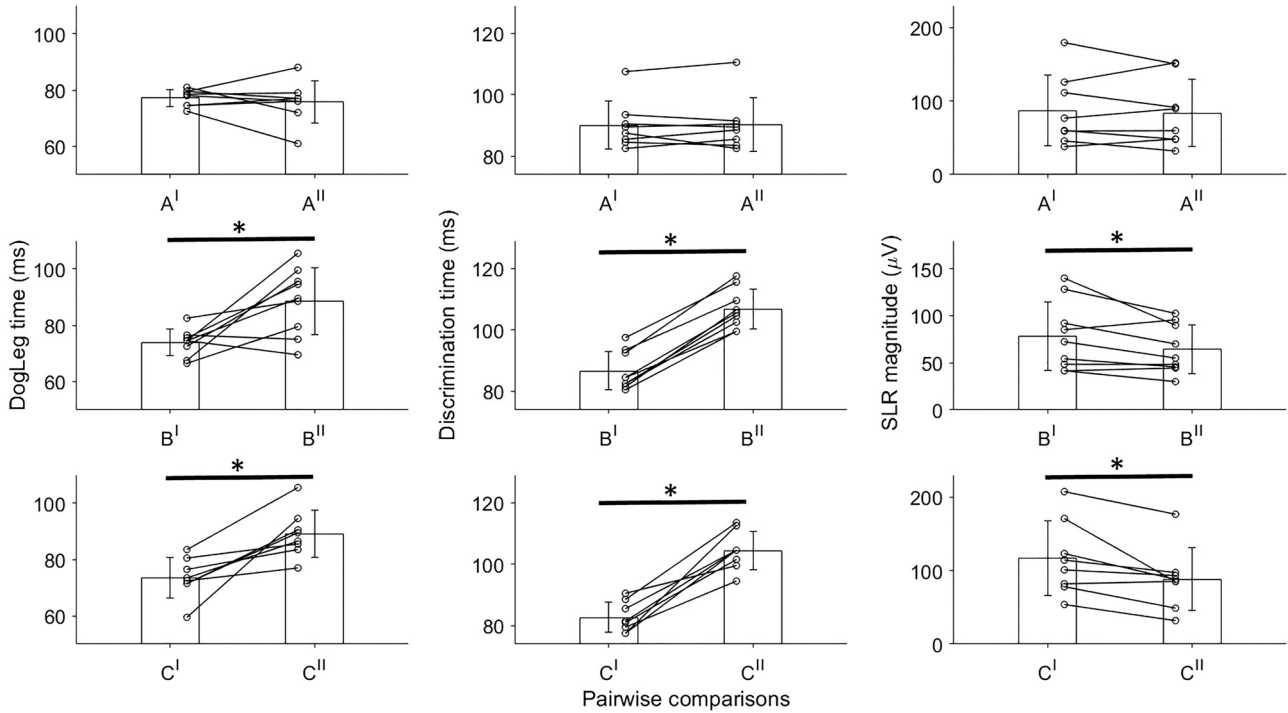
## DISCUSSION

### Methodological Factors in SLR Prevalence

The distinctive short latency of the SLR suggests that it is a behavioral marker for the contribution of a subcortical system to the expression of rapid visuomotor behaviors. However, because early reports found such rapid responses to be sporadic across subject and conditions, the SLR has mainly remained a curiosity. Methods to consistently record robust SLRs across participants are therefore needed to facilitate research on this phenomenon, including whether or not it can be exploited for practical applications (e.g., training, rehabilitation). One objective of the current study was to identify experimental conditions that can generate robust SLRs in most subjects. Notably, Kozak et al. (19) detected SLRs in all five of the participants that they tested, by adopting a moving target paradigm involving a visual barrier to partially occlude the target trajectory of motion. Here, we observed +SLRs among all but one of the 21 unique subjects tested with different versions of the moving target paradigm. This suggests that the low SLR prevalence that was previously reported (see 3) is not due to an absence of the neural circuitry necessary to generate an SLR but rather to the use of stimulus paradigms that were suboptimal for the relevant neural pathway. Indeed, a negative SLR producer in one paradigm may become a +SLR producer in another (e.g., the

eight subjects that exhibited SLRs only with predictably timed targets, Table 1, Fig. 6). We expect that most humans can be primed to produce SLRs given appropriate task conditions. This would imply that a subcortical system for visuomotor transformations is a ubiquitous feature of human sensorimotor control systems, which should be considered as a potential contributor in general theories of human motor behavior.

Our experimental setup had some key differences from that adopted by Kozak et al. (19). In that study, the authors presented the paradigm via a horizontal mirror that reflected a down-facing monitor, which also projected a real-time cursor to provide the participants with the visual feedback of the hand location. This resulted in a veridical spatial representation of both the hand and the target and allowed the participants to bring the hand exactly to the physical target locations. By contrast, we projected our stimulus on a monitor located in front of the participants and we limited their arm movements to the transverse plane, irrespective of the target location in the vertical axis. Indeed, the participants did not move their hand toward the exact target positions. Despite these differences, we replicated the high (>90%) SLR detection rate that was reported by Kozak et al. (19). Thus, the emerging target paradigm may be a powerful tool to elicit consistent and robust SLRs, irrespective of minor differences in setup.

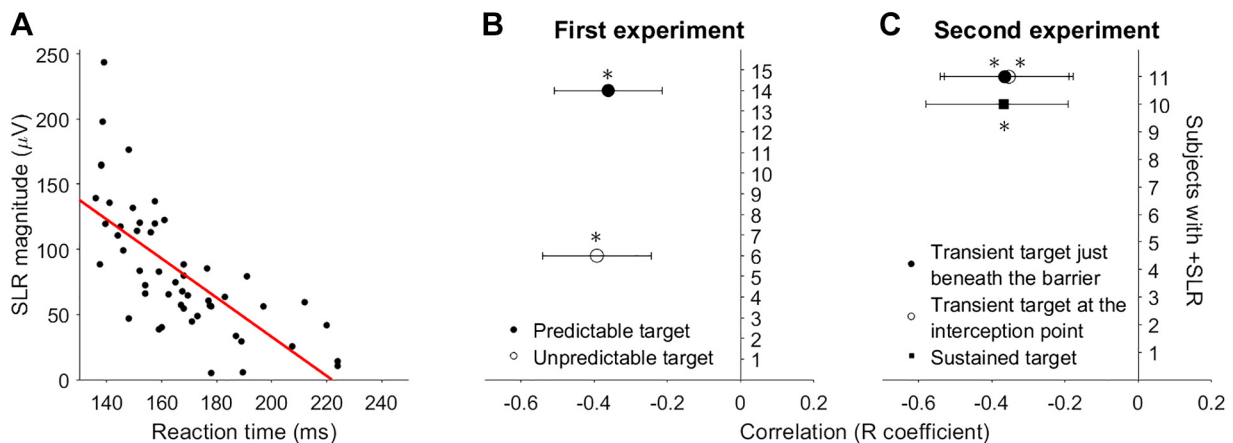


**Figure 8.** Latencies and magnitudes of the visuomotor responses to stimulus presentation. The DogLeg time represents the point in time at which the AUC starts to deviate from chance, whereas the discrimination time represents the point in time at which the target location could be discriminated from the SEMG activity above the threshold in the ROC area under the curve (see MATERIALS AND METHODS). Each solid black line represents one subject having + SLRs on both target types used for the pairwise contrasts, as consistent with the design of the second experiment (see MATERIALS AND METHODS and Fig. 2). The first row of panels shows the absence of significant differences between the transient target appearing just beneath the barrier (A<sup>I</sup>) and the transient target appearing at the interception point (A<sup>II</sup>). The second and third rows show that the transient target (B<sup>I</sup> and C<sup>I</sup>) led to significantly faster ( $*P < 0.01$ ) and stronger ( $*P < 0.05$ ) SLRs than the sustained targets (B<sup>II</sup> and C<sup>II</sup>), regardless of the location of the transient targets (B<sup>I</sup> transient target just beneath the barrier; C<sup>I</sup> transient target at the interception point). AUC, area under the ROC curve; EMG, electromyogram; ROC, receiver operator characteristic; SEMG, surface electromyogram; SLR, stimulus-locked response.

Like Kozak et al. (19), we recorded the muscle activity via surface EMG electrodes. The emerging target paradigm might therefore help to broaden the investigation of SLRs among populations that may be less tolerant of intramuscular electrodes (e.g., young, old, and clinical populations).

### Neural Mechanisms of SLR Generation

In the first experiment, we investigated whether the SLR-facilitation effect of the emerging target paradigm relies on the temporal predictability of the stimulus presentation. We observed that the expression of SLRs in the emerging target



**Figure 9.** A shows the correlation between the reaction time and SLR magnitude from the pectoralis major clavicular head for an exemplar participant. Each data point represents a single trial, and the solid red line is the linear regression function. B and C show the average correlation coefficient of all participants who exhibited an SLR in experiments 1 and 2. Regardless of target onset predictability (first experiment) and target spatiotemporal attributes (second experiment), the magnitude of the SLR demonstrates a significant negative correlation ( $*P < 0.001$ ) with the movement initiation. SLR, stimulus-locked response.

paradigm is facilitated when the target onset time is predictable. The positive effects of stimulus onset time predictability on the expression of rapid visuomotor behaviors is consistent with earlier work that used the gap task paradigm (i.e., constant time gap between the warning stimulus and the imperative stimulus; 3, 5, 9, 10). Pruszynski et al. (3) observed only a ~44% of +SLR prevalence with the gap task, whereas the emerging moving target paradigm led to 100% SLR detection score in the work by Kozak et al. (19), and above 90% in the present investigation, at least for the PMch sample. This suggests that the internal timing mechanism necessary to anticipate a temporally predictable stimulus may be facilitated if the target timing information is conveyed through a moving stimulus, rather than by the offset of a static fixation spot as in the gap task paradigm (3, 9, 10).

The SLR implies the existence of a short-latency neural pathway that quickly connects the retinal information with limb muscles, thus producing rapid visuomotor transformations. This pathway has been proposed to include the superior colliculus and its projections to the reticular formation, which in turn is connected with spinal interneurons and motoneurons (3, 9–14, 17). We propose that the baseline activity in superior colliculus neurons can be enhanced by prediction and motor preparation signals, likely originating from frontal and parietal cortical areas that project to superior colliculus (15, 32). Such known cortico-collicular projections might raise the activity of the collicular neurons closer to threshold level, thus facilitating a visually evoked SLR from the retino-tectal or retino-geniculo-cortico-tectal pathways. This idea is supported by previous work showing that the generation of an express saccade is predicted by the prestimulus firing rates of superior colliculus neurons, which can be enhanced by the predictability of visual stimulus onset time (1, 33). Decrements in the production of express saccades in nonhuman primates were observed consistently in association with reduced collicular prestimulus preparatory activity, which was induced by transiently inactivating the frontal eye field area (32).

Considering that both express saccades and SLRs are thought to rely on the activity of neurons in the intermediate layers of the superior colliculus, we propose that target onset time predictability facilitates the expression of SLRs through a top-down priming of the superior colliculus. The assumption of top-down modulation of the SLR system is consistent with previous work from Gu et al. (17), who showed that the magnitude of the SLR was lower in the antireach than proreach tasks. This suggests that the task context influences the state of the SLR circuitry and the relative vigor of the rapid visuomotor response in muscles, potentially via cortical top-down modulation of the superior colliculus. Here, we add to this literature by showing that the expression of an SLR is facilitated when the stimulus onset time can be predicted from contextual information that must be interpreted within each trial, consistent with continuous cortical modulation of the superior colliculus. However, the SLR-facilitation effect induced by target temporal predictability might also result from a modulation of reticular formation or spinal cord circuits. In these circumstances, the predictability-induced SLR modulation might result from a subtectal integration between the descending collicular signals and the temporally tuned reticular/spinal circuits.

In the second experiment, we compared the SLR with a transient flashing target that appeared just beneath the barrier with a transient flashing target that was presented at the interception point (see MATERIALS AND METHODS; A series, Fig. 2). We found that the SLR did not depend on the location of the transient target in the vertical axis, at least within the range of vertical visual angles (~6 dva) explored in this experiment. Broader ranges of vertical distance between the target emerging spots should be investigated in future studies to understand the spatial resolution of a priming pathway. Trial-by-trial, the target moved at a constant velocity (~35 dva/s) before disappearing behind the barrier and emerged (transiently) at a constant time (~540 ms) from the trial start. If the implied motion of the target behind the barrier was extrapolated assuming a constant target velocity, then it should have enabled the temporal prediction of the target that appeared just beneath the barrier. By contrast, the timing predictability of the target that appeared at the interception point would require the extrapolation of a target that seems to start accelerating while it is hidden by the barrier. In our setup, we randomized target location from trial-to-trial, thus making impossible for the participants to know in advance the final location of the target and thereby the implied target kinematics (acceleration = 0 or acceleration  $\neq$  0) from which to extrapolate its implied motion behind the barrier. The absence of significant target location-induced effects on SLR expression suggests that implied target motion per se is not necessary to facilitate the SLR. More likely, the disappearance of the moving target behind the barrier enables more precise initiation of the internal timing signal than simply extinguishing the target, which would be consistent with the results of the first experiment. A cortical origin for this hypothetical internal timing signal seems likely but has not been specifically addressed here and needs further elucidation.

The previously reported effects of a moving target for facilitating SLRs might have been the result of its kinematic-related salience as a stimulus instead of (or in addition to) its utility for extrapolating timing information. Another question is whether the SLR circuitry responds differently to a target that suddenly appears and starts moving and to a static target that flashes briefly. In both experiments, we compared responses to sustained moving targets and transiently flashed targets that appeared at predictable times. Previous work suggests that the visual neurons of the mammalian superior colliculus are sensitive to the kinematic features of visual stimuli. An fMRI study showed that the presentation of a cluster of dots, which were equally distributed around a fixation spot, enhanced the response of the human superficial collicular layer when the dots changed their state from static to dynamic (radial movements toward, or away from, the fixation spot; 21). Another fMRI study showed that the activity of the rat superior colliculus neurons was larger when a moving stimulus passed through their receptive visual field than when a static stimulus appeared within their receptive field (22). Noteworthy, earlier work also showed that the superficial layer of the human superior colliculus responds well to transient stimuli (21). More precisely, Schneider and Kastner (21) reported larger collicular responses with a flickering stimulus than with a moving stimulus. Further, Chen and Hafed (34) observed

that the nonhuman primate superior colliculus neurons have preference for low flicker stimulus frequencies (e.g., 3–10 Hz). Specifically, the collicular neurons responded to low flicker frequencies with transient increments in firing rate (>160 spikes/s) encoding each individual flicker cycle. By contrast, higher stimulus flickering frequencies resulted in a less transient and more sustained response characterized by low-frequency firing rates (~40 spikes/s), especially when the stimulus approached the flicker fusion frequency for perception (i.e., ~60 Hz of flickering frequency; 34). This suggests that the superior colliculus is sensitive to the duration of the visual stimulus. The temporal events of visual stimuli are encoded by different cell types located in the superficial layers of the mammalian superior colliculus: “On,” “Off,” “On-Off” cells (35). Notably, the On-Off cells outnumber the other cell types and their receptive fields overlap those of the other cells (35), suggesting a preferential superior colliculus representation for transient visual stimuli.

In the first experiment, we successfully detected SLRs in 14 people when the transient target appeared via a single flash of 8 ms at the interception point, and in nine people when the sustained moving target appeared just underneath the barrier (PMch; Table 1). This is consistent with a stronger effect from transience than motion, but contextual features of the paradigm might also have contributed to this result. Specifically, the subjects knew that if the target did not appear just beneath the barrier at a time consistent with the target velocity (540 ms from the initial target drop), then it could only appear transiently at the lower location. The SLR facilitation observed with the transient target conditions could therefore be due to spatial predictability of the target re-emerging location. In the second experiment, we made the target location unpredictable from the trial context by matching the timing of the transient and sustained moving targets. The more powerful and earlier SLRs with the transient target suggests that its effectiveness is related to its transient nature rather than the spatial predictability of the target location.

In the second experiment, the two transient targets and the sustained moving targets always appeared underneath the barrier after ~540 ms from the start of the trial. This made it impossible for the participants to distinguish the spatiotemporal attributes of the transient and sustained moving targets at the first stimulus presentation frame. That is, the earliest information for the generation of a target-directed visuomotor response, including an SLR, was equally available at ~540 ms from trial start, irrespective of the target trial type. The different SLR timing between the sustained moving and transient targets must be due to sensory events subsequent to this. In our paradigm, the transient target turned off ~8 ms after its appearance, whereas the sustained target moved downward by ~0.25 dva/frame. The fact that the transient target led to an SLR with an earlier onset latency (10–20 ms) indicates that the disappearance of the target after 8 ms is a more salient stimulus for the circuits operating express visuomotor transformations than is target motion of 0.25 dva every 8 ms. It is unclear how many position change samples are required for the visual system to integrate the motion of the target or whether a faster moving target would provide a more salient stimulus for the SLR. Nonetheless, our target speeds were close to the limit of

what was possible for our subjects to intercept, so our data show that transient targets generate earlier and larger SLRs than moving targets for motion trajectories that are feasible for human subjects to intercept. The fast and strong SLRs expressed to transient targets are consistent with a synchronized and high-frequency collicular response (34) to both the onset and the offset (8 ms later) phases of the target, and in all the cells that can encode these temporal events (i.e., On, Off, and On-Off cells; 35). The strong and rapid transient collicular responses should result in the generation of high-frequency trains of action potentials whose spatiotemporal integration would facilitate rapid transmission through the projecting neurons of the brainstem reticular formation and spinal interneurons required to reach the motoneurons. By contrast, given its extended “on” phase, the sustained moving target would be encoded by the subpopulation of superior collicular On cells (35), including low-frequency response (34), which may take longer for spatiotemporal integration and final SLR release. From an ethological standpoint, transient stimuli might trigger particularly brisk responses to orient the eyes, head, and limbs toward targets that may soon become unavailable. This correlates with the primitive function of the superior colliculus to acquire unknown but salient visual stimuli (15). Nonetheless, we are mindful that further studies are needed to elucidate the effective timing and intensity of the collicular visual response in these behavioral paradigms.

### Behavioral Function of SLRs

A key outstanding question about the SLR concerns its functional role in motor behavior. The term “stimulus-locked response” was originally coined by Pruszynski et al. (3) to describe short-latency muscle responses that were more invariant to the time of stimulus presentation than to movement initiation. We acknowledge that the timing of the SLR is variable trial-by-trial; similar variability is also seen in the first spike timing of visual responses in the intermediate superior colliculus (36). Regardless, we caution that the term SLR or similar terms such as “rapid visuomotor responses” (9) or “visual responses on muscles” (7) may incorrectly impute a sensory rather than motor function. The selective muscle activation or inhibition that is tuned correctly to the direction of the reach would be expected to contribute to the reach mechanics. We replicated previous correlation analyses (3, 17) to show that the magnitude of the SLR predicts the onset time of the voluntary movement. For every subject exhibiting a +SLR, we observed a significant negative correlation between SLR magnitude and RT, indicating that stronger SLRs were associated with quicker mechanical responses.

Mechanistically, large and rapid activation of an agonist muscle and inhibition of a tonically active antagonist will shorten the time at which sufficient net torque is produced to overcome limb inertia and start accelerating the arm (i.e., RT). During the so-called long-latency voluntary phase of the reaching movement, the time needed by the rising force to start accelerating the arm will be reduced if the same motor units have already fired once during the earlier SLR. When the interval between action potentials in a muscle fiber is substantially shorter than the typical interspike interval for voluntary muscle recruitment (a phenomenon known

as doublets; 37), the total muscle contractile activation so produced is greatly accelerated and sustained as a consequence of calcium diffusion and reuptake kinetics in the muscle fibers, a phenomenon called the catch property of muscle [originally reported by Burke et al. (38) and reviewed mechanistically in Tsianos and Loeb (39)]. If the same motor units participate in both the SLR and the voluntary reaction, the enhanced force output would be expected to contribute to a shorter RT. This could be resolved with intramuscular recording of discriminable, single-unit EMG signatures such as employed by Van Cutsem et al. (37) to identify doublets in human muscles.

### Further Methodological Considerations and Future Experiments

It is worth noting that our experimental paradigm explored only conditions with tonic activation of the shoulder flexor muscles, including the PMch, against an extensor load. This may account for the large asymmetry of agonist-antagonist SLR production reported here and suggests further experiments to study the effects of direction and magnitude of such preloads.

In this study, we did not test predictable target conditions in which the target timing information is provided by extinguishing a static target. Future work should compare the “original” emerging target paradigm with a task akin to our unpredictable target conditions, but with a constant time between the offset of the target and its re-emergence underneath the barrier. This would provide a direct test to disentangle the effective influence of moving and static warning stimuli on the SLR expression when the target onset time is matched. Future experiments should also compare our target conditions with static targets that remain detectable for an extended period of time, such as that in which the moving target stayed visible underneath the barrier. This would aid the definition of the optimal task conditions for SLR expression. Moreover, it could further improve the understanding of mechanisms behind the generation of SLRs by comparing them with the known target-related responses of the neural networks operating visuomotor transformations, such as the superior colliculus.

### Conclusions

Our results suggest that the effectiveness of the emerging target paradigm for eliciting SLRs is related to the temporal predictability of target presentation. Predictability of the stimulus onset time appears to prime the putative subcortical circuit responsible for SLRs, potentially via the generation of an internal timing signal. A plausible source of the timing signal is the descending cortico-collicular projections, suggesting a top-down modulation of the SLR circuitry. The fact that transient targets are especially effective in promoting SLRs is consistent with the known sensitivity of the superior colliculus to the onset and offset phases of transient visual stimuli. The effectiveness of the emerging target paradigm for facilitating consistent and robust SLRs greatly enhances the capacity of researchers to investigate the neural processes underling these express visuomotor responses, as well as their potential use in clinical and sporting applications.

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## DISCLOSURES

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

## AUTHOR CONTRIBUTIONS

S.C. and T.J.C. conceived and designed research; S.C. performed experiments; S.C. analyzed data; S.C., G.E.L., G.W., and T.J.C. interpreted results of experiments; S.C. prepared figures; S.C. drafted manuscript; S.C., G.E.L., B.D.C., G.W., and T.J.C. edited and revised manuscript; S.C., G.E.L., B.D.C., G.W., and T.J.C. approved final version of manuscript.

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