High contrast, moving targets in an emerging target paradigm promote fast visuomotor responses during visually guided reaching

Abbreviated title: Moving targets promote fast visuomotor responses

Rebecca A. Kozak[1,4], Brian D. Corneil[1,2,3,4]

[1]Graduate Program in Neuroscience, Western University, London, On, Canada, N6A 5B7
[2]Department of Psychology, Western University, London, Ontario, Canada, N6A 5B7
[3]Department of Physiology and Pharmacology, Western University, London, Ontario, Canada, N6A 5B7
[4]Robarts Research Institute, 1151 Richmond St. N, London, Ontario, Canada, N6A 5B7

*Corresponding Author: Brian D. Corneil, bcorneil@uwo.ca

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Abstract

Humans have a remarkable capacity to rapidly interact with the surrounding environment, often by transforming visual input into motor output on a moment-to-moment basis. But what visual features promote the shortest-latency reach responses? To address this question, we had human subjects perform visually guided reaches to moving targets varied by speed (experiment 1), or speed and contrast (experiment 2) in an emerging target paradigm, which has recently been shown to robustly elicit fast visuomotor responses. Our analysis focused on stimulus-locked responses (SLRs) on upper limb muscles. SLRs represent the first wave of muscle recruitment tied to visual target onset, appearing within <100 ms. Across 32 subjects studied in both experiments, 97% expressed SLRs in the emerging target paradigm. In comparison, 69% of these subjects expressed SLRs in a visually-guided reach paradigm. Within the emerging target paradigm, we found that target speed impacted SLR magnitude, whereas target contrast impacted SLR latency and magnitude. Thus, high contrast, faster-moving targets in the emerging target paradigm robustly recruited the circuitry mediating the most rapid visuomotor transformations for reaching, and such responses were associated with shorter latency RTs. Our results support the hypothesis that a subcortical pathway originating in the superior colliculus may be involved in the earliest wave of muscle recruitment following visual stimulus presentation. In scenarios requiring expedited responses, cortical areas may serve to prime this subcortical pathway, and elaborate subsequent phases of muscle recruitment following the SLR.

Significance Statement

Humans have a remarkable capacity, when necessary, to rapidly transform vision into action. But how does the brain do this? Here, by studying human subjects reaching to suddenly-appearing

targets, we find that the earliest visually-guided actions are produced in response to high-contrast, moving targets. A millisecond-resolution examination of upper limb muscle recruitment shows that motor output can begin within less than 100 ms of target presentation. We surmise that this earliest recruitment arises from a phylogenetically-conserved brainstem circuit originating in the superior colliculus. Rather than being directly involved in the earliest phase of visuomotor actions, cortical areas may prime this brainstem circuit to produce initial muscle recruitment, and then elaborate subsequent phases of recruitment when time is of the essence.

Introduction

To perform a visually-guided reach, for example to pick-up a baseball off a table, visual information such as the shape and size of the ball is transformed into motor commands which are communicated to the motor periphery. However, if the ball is thrown to us, time is of the essence and we must perform a rapid reach in order to catch the ball. In such situations, the latency of the response depends on the visual attributes of the stimulus; for example, earlier responses are elicited by larger or higher contrast targets, or stimuli defined by lower spatial frequencies (Veerman et al., 2008; Wood et al., 2015; Kozak et al., 2019). Other work has suggested that the most rapid visuomotor transformation for reaching is mediated by a tecto-reticulo-spinal pathway, which lies in parallel to the well-studied corticospinal pathway (Day and Lyon, 2000; Pruszynski et al., 2010; Gu et al., 2016; Glover and Baker, 2019).

In order to better understand the most rapid visuomotor transformation at the limb, we and others have recorded electromyographic (EMG) activity from upper limb muscles during rapid visually-guided actions. Doing so has led to the identification of stimulus-locked responses (SLRs; also termed rapid visuomotor responses by (Glover and Baker, 2019) or express responses by (Contemori et al., 2020)), which are the first waves of muscle activity influenced by the visual stimulus. SLRs evolve within < 100 ms of stimulus onset, preceding some response latencies in visual and motor cortices (Maunsell and Gibson, 1992; Schmolesky et al., 1998; Lara et al., 2018). In contrast, visual responses latencies in the superior colliculus (SC; from which the tecto-reticulo-spinal track originates) precede the SLR (Stuphorn et al., 1999; Rezvani and Corneil, 2008), which makes the SC a potential candidate for mediating the SLR. Further, high contrast (Li and Basso, 2008; Marino et al., 2012; Wood et al., 2015) or low spatial frequency (Chen et al., 2018; Kozak et al., 2019) targets elicit larger-magnitude and shorter-latency visual

responses in the SC and SLRs. Robust SC responses are also elicited by moving visual targets (Marrocco and Li, 1977); however, a systematic investigation of target motion on the SLR has not been performed.

Previous research investigating the most rapid visuomotor transformations involved in visually guided reaching has typically relied on targets that either suddenly appear (a *static target paradigm*; (Pruszynski et al., 2010)), or are displaced during a reach (*target jump paradigm*; (Soechting and Lacquaniti, 1983; Day and Lyon, 2000)). Recently, we have presented an *emerging target paradigm*, where a target travels down an inverted 'Y' path before disappearing and then emerging from behind an occluder (Kozak et al., 2020). Benefits of the emerging target paradigm include the stability of the arm when the target emerges (which is not the case in the target jump paradigm), and the generation of robust fast visuomotor responses in almost every subject (which is not the case in the static target paradigm). In Kozak et al. (2020), while only 3 of 5 subjects expressed an SLR in the static target paradigm, all 5 subjects expressed an SLR in the emerging target paradigm, with the SLR being four to five times larger in the emerging target paradigm. The efficacy of the emerging target paradigm in generating SLRs has been replicated in a larger sample of subjects using the emerging target paradigm, wherein 20 of 21 subjects expressed an SLR (Contemori et al., 2020). Thus, essentially every subject has the circuitry to generate fast visuomotor responses; the failure to do so in past studies arose from the reliance on suboptimal stimuli and/or tasks.

The goal of the current study is to systematically investigate how target speed and contrast impact fast visuomotor responses in the emerging target paradigm. Based on the hypothesis that transient visual responses in the SC initiate the SLR, larger and more robust SLRs should accompany the presentation of fast moving, high-contrast targets. Accordingly, we

tested the influence of targets varied by speed (experiment 1) or speed and contrast (experiment 2) on the SLR, in both static and emerging target paradigms. A secondary goal is to better understand how the emerging target paradigm promotes the generation of SLRs. Hence, we also presented non-moving stimuli in the context of both the static target and emerging target paradigms in Experiment 1. In such cases, the retinal stimulus is exactly the same, meaning that any differences in the SLR arise from differences related to the behavioural task. Overall, we find that high contrast, fast moving targets in the emerging target paradigm robustly recruits the circuitry mediating the most rapid visuomotor transformations for reaching movements.

Materials and methods

Subjects

A total of 34 subjects (18 females, 16 males; mean age: 24.2 years SD: 5.6) completed at least one of the two experiments. Two subjects completed both experiments. All subjects provided informed consent, were paid for their participation, and were free to withdraw from the experiment at any time. All but 1 subject was right-handed. All subjects had normal or corrected-to-normal vision, with no current visual, neurological, or musculoskeletal disorders. All procedures were approved by the Health Science Research Ethics Board at the University of Western Ontario. Two subjects (1 from each experiment) were excluded due to low quality EMG recordings.

Apparatus

Subjects were seated in either a KINARM robotic Exoskeleton (experiment 1) or a KINARM End-Point Lab (experiment 2) (KINARM Technologies, Kingston, ON, Canada), and performed reaching movements with their right arm. Both platforms relied on the same experimental

software. Visual stimuli were projected onto an upward facing mirror from either a downward facing monitor in experiment 1 (LG 47LS35A; size: 47” resolution: 1920x1080 pixels (Exoskeleton)) or custom built in projector in experiment 2 (PROPixx projector by VPixx, Saint-Bruno, QC, Canada; custom integrated into the KINARM End-Point Lab). In both experiments, a shield below the mirror occluded direct vision of the hand, but real-time hand position was represented on the monitor via a real-time cursor projected onto the screen. A photodiode was used to indicate the precise time of visual stimulus presentation, and all kinematic and electromyographic (EMG) data were aligned to photodiode onset. Eye movements were not measured.

Experimental design:

In experiment 1 and 2, we used an emerging target paradigm as previously described in ((Kozak et al., 2020) see **Figure 1**). Briefly, a target travels down an inverted ‘y’ path, disappears behind an occluder before reappearing, continuing to move, and evoking a reach from a subject. In both experiments, we also collected data in a *static task*, where subjects performed visually guided reaches towards stationary targets in a separate block of trials. This allowed us to directly compare SLRs in the emerging target paradigm to those obtained with a static task typically used to evoke the SLR (Pruszynski et al., 2010; Wood et al., 2015; Gu et al., 2016; Kozak et al., 2019).

Experiment 1: effects of speed.

In the static task in Experiment 1, subjects (n = 16) performed visually guided reaches from a stationary arm position to static targets appearing pseudorandomly to either the right or left of

the start position. Throughout this task, a constant torque of 2 Nm was applied to the shoulder, increasing tonic activity on the muscle of interest. Doing so allows for the SLR to be expressed as either an increase or decrease in muscle activity following target appearance to the left or right, respectively. Each trial was initiated when a subject moved the real time cursor (RTC) representing their hand into a start position (T0). T0 was 1.5 cm in diameter, located approximately 45 cm in front of the subject relative to midline, and changed to grey once the RTC was in the start position. If the subject exited the start position before completion of a constant hold period (1s), the trial was reset, and T0 changed back to white. Subjects were instructed to also look at T0 before the onset of the target (T1). After the hold period, a white T1 was presented on the black background 17 cm to the left or right of the start position (~17.5 degrees of visual angle). A 17 cm eccentricity was chosen as it resembled the interception point of the emerging target paradigm. Subjects were instructed to reach towards the peripheral target as quickly as possible, and the trial ended when the RTC made contact with the center of T1. T0 remained visible as a grey target, changing back to white once the trial ended. Subjects completed 1 block of 220 trials (110 trials towards each target), before they performed the emerging target paradigm. In contrast to previous static tasks which used a randomized hold delay for T0 (Gu et al., 2016; Gu et al., 2018), we chose to have a constant hold delay (1s), and allowed T0 to remain visible during the reach. These conditions more closely resembled the conditions in the emerging target task which allowed for a more direct comparison between a static task and an emerging target task.

After completing the static task, the same 16 subjects performed visually guided reaches towards moving targets that emerged below an occluder in the emerging target paradigm (See **Figure 1** for protocol). The emerging target paradigm involves a target starting at the top of an

186 inverted y (**Figure 1a**), moving towards an occluder and disappearing behind it (**Figure 1b**), then
187 emerging below the occluder at one of two outlets. Subjects were instructed to reach and
188 intercept the target after it emerged from behind the occluder (**Figure 1c**) (Kozak et al., 2020). In
189 experiment 1, we varied the speed of the moving target. The start position, RTC, hold period,
190 background loading torque, and target radius were the same as in the static task.

191 We implemented three target speeds in our paradigm (10, 15 or 20 cm/s), translating to
192 initial velocities of approximately 10, 15 or 20 retinal degrees per second, respectively. These
193 speeds were chosen to span a range from 'slow' to 'fast' while still permitting target interception
194 of the fastest target. The duration that T1 was visible above the occluder was constant (.5s)
195 regardless of target speed; as targets travelled at different speeds, this meant that they started at
196 different heights above the occluder. The occluder was 30 cm wide by 15 cm high, and the center
197 of the occluder was located ~63 cm away from the subject. Behind the occluder, the target
198 moved at a constant speed of (15 cm/s) regardless of initial or final target speed. Thus, the target
199 consistently disappeared behind the occluder for 1s on trials with a moving target. The target
200 only became visible once it had fully moved past the occluder (i.e., the target was presented in its
201 entirety, rather than sliding past the occluder to avoid a half-moon stimulus). After emergence,
202 the target stayed visible and usually continued down the inverted y path. To control for eye
203 position, subjects were instructed to foveate a notch located on the bottom of the occluder
204 halfway between the exit points, while the moving target was occluded. The trial ended as soon
205 as the RTC contacted the peripheral target, or if the target passed the bottom of the screen.

206 We also included a static T1 within the emerging target paradigm, where T1 began
207 moving at a speed of 20 cm/s but appeared ~ 17 cm to the left or right of the start position and
208 did not move; we term this the 0 cm/s target. Thus, the initial conditions where the target drops

209 into the occluder were the same for the 0 cm/s and 20 cm/s targets. On the 0 cm/s trial, the trial
210 ended when the subjects made contact with the target. Due to an oversight, the target disappeared
211 behind the barrier for 900 ms on 0 cm/s trials, rather than 1000 ms as on moving target trials. If
212 the slightly shorter time the target was obscured behind the barrier on 0 cm/s trials were to be
213 relevant, then results by Contemori and colleagues (2020) would suggest that SLR should be
214 weaker on such trials given less temporal certainty. Instead, as we will show, we observed robust
215 SLRs to both moving and non-moving targets in the emerging target task. Further, no subject
216 reported perceiving any difference in the time the target was behind the occluder on trials with a
217 moving versus a non-moving target.

218 All targets in experiment 1 were white (110 cd/m^2) presented against a black (.6 cd/m^2)
219 background (contrast ratio: 183:1). There were 8 unique trial conditions (4 target speeds 0, 10, 15
220 and 20 cm/s presented to the left and right). Subjects completed 2 blocks of 480 trials, with each
221 block containing 60 repetitions of each unique trial condition presented pseudorandomly without
222 replacement, yielding a total of 120 trials for each unique trial condition.

223

224 *Experiment 2: effects of contrast and speed*

225 Experiment 2 was designed to investigate the interaction between target speed and contrast on
226 the SLR. This experiment was conducted in a different apparatus, the KINARM End-Point
227 system. As in experiment 1, two tasks were run in separate blocks.

228 In the *static task* in experiment 2, subjects (n = 18) performed visually guided reaches
229 initiated from a stationary position, towards static left or right targets. As in experiment 1, each
230 trial was initiated when a subject moved the real time cursor (RTC) representing the subjects
231 hand position into a start position (T0). We used a constant torque throughout the experiment

232 (2Nm down, 5Nm right) applied to increase the baseline activity of the muscle of interest. This
233 torque is different than experiment 1, due to a different apparatus and subject posture. T0 was
234 aligned with the subject's midline (0, -42 cm relative to the midpoint between the robot
235 manipulanda; radius 1 cm). T0 changed from white to grey once the RTC was moved into it. The
236 trial was reset if the subject exited T0 before completion of the hold period (randomized time
237 between 1000 to 2000 ms). Our use of a randomized hold time in experiment 2 resembles that
238 used in the work by Wood and colleagues (2015), which also manipulated stimulus contrast.
239 Recall that the static task in experiment 1 used a fixed hold time of 1 s, which matched the time
240 the target disappeared behind the barrier in the emerging target paradigm in experiment 1.
241 Subjects were instructed to foveate T0 before the onset of the target (T1). After the hold period,
242 T1 (target with a 1 cm radius) appeared 10 cm to the left or right (~15.4 degrees of visual angle).
243 Subjects were instructed to reach towards the peripheral target as quickly as possible, and the
244 trial ended as soon as RTC made contact with the peripheral target. There were 4 unique trial
245 conditions; a high contrast white (275 cd/m^2: contrast ratio 793.8:1) or low contrast grey (18
246 cd/m^2: contrast ratio 50:1) target presented against a black (.36 cd/m^2) background to either the
247 left or right side. T0 remained visible as a grey target, changing back to white once the trial
248 ended. Subjects completed 1 block of 400 pseudorandomized trials, yielding a total of 100 trials
249 for each unique trial condition.

250 After completing the static task, the same 18 subjects completed the emerging target
251 paradigm. As in experiment 1, subjects performed visually guided reaches initiated from a stable
252 posture towards moving targets that emerged suddenly beneath an occluder. Throughout the
253 experiment, the same torque was applied as used in the static task. Each trial was initiated when
254 a subject moved the RTC into a start position (T0), and the trial was reset if the subject exited T0

before completion of the hold period (1s). In experiment 2, we used a two-by-two design, where we modulated speed (including a ‘slow’ and a ‘fast’ target (10 cm/s, 20 cm/s; translating to approximately 10 and 20 degrees of visual angle); and contrast (the ‘low’ and ‘high’ contrasts). In experiment 2, the occluder was 30cm by 15cm, centered at the midpoint between the manipulanda (0, - 29 cm). To control for eye position, subjects were instructed to foveate a notch located on the bottom of the occluder halfway between the exit points, while T1 was occluded. As in experiment 1, we controlled for the amount of time that T1 was visible before being obscured by the occluder (.5s) by starting T1 at different heights above the occluder for different target speeds. The time T1 disappeared behind the occluder in experiment 2 is shorter (0.5 s) than in experiment 1 (1 s). T1 was made visible only after it had fully emerged beneath the occluder, avoiding an initial half-moon stimulus. T1 then continued on the inverted y path. The trial ended as soon as the RTC made contact with T1 or if the target passed the bottom of the screen. There were 8 unique trial conditions (2 speeds, 2 contrasts, leftward or rightward targets). The same contrasts were used from the static task. Subjects completed 2 blocks of 400 pseudorandomized trials, yielding a total of 100 trials for each unique trial condition.

Data acquisition and analysis

Surface electromyographic (EMG) activity was recorded from the right pectoralis muscle with double-differential surface electrodes (Delsys Inc. Bagnoli-8 system, Boston, MA USA). As stated in (Kozak et al., 2020), hair or excess adipose may compromise the EMG signal; therefore, we targeted either the medial or lateral portion of the clavicular head, or the sternal portion, depending on such idiosyncratic factors. We placed two electrodes on each subject, and during post-hoc analysis we used the recording exhibiting the higher level of EMG activity.

EMG signals were sampled at 1 kHz, amplified by 1000, full-wave rectified off-line, and smoothed with a 7-point smoothing function. We excluded two subjects with poor quality muscle recordings, which was defined as an increase in peak EMG activity above baseline of less than 40 μV during leftward reaching movements.

Kinematic data were sampled at 1 kHz by the Kinarm data acquisition system in both experiments. Reaction time (RT) was calculated as time from peripheral target (T1) appearance (measured by the photodiode) to reach initiation. Reach initiation in both experiments was defined as 8% of the peak tangential velocity. We excluded trials with RTs less than 120 ms due to presumed anticipation, and also excluded trials with RTs exceeding 500 ms due to presumed inattentiveness.

As described previously (Kozak et al., 2020), we used a receiver-operating characteristic (ROC) analysis to define the presence and latency of the SLR. Briefly, the time-series ROC analysis indicates the likelihood of discriminating stimulus presentation based on EMG alone. As the SLR is the first wave of muscle activity influenced by the visual stimulus, we rely on this method to discriminate the moment a visual stimulus influences EMG activity. The ROC value (i.e., the area under the ROC curve) was calculated and plotted at every time sample (1ms) from 100 ms before to 300 ms after target presentation (an example may be seen in **Figure 2d** overlaid with mean +/- SE of EMG activity for the data shown in **Figure 2a**). A ROC value of .5 indicates chance discrimination, whereas values of 1 or 0 indicate perfectly correct or incorrect discrimination relative to target presentation, respectively. Discrimination thresholds were set to 0.6, and the discrimination latency was determined as the first of 8 of 10 consecutive points that exceeded this value.

To define the presence of an SLR, an RT split analysis was used (as described in: (Wood et al., 2015; Kozak et al., 2020)). The purpose of the RT split analysis is to empirically test whether EMG activity is more likely to evolve with stimulus presentation, or arm movement over a large number of trials. This method is used as an additional conservative approach to relying on pooled EMG, which may be unfairly biased towards a subset of the shortest latency trials. To perform the RT split analysis, separate time series ROC analyses were conducted on early and late RT trials (purple or green highlighted trials in **Figure 2a**; see also mean EMG traces in **Figure 2b**), defined relative to mean RT. We then plotted the mean RT for the early or late RT subsets versus the ROC discrimination time, and then connected these two points with a line (**Figure 2c**). The slope of this line is used to determine whether the initial change in EMG activity is more locked to stimulus onset (slope ≥ 67.5 deg.) or not (slope < 67.5 deg.). The example shown in **Figure 2** illustrates an example where an SLR was detected (termed SLR+; versus SLR-).

We used the same criterion for determining latency and magnitude of the SLR as used in (Kozak et al., 2020). For SLR+ observations, SLR latency was defined as the first point where the time-series ROC constructed from all trials (regardless of RT) surpassed .6 for 8 out of 10 trials (see **Figure 2d)**. SLR magnitude was defined as the area between leftward and rightward mean EMG traces for an interval spanning from SLR latency to 30 ms later.

Statistical analyses

Statistical analyses were performed in MATLAB (version R2016a, The MathWorks, Inc., Natick, Massachusetts, United States). Chi-squared tests were used to determine differences in the proportion of subjects exhibiting an SLR (termed SLR prevalence). To compare SLR

323 latencies and magnitudes, we used a one-way ANOVA for experiment 1 and a 2 by 2 ANOVA
324 for experiment 2. Post-hoc pairwise comparisons relied on the Tukey-Kramer critical value, as
325 well as paired and unpaired t-tests when appropriate. We relied on non-normalized EMG for our
326 magnitude analysis. When comparing SLR magnitudes between subjects, all SLR+ values were
327 normalized to a maximum SLR magnitude within participants. For example, if a subject
328 exhibited SLRs in 5 conditions, the largest SLR condition for that subject is given a value of 1
329 and all other magnitudes are presented as a fraction of 1. When comparing SLR magnitudes to
330 recruitment associated with voluntary movement, we divided the magnitudes attained from the
331 SLR epoch (non-normalized) by the sum of the movement-aligned activity with a 30 ms window
332 surrounding peak EMG activity. Correlational analyses were performed on latency, magnitude
333 and RT measures on a subject-by-subject basis.
334
335 **Results**
336 *An emerging target paradigm increases SLR prevalence*
337 The emerging target paradigm is highly effective at eliciting stimulus-locked responses (SLRs)
338 and other fast visuomotor responses, such as short-latency reach reaction times (RTs)(Kozak et
339 al., 2020). Here we sought to investigate the features of the stimulus which best elicit SLRs by
340 altering the speed (experiment 1) or the speed and contrast (experiment 2) of the target. We first
341 determined how effective a given target condition was at eliciting an SLR.
342 All 32 subjects exhibited an SLR in at least one condition in both experiment 1 and 2
343 (**Figure 3;** recall 2 subjects performed in both experiments); as can be seen in this figure, each
344 subject had at least one diamond above the dotted line, indicating a detectable SLR. Previous
345 studies have reported that less than 65% of subjects exhibit an SLR to static high contrast targets

346 (Wood et al., 2015). In our sample, we found that 31 (97%) exhibited an SLR to a moving target
347 condition, whereas only 22 (68.7%) exhibited an SLR in the static target task. These differences
348 in detection are statistically significant (chi-squared test: $p= 0.0189$, $\chi2= 5.51$, $df= 1$), and
349 reaffirm previous observations that subjects not exhibiting an SLR to static targets almost always
350 exhibit an SLR to targets in the emerging target task (Kozak et al., 2020).

351 We further investigated whether SLR prevalence was influenced by target speed and/or
352 contrast. In experiment 1, the target could move at three different speeds; 'slow' (10 cm/s),
353 'medium' (15 cm/s), or 'fast' (20cm/s). We found that stimulus speed did not influence the
354 probability of detecting an SLR (10 v. 15 v. 20 cm/s- chi-squared, all $p> .05$). Therefore,
355 although subjects are more likely to exhibit SLRs in response to moving versus static targets, the
356 speed at which the target moves does not increase the likelihood of detection.

357 Recall that in experiment 1, we presented a static target either in the emerging target task
358 (i.e., the 0 cm/s target, which was intermixed with other moving targets), or in a standard static
359 task used previously (S1). We found that all 16 subjects (100%) exhibited an SLR to a static
360 target in the emerging paradigm, but only 9 of these subjects (~56%) exhibited an SLR in the
361 standard, static task (S1). This difference in prevalence was statistically significant (chi-squared
362 test: $p= 0.00275$, $\chi2= 8.96$, $df=1$), indicating that an emerging target paradigm promotes the
363 expression of an SLR regardless of whether the target is moving or not.

364 In experiment 2, we investigated whether the contrast and speed of a target impacted SLR
365 expression. As shown in experiment 1, we confirmed that target speed does not impact SLR
366 prevalence, therefore we grouped together both fast- and slow- moving target conditions and
367 determined that a high contrast moving target is more likely to evoke the SLR than a low
368 contrast moving target (chi-squared test: $p= 0.00075$, $\chi2= 11.361$, $df=1$). In fact, low contrast

moving targets were not significantly better at evoking SLRs than static targets (slow + fast low contrast moving targets versus high + low contrast static targets: chi-squared test: $p>.05$, $\chi 2= .056$, df=1). These results demonstrate that high contrast, moving targets are better at evoking SLRs than static or low contrast targets, furthermore, low contrast targets are equally as effective as static targets.

Next, we sought to characterize the latency and magnitude of the SLR. As can be seen in representative data from experiment 1 (**Figure 4**) and experiment 2 (**Figure 5**), various SLR features changed with different target conditions. In these plots, the SLR appears as a vertical banding of EMG activity, due to EMG changes occurring around the same time after target emergence on every trial (grey boxes, two left columns in **Figure 4** and **Figure 5**). **Figure 4** and **5** also shows the mean +/- SE EMG traces and time-series ROC plots (3rd column), and a depiction of how the presence of an SLR is detected (see methods- RT split analysis; slopes >67.5 indicate an SLR is present). In **Figure 4**, the representative subject from experiment 1 exhibited SLRs in all conditions; note the vertical banding in the color plots, and the slopes of the lines in the rightmost plots. SLRs in this subject began ~90 ms after target emergence in all conditions, regardless of target speed, or whether a stationary stimulus was presented in the emerging target task or static task. In contrast, the representative subject from experiment 2 (**Figure 5**) did not exhibit an SLR in the static task (rightmost columns, slope <67.5) but did exhibit an SLR to both high and low contrast moving targets in the emerging target task. Data from this subject illustrates an example of an SLR following target appearance in the emerging target but not static task (compare first two rows to final four rows). In the following sections, we further investigate the impact of varying target speed and contrast on the latency and magnitude of the SLR.

Experiment 1: Faster moving targets elicit larger magnitude SLRs that evolve at similar latencies

We have previously reported that SLRs may differ in magnitude (Gu et al., 2016) and/or latency (Kozak et al., 2019) depending on task context and stimulus properties, respectively. We examined the data from experiment 1 to investigate the effect of target speed on SLR latency and magnitude. There were 5 different conditions associated with experiment 1: either a static target appearing in the static task (S1), or static (0cm/s), 'slow' (10 cm/s), 'medium' (15 cm/s) or 'fast' (20 cm/s) targets in the emerging paradigm. Intriguingly, as seen in (**Figure 6a**), there were no differences in SLR latency in any of the conditions (one-way ANOVA, $F(4,53) = .58$, $p = .68$). These results are also apparent in the individual subject data shown in **Figure 4**; as can be seen in the trial-by-trial colour plots on the left-hand side, irrespective of the condition, the banding of activity defining the SLR evolves consistently at ~90 ms.

Although it is clear that the latency for the SLR is not affected by target speed, we observed clear evidence that SLR magnitude is impacted by target speed (**Figure 6b**). From the left side of **Figure 6b** (S1) to the right side of the subplot (fastest moving targets), magnitude values are increased for moving targets (one-way ANOVA (all conditions), $F(4, 53)= 15.15$, $p= 2.53e-8$), with all emerging targets evoking larger magnitude SLRs than static targets (all $p<.0005$). Indeed, SLRs evoked by the fastest moving target in the emerging target paradigm were approximately twice as large as SLRs evoked by the target in the static paradigm (S1 versus 20 cm/s; unpaired t-test; $t= -7.78$, $p= 3.61e-7$, $df= 18$). Even when removing the influence of both static targets from our analysis (s1 and 0cm/s), we found that faster moving targets in the

414 emerging target paradigm promote larger magnitude SLRs (one-way ANOVA (10, 15 and 20
415 cm/s speeds), $F(2, 32)= 4.59$, $p= .0183$).

416 While SLR magnitude tends to increase for faster moving targets, **Figure 6b** shows that
417 SLR magnitudes were comparable for the fastest (20 cm/s) and the non-moving (0 cm/s) target in
418 the emerging target paradigm. Recall as well that the 0cm/s target presented in the emerging
419 target paradigm evoked SLRs more often than targets in the static paradigm. These results (large
420 magnitudes and high prevalence) were very interesting to us given that in both conditions the
421 stimulus presented to the visual system is the same (blue rectangle in **Figure 6**). A direct
422 comparison showed that 0 cm/s targets in the emerging target paradigm evoked larger magnitude
423 SLRs than target in the static paradigm (unpaired t-test; $t= -6.1$, $p= 3.02e-6$, $df= 23$). Thus, the
424 behavioural context in which a static target is presented influences both the prevalence and
425 magnitude of the SLR, but not the latency.

426 We were also interested in how SLR magnitude related to the maximal movement
427 aligned activity. Therefore, we took the magnitude of the EMG activity in SLR epoch and
428 compared it to movement aligned magnitude for a 30 ms window around the peak (this is the
429 same duration used for the SLR magnitude). As shown in **Figure 6c**, we observed substantial
430 variability in how SLR magnitudes compared with the peak EMG activity aligned to movement
431 onset, with SLRs being anywhere between ~10-90% as large. We did not detect any differences
432 in this scaled measure of SLR magnitude across conditions (one-way ANOVA, $F(4,53)=.62$, $p =$
433 $.65$). On average, SLRs tended to be ~50% as large as the activity aligned to movement onset.
434 Despite such large variability, the SLR magnitudes reported here are significantly larger than any
435 reported previously (Pruszynski et al., 2010; Gu et al., 2016; Kozak et al., 2019).

436 Overall, when using targets moving at different speeds in an emerging target paradigm,
437 all moving targets are equally capable of eliciting SLRs and do so at similar latencies. However,
438 faster moving targets are associated with larger magnitude SLRs. An emerging target paradigm
439 was also more effective than a static target paradigm at eliciting more prevalent and larger
440 magnitude SLRs. Static targets presented in the context of an emerging target paradigm,
441 intermixed with moving targets, were equally effective at eliciting large magnitude and prevalent
442 SLR responses.
443
444 *Experiment 2: Higher contrast targets evoke shorter latency and larger magnitude SLRs*
445 The most intriguing finding in experiment 1 was that the latency of the SLR did not depend on
446 the speed of the target; all targets (whether statically presented or the fastest moving) evoked
447 SLRs at the same latencies. This was intriguing given that previous studies which systematically
448 varied visual features (contrast, spatial frequency) found that lower magnitudes accompany
449 longer-latency SLRs (Wood et al., 2015; Kozak et al., 2019). However, the results from
450 experiment 1 indicate that manipulations of stimulus features, and specifically stimulus velocity,
451 can influence SLR magnitude without influencing SLR latency. Therefore, we further probed
452 this finding by introducing targets varied by contrast, which have been shown to alter SLR
453 latency for static targets (Wood et al., 2015). In particular, we examined if SLR latency and
454 magnitude would negatively correlate across the speed of motion of lower-contrast targets. These
455 lower contrast targets would avoid possible 'floor effects' on SLR latency, which may have been
456 caused by the use of salient, high contrast moving targets in experiment 1. In experiment 2, we
457 examined the SLR in response to high and low contrast targets moving at a 'fast' (20 cm/s) or
458 'slow' (10 cm/s) speed.

We first examined the effect of target contrast on SLR latency. We found that the contrast, but not the speed of the moving target, impacted the SLR latency (2 x 2 ANOVA, $F(1,47) = 72.85$, $p = 4.1e\text{-}11$). High contrast targets evoked shorter latency SLRs by approximately 14ms compared to low contrast targets (**Figure 7a**; $p = 2.07e\text{-}8$). This trend is consistent with previous results (Wood et al., 2015). We also found that targets with the same contrast, regardless of the speed they were moving, evoked SLRs of similar latencies ($p > .05$; **Figure 7a** no differences within green points or blue points), which confirms results from experiment 1. Thus, the same contrast targets evoke similar latency SLRs, regardless of how fast they are moving. Thus, the results from experiment 1 were not simply due to a floor effect on SLR latency, beyond which the SLR latency could not be further lowered.

In contrast to experiment 1, static targets in experiment 2 tended to be longer latency compared to emerging targets, (**Figure 7a**; unpaired t-test; $t(18) = -3.27$, $p = .004$), but were similar latencies to those reported previously (Wood et al., 2015). We contend that the most likely reason for longer latency SLRs in the experiment 2 static target task is due to differences in experimental set up between experiment 1 and 2, related to randomized hold time (see discussion).

We next examined the influence of target contrast and speed on SLR magnitude (**Figure 7b**). Here we found that both the speed and the contrast impacts SLR magnitude (2 x 2 ANOVA, speed: $F(1,47)=67.8$ $p = 1.1e\text{-}10$; contrast: $F(1,47)=11.7$ $p = .001$). Higher contrast targets evoked larger magnitude SLRs compared to lower contrast targets (**Figure 7b**, all blue points lower than all green points; unpaired t-test; $t= 2.7$, $p= .01$, $df= 49$). We also found that faster moving targets evoked larger magnitude SLRs compared to slower moving targets (all second points within a condition are higher than first points; unpaired t-test; $t= -7.8$, $p= 4.1e\text{-}10$, $df= 49$).

482 This supports the results from experiment 1, where faster moving targets evoked larger
483 magnitude SLRs. We did not observe interaction effects between target speed and contrast (2 x 2
484 ANOVA, p=.87). We also did not observe any differences in magnitude for static targets. Taken
485 together, higher contrast and faster moving targets evoked shorter latency and larger magnitude
486 SLRs, compared to low contrast or static targets.

487 When examining SLR magnitudes in relation to the magnitude of reach-related activity in
488 experiment 2 (**Figure 7c)**, we also observed large variability as seen in experiment 1 (**Figure**
489 **6c**). However, in experiment 2, SLR magnitudes in the emerging target paradigm tended to be
490 even larger than in experiment 1. SLR magnitudes for moving targets reached ~75% of the level
491 of reach-related activity (~20% higher than experiment 1; compare **Figures 6c** versus **7c**), with a
492 few values approaching 150%. An example of such a phenomenon is shown in **Figure 8**. As seen
493 in **Figure 8a**, the differences between red lines defining the SLR epoch highlighted by the grey
494 box, are approximately equal to, and slightly greater than the differences between lines of
495 movement aligned activity shown in **Figure 8b** (movement aligned magnitude epoch highlighted
496 by grey box). This figure demonstrates that SLR magnitude may be on par, or even greater than,
497 movement-aligned activity. We consider that the most likely reason for larger SLR magnitudes
498 in experiment 2 is due to differences in the apparatus used (see discussion). **Figure 8** also
499 illustrates the variability in the appearance of the SLR across subjects. For example. while the
500 SLR in **Figure 8** is crisp and distinct from subsequent recruitment, those seen in previous figures
501 (e.g., see mean EMG activity in **Figures** 4 and **5**) show a 'smoothing' of fast visuomotor activity
502 into voluntary activity.

503 To summarize, the results from experiment 2 concurred with the results from experiment
504 1 in that SLR latency was not influenced by target speed, regardless of target contrast. A target

of the same contrast will elicit SLRs of the same latency, regardless of how fast the target is moving.

The SLR and its relationship to reaching behaviour

So far, we have shown that 97% of tested subjects were capable of generating an SLR towards emerging targets, and furthermore that visual features such as speed and contrast of a target alter the latency and magnitude of the SLR. We now turn to the relationship between the latency and magnitude of the SLR, and how these features impact ensuing RT.

In both experiments SLR latency and magnitude were negatively correlated with each other (**Figure 9a** exp. 1; R=-.48, p=.00012; **Figure 9d** exp. 2; R=-.41, p=.00038), indicating that larger magnitude SLRs are associated with shorter latency SLRs. Recall that there were no significant latency differences for any target conditions found in experiment 1. This negative correlation indicates that short latency SLRs, even with small variability and a narrow range of latencies (all SLR latencies between ~90-110 ms **Figure 9a**), still tend to be associated with larger magnitude SLRs.

When examining how the SLR relates to RT, we found a positive correlation between latency and RT in both experiments (experiment 1- **Figure 9b**; R=.36, p=.0047; experiment 2- **Figure 9e**; R=.67, p=8.4e-11); indicating that longer SLR latencies were associated with longer latency RTs. Conversely, there was a strong negative correlation between magnitude and RT for both experiments (experiment 1- **Figure 9c**; R=-.75, p=8.69e-12; experiment 2- **Figure 9f**; R=-.40, p=.0005), indicating that decreasing SLR magnitudes are correlated with increasing RT latency. Thus, in conditions where stimulus appearance evoked larger and earlier SLRs, subjects generally produced shorter RTs.

These findings raise the question of how much RTs change in accordance with the changes in SLR latency and magnitude. In both experiments, we saw a significant reduction in RT latency for faster moving, or higher contrast targets, compared to static targets (see **Figure 10**). In experiment 1, we found that faster moving targets were associated with shorter latency RTs (one-way ANOVA, F(4, 79)= 2.71, *p*= .036). RTs decreased by an average of ~20 ms for static versus fast targets (static versus fastest; 250ms+/-25 versus 231ms+/- 16; paired t-test; t= 3.25, p=.005, df= 15) (see **Figure 4** for an example; note the leftward shift of white boxes indicating RTs in the first row versus the last row). In experiment 2, we found that both target speed (two-by-two ANOVA, F(1, 107)= 17.33, *p*= 6.5e-5) and contrast (two-by-two ANOVA, F(2, 107)= 103.07, *p*= 3.25e-25) impacted RT. RTs significantly decreased in experiment 2 by an average of 62 ms for high contrast moving targets (static versus fastest; 243ms+/-26 versus 181ms+/- 9; paired t-test; t= 10.2, p=5.7e-9, df= 17), and 57 ms for low contrast moving targets (static versus fastest; 253ms+/-26 versus 196ms+/- 11; paired t-test; t= 9.7, p=2.2e-8, df= 17). Of great interest, the RTs shown in **Figure 10** strongly resemble our manipulated SLR characteristics depending on the experiment, for both magnitude (compare **Figure 6b** to experiment 1 in **Figure 10)**, and latency (compare **Figure 7a** to experiment 2 in **Figure 10).** Taken together, these results indicate that strongly evoking a fast visuomotor system (indicated by short latency and large magnitude SLRs) is correlated to decreasing RT. RTs may be expedited by as much as 62 ms in an emerging target paradigm with high contrast fast moving targets, compared to static targets.

Recall in experiment 1 that we presented two different static conditions, one in the context of an emerging target paradigm (0 cm/s), and one in the standard static task (S1). The 0 cm/s target evoked larger and more prevalent SLRs compared to S1 targets presented out of the

emerging target paradigm. Therefore, we also investigated whether differences in SLRs related to differences in RT. Averaged across subjects, RTs in the 0cm/s condition were not different than RTs in the S1 condition (250 +/- 22 ms versus 250 +/- 25 ms; n.s.). Thus, despite differences in SLR magnitudes between static targets, there was little difference in RTs. Taken together, these results indicate that fast visuomotor relates to, but is not fully predictive of, the ensuing RT.

Interestingly, we noticed in **Figure 6a** and **Figure 7a**, that there were latency differences between experiments 1 and 2, despite both using 'high contrast' targets (unpaired t-test; t= 7.99, p= 2.35e-8, df= 25). We found that experiment 2 targets were associated with shorter latency SLRs by approximately 15 ms (99 +/-5 ms versus 84 +/- 4ms). However, when we compared SLR latencies between experiment 1 and low contrast fast moving targets in experiment 2, we did not find any differences (unpaired t-test; t= 1.2, p= .22, df= 25). Therefore, its possible that the reason for this RT difference is due to differences in monitors, where the 'high contrast' target in experiment 1 is similar to the low contrast target in experiment 2 (see discussion).

Here we have demonstrated that fast moving, and high contrast targets presented in an emerging target paradigm tended to elicit the most prevalent, shortest latency and largest magnitude SLRs, which were correlated with shorter latency RTs. We found that RTs decreased by as much as 62 ms when using these targets. These results indicate that the neural circuitry mediating a fast visuomotor response are best evoked by a faster moving, higher contrast targets.

Discussion

The brain has a remarkable capacity to rapidly transform vision into action, allowing us to initiate reaches towards a target within fractions of a second. Previous research has shown that

some visual attributes, such as stimuli composed of lower spatial frequencies or higher contrast, can elicit earlier reaching responses than others (Veerman et al., 2008; Wood et al., 2015; Kozak et al., 2019). Here, by using a newly-described emerging target paradigm (Kozak et al., 2020), we show that high-contrast, moving stimuli are particularly capable of eliciting fast visuomotor responses such as SLRs and expedited reach reaction times. Further, as the same subjects performed both the novel emerging target paradigm and a visually-guided reach paradigm used previously, we can better understand the sensory and cognitive factors promoting fast visuomotor responses. Finally, by studying a variety of stimuli in the emerging target paradigm, we can gain further insights into the relationship between the earliest phase of stimulus-related EMG recruitment, subsequent phases of EMG recruitment leading up to movement onset, and the RT of the movement itself. Together, our results contribute to a growing understanding of the interplay between the cortical and subcortical substrates mediating visually-guided reaches in conditions requiring expedited responses.

Comparison to past studies

Previous research on rapid visually-guided reaches have typically used either target-jump paradigm where a visual target is displaced during an arm movement (Soechting and Lacquaniti, 1983; Day and Lyon, 2000), or a static target reaching paradigm where a suddenly appearing target evokes reaches from a stationary arm position (Pruszynski et al., 2010). While useful, such approaches have limitations: the response of interest evolves during an on-going movement in target-jump experiments, or not all subjects exhibit SLRs in a typical static target paradigm, even with intramuscular electrodes (Pruszynski et al., 2010; Gu et al., 2016). In contrast, in the emerging target paradigm, the arm is stationary at the time of target emergence and evokes

597 highly prevalent fast visuomotor responses that can be recorded even with surface electrodes
598 (Contemori et al., 2020; Kozak et al., 2020).

599 The results in experiment 1 show that much larger SLRs are provoked by the appearance
600 of a stationary target in the emerging target paradigm rather than the static task (blue rectangle,
601 **Figure 6,** approximately 2 times larger). Larger magnitude SLRs likely relate to the increased
602 proportion of subjects expressing an SLR to a stationary target in the emerging target paradigm
603 rather than static task (100% vs 56%). We speculate that a signal of implied motion of the target
604 behind the barrier is central to the increased SLR magnitude in the emerging target paradigm
605 (Kozak et al., 2020). Recent work has shown that the certainty of the time of target emergence
606 also facilitates the expression of more prevalent and larger SLRs (Contemori et al., 2020). Note
607 that temporally predictable targets still have to be presented within the emerging target paradigm,
608 as smaller magnitude and less prevalent SLRs are elicited in static tasks that had high temporal
609 certainty via a predictable gap between the offset of a central hold stimulus and target
610 presentation (Pruszynski et al., 2010; Wood et al., 2015).

611 Past work has shown that stimuli composed of progressively higher contrast (Wood et al.,
612 2015) or lower spatial frequencies (Kozak et al., 2019) elicit progressively larger magnitude and
613 lower latency SLRs. Indeed, higher contrast moving stimuli evoked larger and earlier SLRs in
614 experiment 2 (**Figure 7**). Somewhat surprisingly, this inverse relationship between SLR latency
615 and magnitude was not observed in the manipulation of the velocity of moving stimuli. Instead,
616 SLR latency remained invariant while SLR magnitude was greatest for the fastest moving
617 stimulus; this was observed both in experiment 1 (**Figure 6**) and in experiment 2 for stimuli of
618 similar contrast (**Figure 7**). Thus, at least across the parameters explored in this study, SLR

magnitude is impacted by both stimulus contrast and velocity, whereas SLR latency is impacted by stimulus contrast but not velocity.

We speculate that this dissociation between SLR latency and magnitude for stimulus velocity may relate to the displacement of the stimulus across sequential display frames, with larger displacements increasing the vigor of sensory transients that remain timed to the onset of the first frame. Future studies should examine the impact of subsequent display frames on the SLR, given that Contemori and colleagues (2020) found that a stimulus flashed for a single frame (~16 ms) provokes earlier and larger SLRs than moving targets; it is possible that flashed stimuli may prove to be a particularly potent means of evoking vigorous sensory transients from the retina.

Relating the SLR to subsequent RTs

SLRs represent the first change in muscle recruitment following visual stimulus presentation. As such, they demarcate the completion of the most rapid sensory-to-motor transformation at the upper limb. Past reports show that larger magnitude SLRs precede shorter latency movements on a trial-by-trial basis (Pruszynski et al., 2010; Gu et al., 2016; Contemori et al., 2020), and here we show, when pooling across all conditions in which subjects exhibited an SLR, that larger magnitude and earlier SLRs precede shorter reach RTs (**Figure 9;** see also Kozak et al., 2019). These correlative relationships are consistent with a functional contribution of the SLR to the forces necessary to overcome the limb's inertia. However, we are mindful that the SLR is followed by sustained levels of muscle recruitment preceding the onset of the reaching movement, which also contribute to movement initiation. Indeed, comparing SLR latency and magnitude to reach RT in experiments 1 and 2 leads to some interesting insights. For example,

642 while nearly identical SLRs were observed in the emerging target task in experiment 1 to the 0
643 deg/s and 20 deg/s stimulus (**Figure 6**), the reach RTs to the 20 deg/s stimulus were ~20 ms
644 shorter (**Figure 10**). Conversely, while nearly identical reach RTs in experiment 2 were observed
645 to fast moving low-contrast versus slow moving high-contrast targets (**Figure 10)**, the SLRs to
646 these stimuli were different, being larger magnitude but starting later for low-contrast, fast
647 moving targets (**Figure 7**). These distinctions between SLR parameters and RTs likely attest to
648 continued processing of the visual stimulus, and the contribution of such processing to the RT.
649 The judicious selection of stimulus parameters, e.g., to elicit more robust SLRs but longer RTs,
650 may aid the study of the fast visuomotor responses by reducing the overlap between the SLR and
651 activity aligned to movement onset.
652
653 *Plausible neural substrates*
654 The superior colliculus (SC) has been implicated as a potential candidate mediating the SLR
655 (Corneil et al., 2004; Pruszynski et al., 2010). The SC is a midbrain structure whose intermediate
656 and deep layers (SCi) interface with premotor structures for eye, head, and upper limb
657 movements within the reticular formation (Corneil and Munoz, 2014), whereas superficial layers
658 respond to visual input. Our results add further circumstantial evidence for a role for the SC in
659 the SLR. Previous work established that both the SLR and visual responses in the SC
660 preferentially respond to low spatial frequency (Chen et al., 2018; Kozak et al., 2019) and high
661 contrast targets (Li and Basso, 2008; Marino et al., 2015; Wood et al., 2015). Moving targets also
662 evoke robust SC responses (Marrocco and Li, 1977), and we have shown here that moving
663 targets also evoke robust SLRs. Importantly, the target speeds used in the current study resemble
664 those used in the Marrocco and Li (1977) study, which evoked robust responses in the

intermediate and deep layers of the SC where visuomotor and motor neurons activated before arm movements reside (Werner et al., 1997; Stuphorn et al., 1999; Philipp and Hoffmann, 2014) (Stuphorn et al., 1999). The hypothesis that the SC mediates the SLR requires further testing with casual manipulation in tasks that promote SLR expression. Work reporting that SCi inactivation impacted the selection of reach targets but not reach kinematics (Song et al., 2011) employed paradigms that would not promote SLR expression.

An open question is how visual input from target motion accesses the SC. Visual information may access the superficial SC directly via a retinotectal route (summarized in: (May, 2006)), or indirectly via a retino-geniculo-striate loop through cortex, and then on to the SC (Schiller et al., 1979). The SC also receives projections from higher order cortical centers such as MT (an area which responds to target motion (Nhan and Callaway, 2012)); such signals may provide the SC with a pre-target, priming signal related to implied motion that potentiates SLR expression.

Methodological considerations

All of our subjects exhibited an SLR in at least one stimulus condition. This replicates the high prevalence of SLR detection in the emerging target paradigm (Contemori et al., 2020; Kozak et al., 2020), and affirms the contention that most if not all subjects are capable of exhibiting SLRs in an appropriate paradigm. However, subjects did not necessarily exhibit an SLR to every stimulus in the emerging target paradigm, even for high-contrast, fast moving stimuli (**Figure 2**). We speculate that this result may be due, at least in part, to how we detect the presence of the SLR with the RT split analysis, which allows for a direct comparison of SLR prevalence to those reported elsewhere which also used this method (e.g.,(Kozak et al., 2019, 2020; Contemori et al.,

688 2020)). The RT split analysis is somewhat conservative in that it requires an SLR to both short-
689 and long-latency trials. SLR- observations could therefore include those situations where an SLR
690 precedes the short- but not long-RT trials (see top two rows of **Figure 5**, which appear to exhibit
691 SLRs for the shorter-than-average RTs). The RT split analysis is also more suited to paradigms
692 engendering a larger degree of RT variance. As noted previously (Kozak et al., 2020), one
693 potential complication of the emerging target paradigm is that it may shorten RTs too much, not
694 only reducing RT variance but also leading to a potential overlap of SLR with activity linked to
695 movement onset. As noted above, judicious stimulus selection may help avoid such overlap, but
696 we also expect the continued evolution of SLR detection methods suited to a particular
697 paradigm.
698 We noted large differences in the latencies of fast visuomotor responses across
699 experiments, with SLRs evolving ~15 ms earlier and reach RTs being ~50 ms shorter in
700 experiment 2 compared to experiment 1. The most likely reason for these differences is the
701 contrast of the stimuli, as the VPIXX projector used in experiment 2 has a higher level of
702 contrast (275 cd/m2) than the standard monitor used in experiment 1 (110 cd/m2). Consistent
703 with this, the SLR latencies from the high-contrast target in Experiment 1 (**Figure 6b**) resemble
704 those of the low contrast target in experiment 2 (**Figure 7a**). The large difference in reach RTs
705 across experiments, even to targets associated with similar latency SLRs, may relate to postural
706 differences in the exoskeleton-based Kinarm robot in experiment 1 versus the endpoint-based
707 Kinarm robot in experiment 2.
708
709 *Conclusions*

710 The work presented here demonstrates that all subjects can generate SLRs, but are more likely to
711 present one in an emerging target paradigm. As a consequence, reliable SLRs can be recorded
712 even with surface EMG, and here we use this paradigm to show that targets moving at faster
713 speeds elicit larger magnitude SLRs, whereas higher contrast targets decrease SLR latency.
714 Larger magnitude and shorter-latency SLRs tend to proceed expedited RTs, although RTs are
715 also influenced by continued stimulus processing after the SLR. As the SLR is the first wave of
716 muscle recruitment tied to visual target onset, muscle recruitment during this interval may
717 provide a unique window into the contribution of the tecto-reticulospinal signaling that is distinct
718 from subsequent phases of target-related recruitment of corticospinal or cortico-reticulo-spinal
719 circuits. Rather than being directly involved in the SLR, cortical areas may serve to prime this
720 phylogenetically-conserved circuit to produce the first wave of muscle recruitment in situations
721 when time is of the essence, preceding subsequent waves of EMG recruitment that arise
722 following more detailed, cortically-related processing of the sensory signal.
723

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790
791

792 **Figure legends**

793

794 Figure 1. The emerging target paradigm (Kozak et al., 2020). a) A target (T1) appears above an
795 occluder (grey box) and the subject the real-time cursor (RTC; white dot below occluder that
796 represents hand position), into the start position (T0; grey dot below the occluder). b) Once the
797 RTC is in the start position, T1 moves towards the subject along the inverted y path and then
798 disappears behind the occluder. c) The subject makes a visually-guided reach to T1 as soon as it
799 emerges at the right or left outlet below the occluder.

800

801 Figure 2. Detection of SLRs. a) Exemplar trial-by-trial recruitment of activity from right
802 pectoralis muscle during leftward and rightward reaches from a subject with a detectable SLR.
803 Each row is a different trial, with the intensity of color conveying degree of recruitment. Trials
804 sorted by RT (white boxes) and aligned to stimulus onset. The SLR (highlighted by asterisk)
805 appears as a vertical banding of increased or decreased recruitment aligned to left or right
806 stimulus presentation, respectively, rather than movement onset. b) Mean +/- SE of EMG activity
807 for the early- (purple) and late- (green) RT subsets based on mean RT. c) In the RT split analysis,
808 separate time-series ROCs were run for the early and late subsets, and then the mean RT for each
809 subset is plotted as a function of the discrimination time. The slope of the line connecting these
810 points determines whether the divergence of EMG activity is more time-locked to stimulus or
811 movement onset. d) For SLR+ observations, all trials were pooled together regardless of RT to
812 determine the SLR latency (derived from the time-series ROC) and magnitude (derived from the
813 mean EMG waveformes; see methods). Grey rectangle in b) and d) depict the SLR interval.

814

Figure 3. Prevalence of SLRs across the population. Slope of the relationship between discrimination time and average RT for early and late RT groups (e.g. see slope in Figure 2c) Each data point represents a unique subject for a particular condition. Slopes are capped at 90 degrees and a dotted black line is drawn at 67.5 deg. A data point above this line represents a SLR+ observation, whereas a data point below the line represents SLR- observations. a) Experiment 1. Black and grey diamonds represent static conditions in the static and emerging target paradigms, respectively. Blue diamonds represent moving targets in emerging target paradigm, with slower moving targets are represented by darker shades. b) Experiment 2. Purple diamonds represent high contrast targets; green diamonds represent lower contrast targets. Static and slower moving targets are represented by darker shades. 2 subjects completed both experiments; subjects 2 and 16 from experiment 1 are subjects 18 and 12 from experiment 2, respectively.

Figure 4. Data from representative subject in experiment 1, using the same format as in figure 2. From left to right, columns shown trial-by-trial EMG activity for left and right targets sorted by RT, mean +/- SE EMG activity for left and right targets with overlaid time-series ROC, and the RT split analysis for data shown in the corresponding row (the number in each panel is the slope).

Figure 5. Data from representative subject in experiment 2,using the same format as figure 4.

Figure 6. Summary of results from experiment 1, showing SLR latency (a), SLR magnitude (b, normalized within each subject to the largest SLR across all conditions, and SLR magnitude

normalized to the maximum of movement-aligned EMG activity. In c), each asterisk represents data from an individual subject. S1 indicates the results from the static task, which presents the same retinal stimulus to the subject as the 0 cm/s target in the emerging target paradigm . Error bars show SE.. * indicates significance (see results text for more details).

Figure 7. Summary of results from experiment 2 (same format as Fig. 6), with SLR latency (a), SLR magnitude normalized to the within-subject largest SLR (b), and SLR magnitude normalized relative to maximum of movement-aligned activity. All values presented as mean +/- standard error. * indicates significance. HC= high contrast LC= low contrast.

Figure 8. Example subject whose SLR magnitude exceeds the maximum level of EMG activity aligned to target onset. Data, shown as mean +/- SE, are aligned to stimulus onset in a), or movement onset in b). SLR magnitude is measured as area between left and right reaches for the 30 ms interval after the SLR latency (grey box, running from 73-103 ms relative to stimulus onset). + 30 ms. For movement-aligned activity, magnitude is measured as area 15 ms before and 15 ms after RT onset (grey box in b).

Figure 9. Correlations for SLR latency, magnitude and associated reaction time in experiment 1 (top row) or 2 (bottom row). a, d) SLR latency and magnitude correlations. b, d) SLR latency and RT correlations. c, f) SLR magnitude and RT correlations. All correlations shown are significant. Each blue circle represents data from an SLR+ subject in a unique experimental condition. Solid red lines indicates first order fit of the data.

Figure 10. Summary of RTs in experiment 1 (a) and 2 (b), following the formats in figures 6 and 7.

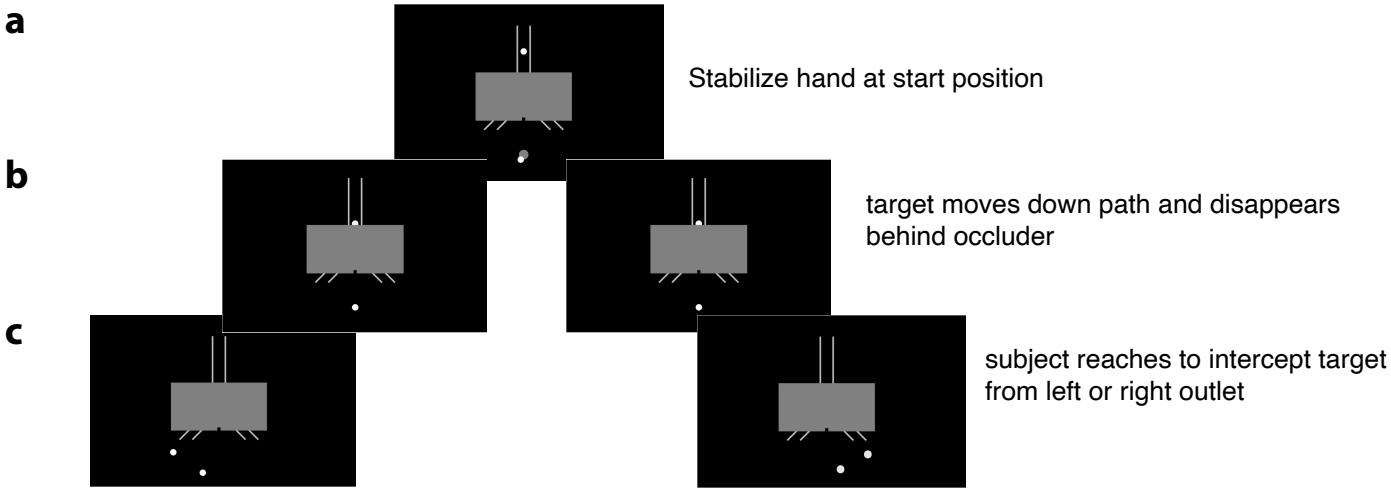

Figure 1- Kozak and Corneil 2021

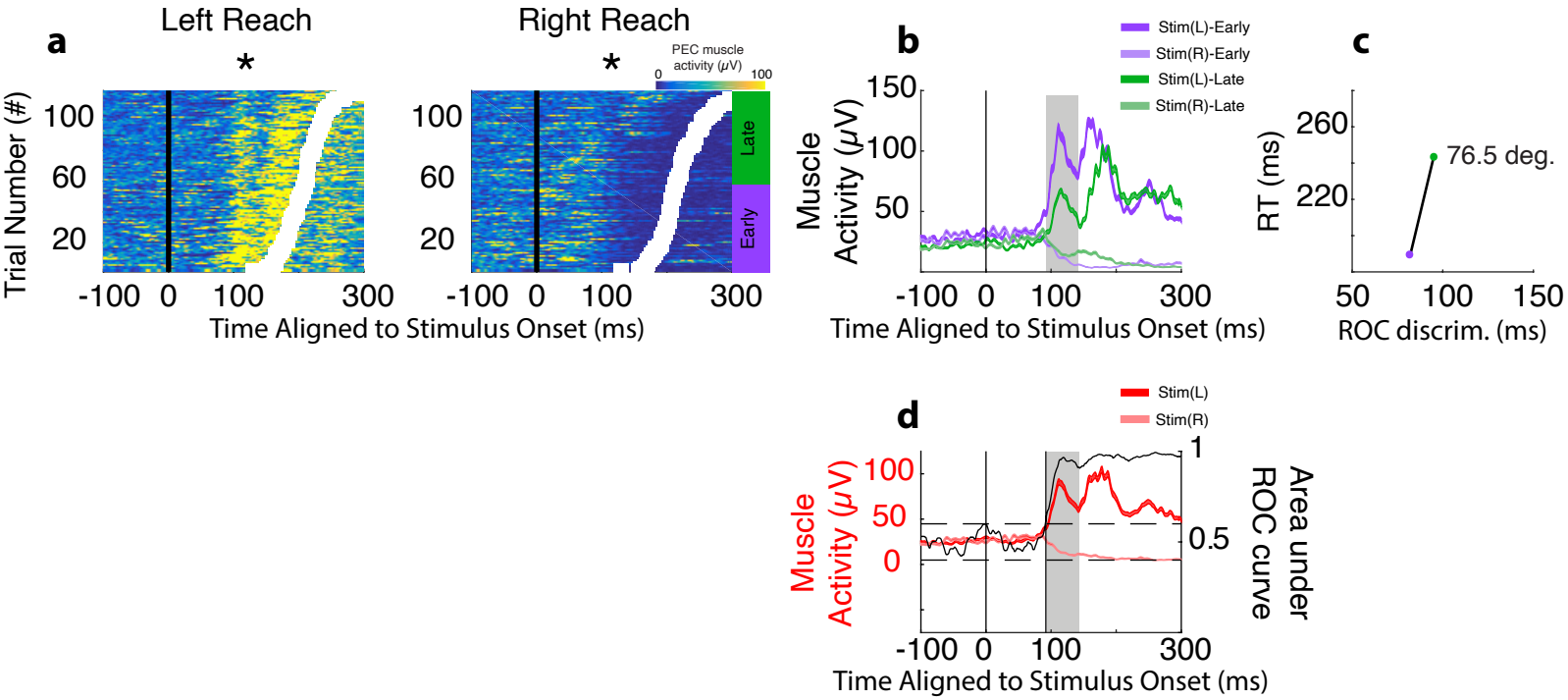

Figure 2- Kozak and Corneil 2021

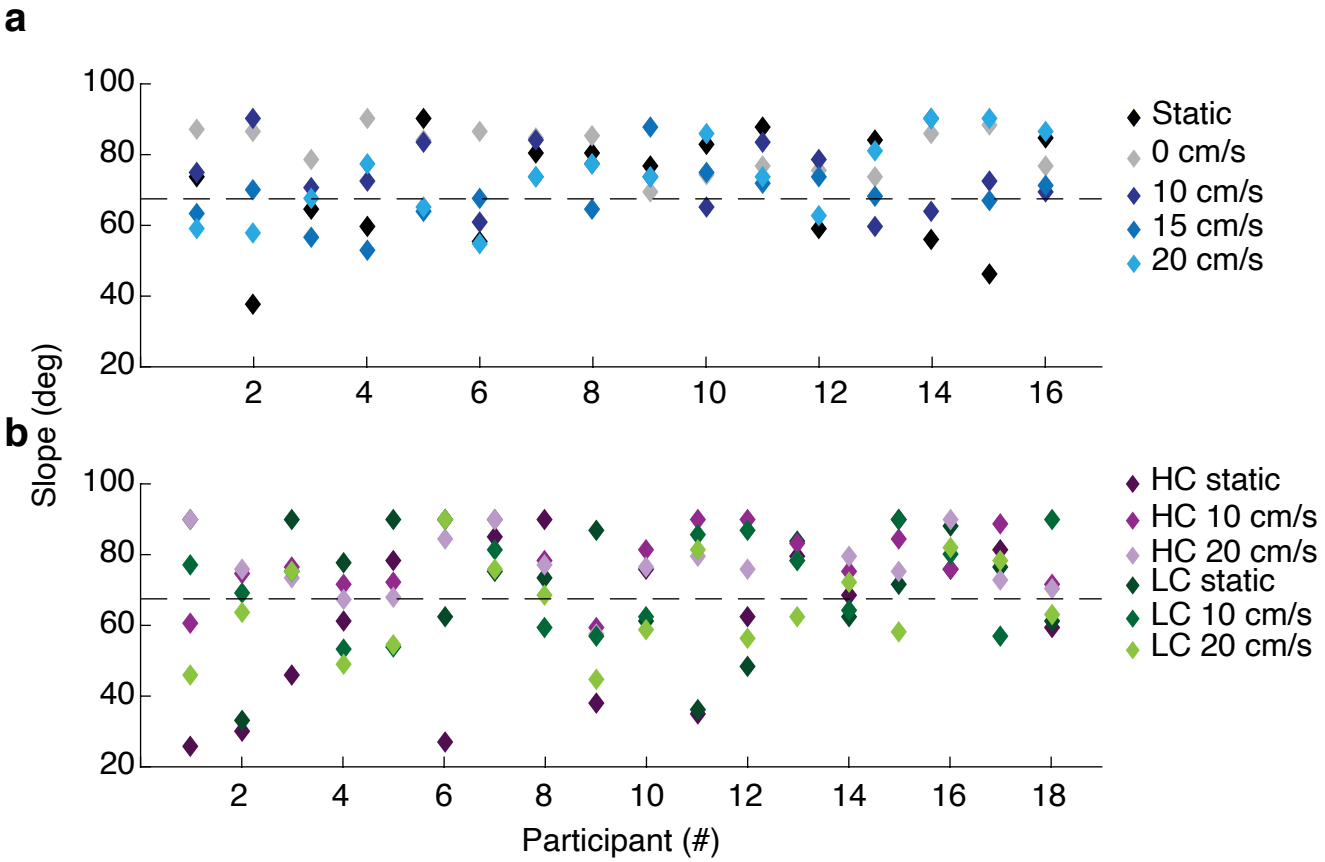

Figure 3- Kozak and Corneil 2021

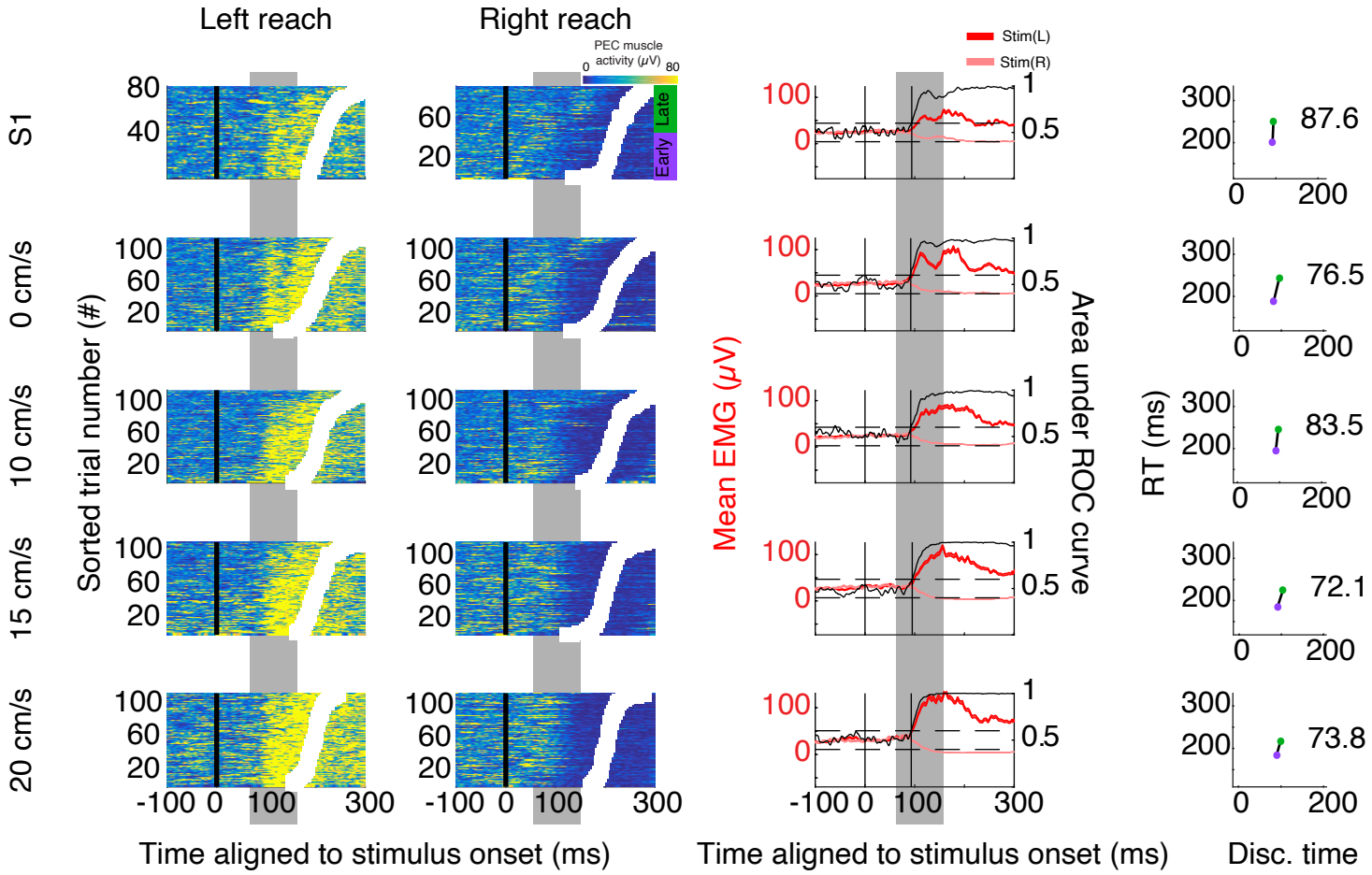

Figure 4- Kozak and Corneil 2021

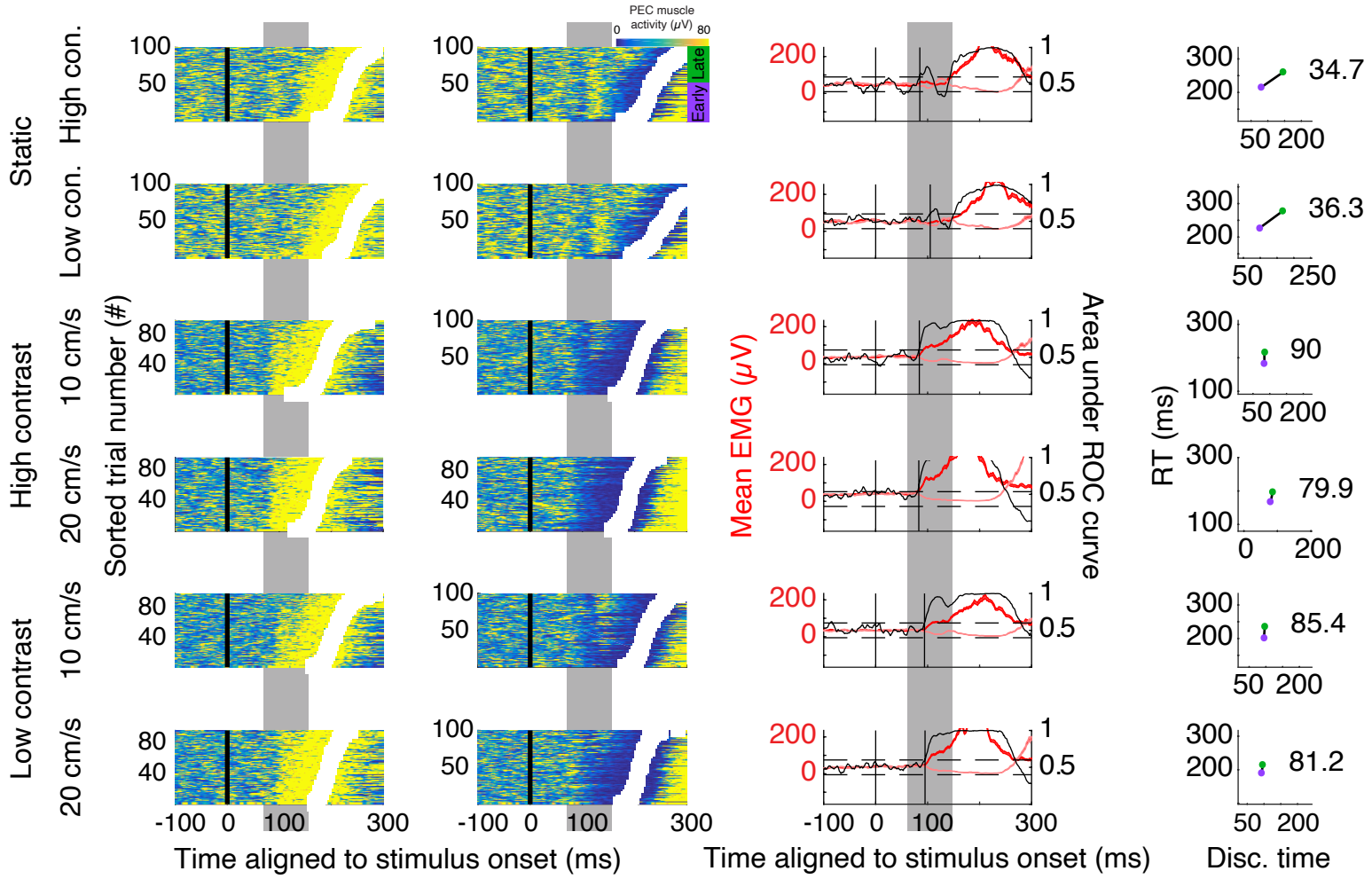

Figure 5- Kozak and Corneil 2021

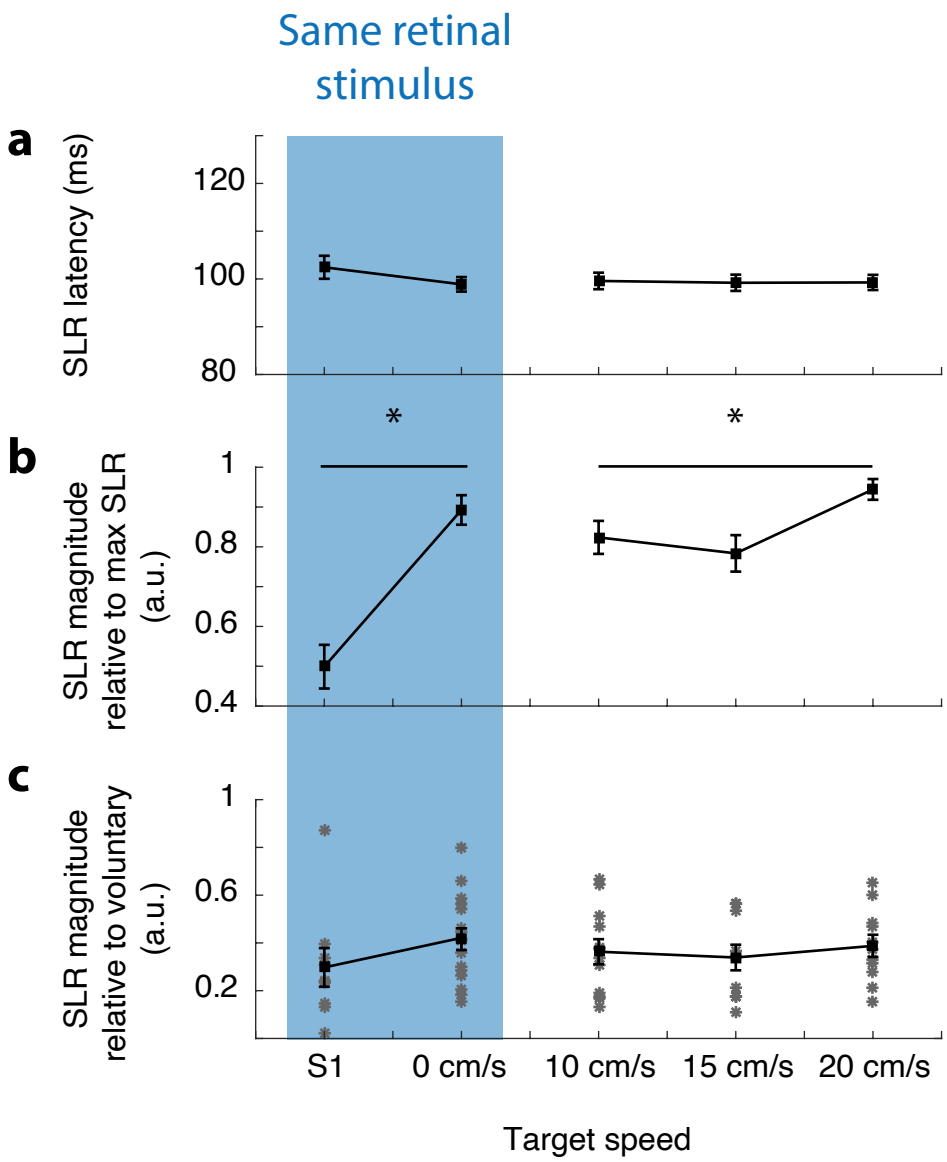

Figure 6- Kozak and Corneil 2021

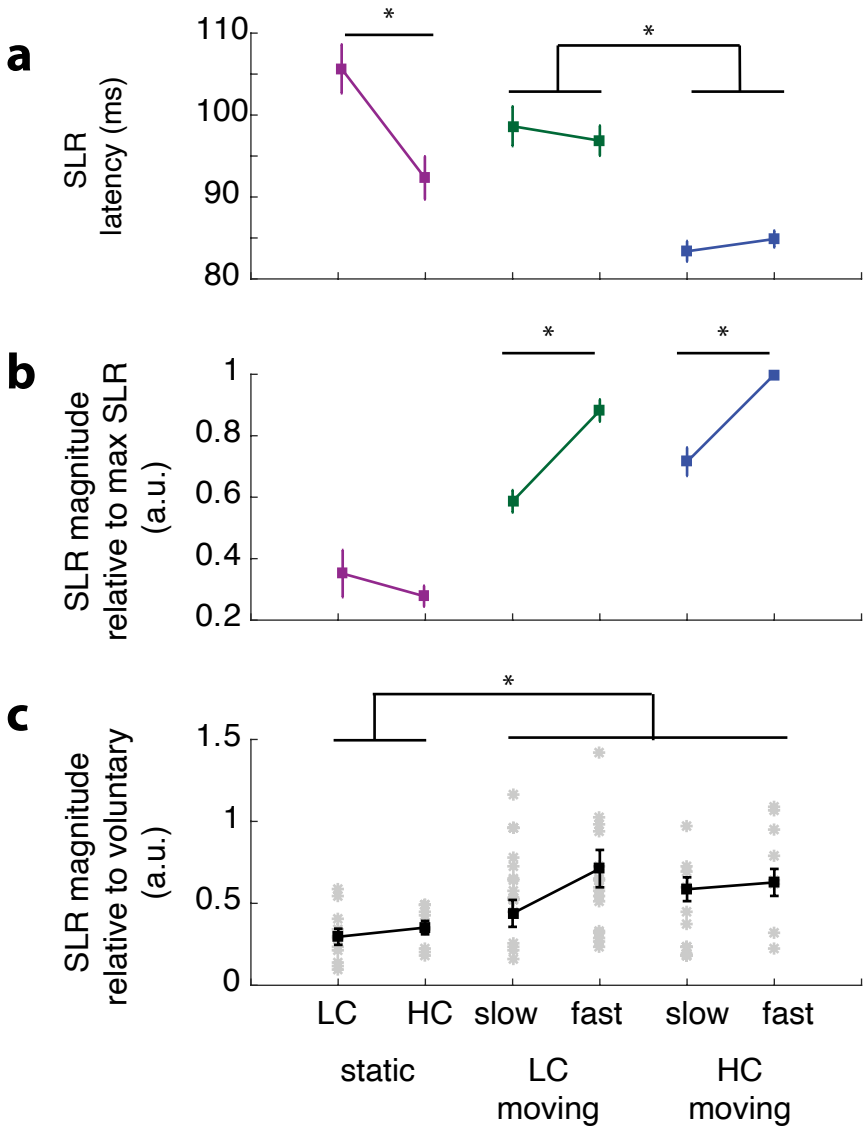

Figure 7- Kozak and Corneil 2021

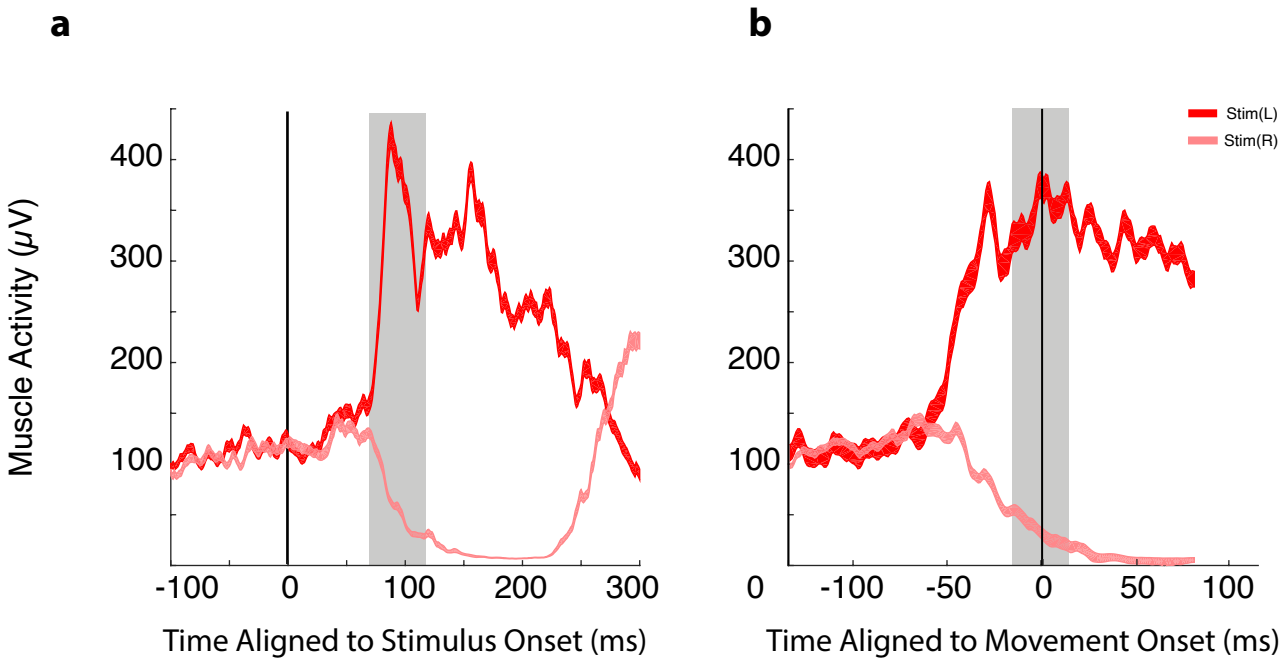

Figure 8- Kozak and Corneil 2021

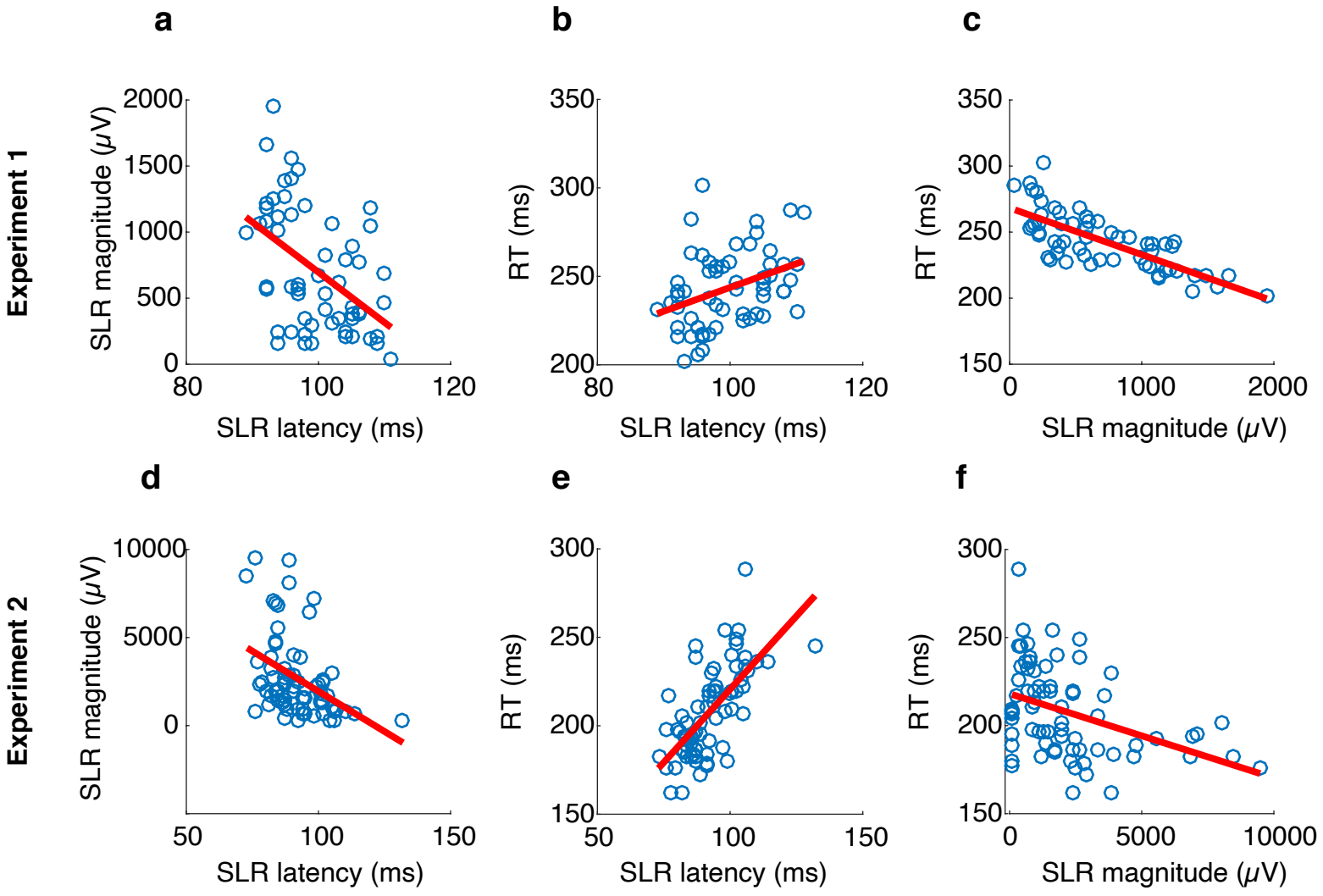

Figure 9- Kozak and Corneil 2021

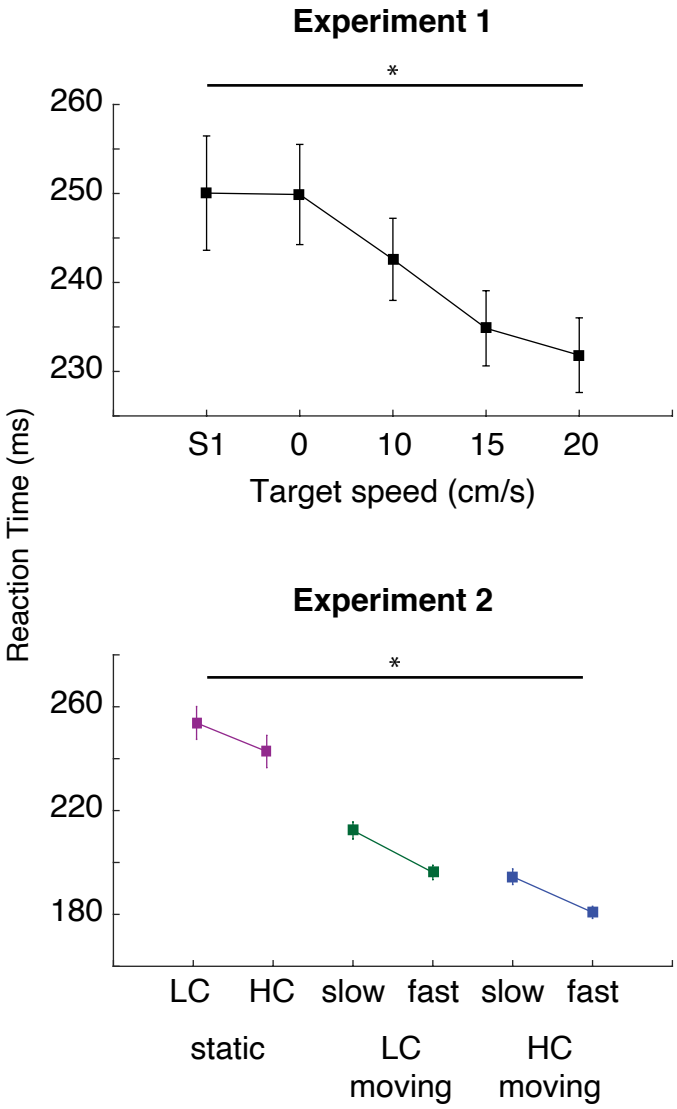

Figure 10- Kozak and Corneil 2021