Startling acoustic stimuli hasten choice reaching tasks by strengthening, but not changing the timing of, express visuomotor responses

Running head: Effects of a startling acoustic stimulus on reflexive reaching

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ABSTRACT

Responding to an external stimulus takes ~200 ms, but this can be shortened to as little as ~120 ms with the additional presentation of a startling acoustic stimulus. This *StartReact* phenomenon is hypothesized to arise from the involuntary release of a fully prepared movement. However, a startling acoustic stimulus also expedites rapid mid-flight, reactive adjustments to unpredictably displaced targets which could not have been prepared in advance. We surmise that for such rapid visuomotor transformations, intersensory facilitation may occur between auditory signals arising from the startling acoustic stimulus and visual signals relayed along a fast subcortical network. To explore this, we examined the StartReact phenomenon in a task that produces express visuomotor responses, which are brief bursts of muscle activity that arise from a fast tectoreticulospinal network. We measured express visuomotor responses on upper limb muscles in humans as they reached either toward or away from a stimulus in blocks of trials where movements could either be fully prepared or not, occasionally pairing stimulus presentation with a startling acoustic stimulus. The startling acoustic stimulus reliably produced larger but fixed-latency express visuomotor responses in a target-selective manner. Consistent with the StartReact phenomenon, it shortened reaction times, which were as fast for prepared and unprepared movements. Our results confirm that the StartReact phenomenon can be elicited for reactive movements without any motor preparation, consistent with intersensory facilitation. We propose the reticular formation to be the likely node for intersensory convergence during the most rapid transformations of vision into targeted reaching actions.

Introduction

Initiation of voluntary movements to visual stimuli typically takes >200 ms. Yet, when a visual 'Go' stimulus is paired with a startling acoustic stimulus (SAS), reaction times (RTs) can be speeded up to a presumed 'reactive' mode of control with RTs of ~80-120 ms (depending on whether EMG- or movement velocity-based readouts are reported; (Valls-Solé et al., 1995; Carlsen et al., 2004)). This *StartReact phenomenon* has been demonstrated in many *simple* reaction tasks involving single or multi-segmental arm and leg movements (for review see (Carlsen et al., 2012; Nonnekes et al., 2015)). However, when the experimental task involves selecting between multiple response options (i.e. *choice* reaction tasks), a SAS typically does not yield accurate target-selective movements at RTs that approach the very fast RTs observed with SAS in a simple reaction task (Carlsen et al., 2004, 2009; Forgaard et al., 2011; Maslovat et al., 2012; Marinovic et al., 2017). These findings have led to the consensus that the StartReact phenomenon depends on the requested movement being fully prepared prior to stimulus presentation, with the prepared movement being involuntarily 'released' by the SAS (Valls-Solé et al., 1999; Carlsen et al., 2012; Carlsen and Maslovat, 2019).

However, there are reports of StartReact effects in choice reaction tasks with RTs just as fast to those observed for 'prepared' movements in simple reaction tasks (Reynolds and Day, 2007; Queralt et al., 2008). Thus, under certain circumstances, a SAS facilitates rapid visuomotor transformations, even without a fully prepared movement. One distinctive feature of these studies is that they both involved online movement corrections, in this case of the lower limb. Online movement corrections may represent a special class of reactive movements where visual input is directly mapped onto motor outputs via a fast subcortical network involving the tecto-reticulo-spinal system (Day and Lyon, 2000; Perfiliev et al., 2010; Kozak et al., 2019). Consistent with this, RTs of online corrections are very short even in the absence of a SAS (Soechting and Lacquaniti, 1983), such movements are initially directed invariably toward a visual stimulus (Day and Lyon, 2000), and their RTs do not follow Hick's law as they remain fixed regardless of the number of possible alternatives (Reynolds and Day, 2012). Other reactive responses like express saccades are also invariably stimulus-driven and do not follow Hick's law (Paré and Munoz, 1996), and are known to rely critically on the subcortical superior colliculus (Schiller et al., 1987; Edelman and Keller, 1996; Dorris et al., 1997). Could the StartReact effect on reactive movements like online corrective movements arise from intersensory facilitation within the reticular formation between the SAS and visual signals relayed along a tecto-reticulo-spinal pathway?

Recent work on intersensory facilitation across multiple sensory modalities suggests that a SAS may indeed strengthen the output of the fast visuomotor network (Glover and Baker, 2019). In the context of center-out visually-guided reaches from a stationary position in a choice reaction task, a SAS increased the mean magnitude of short-latency (~80-120 ms) recruitment of upper limb muscles without drastically impacting its timing. Such recruitment may reflect what are termed express visuomotor responses (EVR; formerly termed stimulus-locked responses). The EVR is a brief increase/decrease in the target-selective recruitment of agonist/antagonist muscles that is relatively time-locked to the visual stimulus at a latency of ~80-100 ms, and is spatially and temporally distinct from the longer-duration burst of muscle activity associated with the generation of the voluntary arm movement (Pruszynski et al., 2010; Wood et al., 2015; Gu et al., 2016; Atsma et al., 2018). Larger but fixed-latency EVRs precede shorter RTs and on-line corrections, and there is compelling evidence that EVRs reflect tecto-reticulo-spinal processing (Pruszynski et al., 2010; Gu et al., 2016; Kozak et al.,

2019; Contemori et al., 2021a, 2023; Kearsley et al., 2022; Billen et al., 2023; Selen et al., 2023). However, as Glover and Baker (2019) reported a generic enhancement of muscle recruitment with SAS across all target directions, it cannot be ruled out that this enhanced recruitment reflected generalized startle reflex-related potentiation, rather than target-selective facilitation of the EVR itself. If this were true, one would expect these SAS-enhanced EVRs to yield a directional bias in StartReact effects due to the preferential recruitment of flexor muscles in the startle reflex (Brown et al., 1991a, 1991b), such that RTs are faster with SAS for movements towards the body, but slower and with more frequent directional errors for those away from the body. In contrast, in the event of intersensory facilitation of the fast visuomotor network itself, where the SAS presumably acts as an accessory stimulus to increase its excitation, RT shortening is expected in all directions in the absence of drastically increased errors. As the Glover and Baker (2019) study did not focus on the StartReact effect, it is not known how the observed facilitation of the SAS on EVR would compare across Choice and Simple reaction tasks, nor how trial-by-trial EVRs relate to the ensuing reactive RTs.

Here, we tested the hypothesis that simultaneous presentation of a SAS with a salient visual stimulus shortens the RTs of reactive reaching movements by strengthening the magnitude of EVRs without changing their latency. We used an emerging target paradigm that increases the generation of EVRs and reactive reaches, even in a choice reaction task on trials without a SAS (Kozak et al., 2020; Contemori et al., 2021b; Kozak and Corneil, 2021). We also interleaved trials where subjects reached toward or away from the emerging stimulus, to better separate the EVR from ensuing voluntary recruitment and to further delineate the target-selective nature of the expected EVR strengthening with SAS. Finally, we also examined EVRs and RTs on a simple reaction task where a movement could be fully prepared prior to stimulus emergence, enabling comparison to results from the choice reaction task.

Materials and methods

Subjects

A total of 17 subjects (10 females, 7 males; mean age: 22.6 years SD: 5.7) participated in these experiments. All subjects provided informed consent, were paid for their participation, and were free to withdraw at any time. All but 3 subjects were right-handed, and 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 the University of Western Ontario and conformed to the Declaration of Helsinki.

Apparatus and experimental design

Subjects performed reaching movements with their right arm in a KINARM End-point lab, moving the end-point of a robotic manipulandum in response to the appearance of visual stimuli that were occasionally accompanied by a loud auditory stimulus. Visual stimuli were produced by a projector (PROPixx project by VPixx, Saint-Bruno, QC, Canada) integrated into the KINARM setup, and projected onto an upward facing mirror. A shield below the mirror occluded direct vision of the hand, and hand position was represented by a real-time cursor projected onto the screen. Subjects were instructed to generate arm movements as quickly and as accurately as possible in response to stimulus emergence in an emerging target task (Kozak et al., 2020), moving either toward (a pro-reach) or away from (an anti-reach) the stimulus depending on an instructive cue provided at the start of each trial (see

below). At the time of stimulus emergence, a second visual stimulus unseen by the subject was provided to a photodiode whose output was fed to the KINARM platform. All kinematic and electromyographic (EMG) data were aligned to photodiode onset. Throughout the entire experiment, a constant load of 2 Nm towards the participant and 5 Nm to the right was applied through the manipulandum in order to increase the activity of the right pectoralis muscle, so that the activity of this muscle would increase or decrease, respectively, following stimulus presentation in the preferred or non-preferred direction of the muscle.

On a subset of trials, a loud acoustic stimulus was presented at the same time as the emergence of a visual target. The acoustic stimulus consisted of a 40 ms white noise burst delivered at an intensity of between 119 and 120 dB. A bilateral sound file was played through a digital output channel in the Kinarm setup and fed into a Rolls stereo line mixer/headphone amplifier, (model RM219) and then delivered bilaterally to Beyerdynamic CT 240 Pro headphones worn by the subject. This output was also routed to an analog in-channel on the KINARM platform, allowing us to confirm the synchronization of the auditory stimulus with visual stimulus emergence measured by the photodiode. Prior to the experiment, the sound intensity from each earpiece was calibrated by placing the earpiece on top of a GRAS Ear Simulator (model RA0039) with a 1／2 '' microphone and held in place by 500g weight. Sound files were recorded with an M-Audio Fast Track Ultra audio interface and analyzed in Praat analysis software (Boersma, 2001). The sound intensity produced by the right and left earpiece was measured at 119.6 dB and 119.1 dB, respectively.

Subjects performed a number of variants of this task in different blocks of trials, and we will describe the results from two such blocks. The order of the blocks was randomized across subjects. Both blocks were variants of the emerging target task (Kozak et al., 2020), which increases the probability of observing EVRs on upper limb muscles (Contemori et al., 2021a, 2021b; Kozak and Corneil, 2021; Kearsley et al., 2022). The structure of this paradigm is provided in Fig. 1. Trials were separated by a 1.5s inter-trial interval. At the start of each trial, the configuration shown at the top of Fig. 1 was presented, with a barrier colored either red or green. The color of the barrier instructed the subject to prepare to make a pro- (toward) or anti- (away from) reach, relative to the side of stimulus emergence below the barrier. Subjects moved the cursor representing their hand position into a start location, at which point a visual stimulus was placed above a barrier. After a 1000 ms hold period, during which subjects were required to maintain the hand position cursor in the start location (if not, the trial was reset), the stimulus began to travel down an inverted “y” path at a speed of 15 cm/s for 500 ms before it disappeared behind the barrier. The junction of the y was obscured by a barrier, hence the stimulus first disappeared behind the barrier, and then emerged from beneath the barrier at either the right or left outlet. The stimulus moved at a constant velocity behind the barrier, and the stimulus was obscured behind the barrier for a fixed period of 500 ms on all trials. During the time the stimulus was behind the barrier, subjects were instructed to keep their hand at the start location, and to fixate a small notch at the bottom of the barrier (eye movements were not measured). The stimulus became visible only after it had fully emerged from beneath the barrier, at which point it continued along the inverted y path. Upon stimulus emergence, subjects were instructed to respond as quickly and as accurately as possible and move to intercept the target on pro-trials, or move in the diametrically opposite direction on anti-trials. The trial ended if the hand cursor made contact with the stimulus on pro-trials, reached the diametrically opposite location on anti-trials, or if the stimulus

moved off screen. On 25% of all trials, stimulus emergence was accompanied by a non-directional SAS.

In a block of Choice reaction task trials, the stimulus could emerge either to the left or right, and subjects could be instructed to either respond with a pro-reach (green barrier) or anti-reach (red barrier). Thus, there were 8 unique trial conditions: stimuli to the left or right, requiring a pro- or anti-reach, with or without a SAS. Subjects completed 1 block of 240 pseudorandomized trials. 60 (25%) trials contained a SAS, and 180 (75%) of trials had no SAS. Thus, there were 15 or 45 unique repeats of trials with or without a SAS, respectively.

In a block of Simple reaction task trials, the stimulus always appeared to the left, and subjects could be instructed to either respond with a pro- or anti-reach. Subjects were explicitly informed of the left-sided stimulus presentation in this block, and they were told that this resulted in 100% certainty of whether a pro-reach to the left or an anti-reach to the right would be required at stimulus emergence. This task thus allowed for full preparation of the requested leftward or rightward hand movement. There were 4 unique trial conditions: a leftward stimulus requiring either a pro- or anti-reach, with or without a SAS. Subjects completed 1 block of 120 pseudorandomized trials, 30 (25%) or 90 (75%) of which contained a SAS or not, respectively. Thus, there were 15 or 45 unique repeats of trials with or without a SAS, respectively.

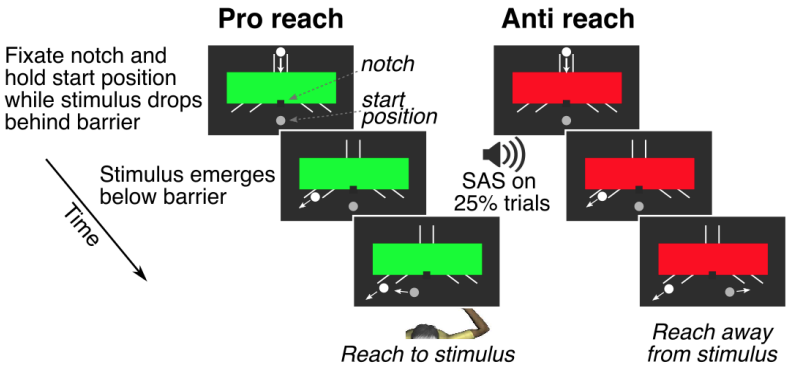

Figure 1. Behavioral paradigm. At the start of each trial, participants acquired the central start position with their hand (grey circle), and fixated a small notch at the bottom of the barrier. The barrier color conveyed the instruction to reach toward (green barrier, a pro-reach) or away from (red barrier, an anti-reach) the stimulus (white circle) upon its emergence below the barrier. On 25% of trials, a starting acoustic stimulus (SAS; 119-120 dB) was presented at the time of stimulus emergence. In a block of Choice reaction task trials, the stimulus could emerge at either the left or right outlet with equal probability. In a block of Simple reaction task trials, the stimulus only emerged at the left outlet.

Data acquisition and analysis

Surface electromyographic (EMG) recordings were made from the following targets: the clavicular head of the right pectoralis major muscle, the sternal head of the right pectoralis major muscle and right and left sternocleidomastoid (SCM) muscles. In all cases, recordings were made with double-differential surface electrodes (Delsys Inc., Bagnoli-8 system, Boston, MA). We found that the recordings from the clavicular and sternal heads of pectoralis major were essentially equivalent, so report the results from the clavicular head. EMG signals were sampled at 1 kHz, amplified by 1000, full-wave rectified off-line, and smoothed with a 7-point smoothing function.

Kinematic data were sampled at 1 kHz by the KINARM platform. RTs were based on acceleration and velocity criteria, finding first the point in time where the arm exceeded 10% of its peak velocity. The RT for a given trial was then determined by searching back in time from this point for the latest point relative to stimulus presentation where the arm's acceleration fell within the 99% confidence interval of arm accelerations determined from all trials spanning from a period of 100 ms before to 50 ms after stimulus appearance. Trials with RTs below 80 ms were excluded as anticipatory, as were trials with RTs exceeding 600 ms due to presumed inattentiveness, resulting in a total of 3.38% of trials excluded in the Choice reaction task, and 34.4% in the Simple reaction task. All trials were inspected by an analyst in a graphical user interface, which permitted rejection of trials with clearly anomalous movement sequences; less than 5% of all trials were rejected by the analyst. On anti-reach trials, subjects often responded with a sequence of two movements where the first movement proceeded toward the stimulus before a second movement went in the opposite, appropriate direction. We excluded such sequences if the first movement went more than 50% toward where the subject landed on pro-reach trials, on the presumption that they may not have consolidated the anti-reach instruction on such trials, or may not have been paying attention. We note that this 50% cutoff is arbitrary, but similar results were obtained if we applied cutoffs of either 25% or 75%. For trials with initial wrong-way hand movements below 50%, we determined the onset latencies of the hand movements in the incorrect as well as the correct directions. The former was determined as explained above, whereas the latter was determined as the time when the reach started to proceed in the correct direction.

As described previously (Corneil et al., 2004), we used a time-series receiver-operating characteristic (ROC) analysis to determine the presence and latency of the EVR in the Choice reaction task. Briefly, we conducted an ROC analysis for each point in time from 100 ms before to 300 ms after stimulus presentation. For each point in time, the area under the ROC curve indicates the likelihood of discriminating the side of stimulus presentation based only on EMG activity alone; a value of 0.5 indicates chance performance, whereas a value of 1.0 indicates perfect discrimination. While our past work (Wood et al., 2015; Kozak et al., 2021) determined the presence or absence of an EVR by conducting separately time-series ROC curves for the shorter- and longer-than-average RT subsets, this was not practical in the current dataset given the fewer number of repeats of each unique stimulus condition, and the relatively small variance in RTs. Instead, we found the time at which the slope of the time-series ROC changed by using the matlab function *ischange*; if this time fell within 70 and 120 ms, then we determined that an EVR was present, and the time at which the slope changed was determined to be the EVR latency EMG magnitude in the EVR time window was calculated as the mean activity over the 80-120 ms interval post stimulus onset. Following subtraction of baseline activity, defined as the 500ms of activity prior to stimulus onset, these EMG magnitudes were normalized with respect to the maximum value of the ensemble-averaged PEC activity on left pro-reach trials without an SAS. Note that these EMG magnitudes were determined regardless of whether an EVR was identified.

Statistical analysis

Unless otherwise stated, linear mixed models were used to investigate main effects and interactions. Linear mixed models were chosen over repeated-measures analysis of variance (ANOVA) because unlike ANOVAs, linear mixed models do not use list-wise deletion in the case of missing data points,

allowing us to maximize the power and reduce the bias of our analysis. This applies where a participant may exhibit an EVR in one condition but not another (e.g., on trials with or without a SAS). The Satterthwaite method was applied to estimate degrees of freedom and generate p-values for the mixed model analyses. We investigated the effect of stimulus presentation side (left vs right), instruction (pro-reach vs anti-reach) and startle (no-SAS vs SAS), specifying these as fixed effects and participant ID as a random effect in the linear mixed models. Post hoc orthogonal contrasts with the Bonferroni correction method for multiple comparisons were used to investigate significant interactions between predictor variables. Data processing was done in MATLAB (R2021a), and statistical analyses were performed using jamovi (version 2.3, 2022), and MATLAB (R2021a).

Results

Choice reaction task - performance and movement RTs

Following our procedure for trial inclusion (see Methods), we retained a total of 3708 trials (90.9 ± 3.8%) for further analysis. Of the rejected trials in the Choice reaction task, 3.4% were due to the RT constraints, ~3% were wrong-way reaches on anti-reach trials that were not corrected, and ~3% were rejected by the analyst.

'Wrong-way' error rates and RTs (means±SE) for each of the experimental conditions are displayed in Figure 2. Participants made more mistakes on anti-reach trials than pro reach trials (15.2±1.6% vs 3.4± 0.9% of trials, respectively) resulting in a main effect of instruction (*instruction*; $\beta = 0.117$, SE = 0.013, $p < 0.001$, 95% CI [0.0926, 0.1422]). Participants also made more wrong-way errors on SAS than non-SAS trials (13.3 ± 1.8% vs 5.3±0.8% respectively; *SAS*, $\beta = 0.080$, SE = 0.013, $p < 0.001$, 95% CI [0.0555, 0.1051]), which effect of the SAS depended on the instruction given (*instruction x SAS*; $\beta = 0.125$, SE = 0.025, $p < 0.001$, 95% CI [0.0751, 0.1742]). A post hoc comparison showed that in anti-reach trials there were more wrong-way errors with SAS than without (22.3± 2.8% vs 8.0± 1.1%; $p < 0.001$), but this was not the case with pro-reach trials (4.3 ± 1.3% vs 2.5± 0.7%; $p = 1.000$). These results were similar between target sides ($p>0.435$ for all main or interaction effects involving *side*).

Movement onset latencies were faster in pro- than in anti-reach trials (148±4 ms vs 198± 5ms, respectively; *instruction*, $\beta = 50.239$, SE = 2.50, $p < 0.001$, 95% CI [45.35, 55.13]). Note that for the wrong-way trials, we here included the onset latency of the movement away from the target (i.e. the instructed direction). The SAS significantly shortened movement onset latencies by, on average, 12 ms in pro-reach trials (142±4 vs 154±4 ms without SAS) and by 6 ms in anti-reach trials (195±5 vs 201±5 ms without SAS; *SAS*, $\beta = -9.443$, SE = 2.50, $p < 0.001$, 95% CI [-14.34, -4.55]), which effect was similar between instructions (*instruction x SAS*, $\beta = 6.4505$, SE = 2.50, $p =0.199$, 95% CI [-3.33, 16.23]). There was no main or interaction effect involving the side of target appearance ($p > 0.3$).

Across participants, the latencies of wrong-way movements (i.e. the RT of the movement towards the target) in anti-reach trials were shorter for SAS than non-SAS trials (127±7 and 147±10 ms, respectively) with no effect of target side (*SAS,* $\beta =-27.77$, SE = 12.66, $p =0.033$, 95% CI [-52.6, -2.98]). The maximum hand displacement in the wrong direction did not significantly differ between SAS and non-SAS trials (9.9% vs 6.2% of the distance to target; *SAS,* $\beta =1.139$, SE = 1.139, $p =0.448$, 95% CI [-1.78, 4.056]) or side of target appearance (*side*, $\beta =-2.122$, SE = 1.50, $p =0.163$, 95% CI [-5.05, 0.810]).

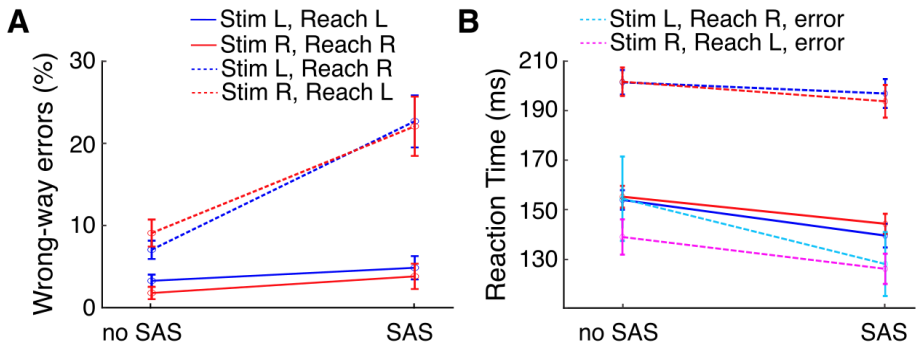

Figure 2. Behavioral results from Choice reaction task. Depiction of mean +/- standard error of error rates (**A**) and RTs (**B**). Errors are defined as anti-reach trials where participants initially moved incorrectly toward the emerging stimulus, and then corrected the movement in mid-flight to reach in the opposite direction. In **B**, the RTs of both the correct movement on anti-reach trials are shown (dashed blue and red lines), as are the RTs for the incorrect component of such error trials (cyan, pink dashed lines).

Choice reaction task – Effects of SAS on EVR Latency and response magnitude

Figure 3a-d shows the EMG responses in the pectoralis (PEC) muscle of a representative subject for each of the reaching conditions with and without a SAS. As the characteristic feature of the EVR, a band of increased PEC activity can be seen in the trials where the stimulus was presented on the left side (i.e left column) at 80-120 ms post stimulus onset, whereas in trials where the stimulus was presented at the right side (i.e. right column) a decrease in activity occurs in this time window. In pro-reaches (i.e. top row) this contrast in PEC activity between left and right stimulus presentation is more pronounced than in anti-reaches (i.e. bottom row). Figure 3e shows the respective time-series ROC analyses for identifying the presence and latency of the EVR (see methods).

All participants had a significant EMG discrimination time in the EVR window (70-120 ms), indicating the presence of an EVR in at least one condition. In pro-reach conditions we observed significant discrimination times in 16/17 participants with the SAS present and 12/17 participants in non-SAS conditions. 12/17 participants had a significant discrimination time in the non-SAS anti-reach condition, and 11/17 in SAS anti-reach condition (Fig. 4A). The Linear Mixed Model yielded no main effect of SAS on EVR latency (*SAS*, $\beta = 2.25$, SE = 1.14, $p = 0.12$, 95% CI [-0.526, 5.02]). Note that this model did not include *side* because to evaluate the EVR, right reaches are already compared to left reaches to determine the ROC curve and subsequently the EVR timing. Discrimination times in pro-reaches (89±1ms) were slightly but significantly faster than in anti-reaches (94±1 ms; *instruction*, $\beta = 3.87$, SE = 1.42, $p = 0.01$, 95% CI [1.085, 6.65]), irrespective of the SAS (*SAS x instruction,* $\beta = 1.28$, SE = 2.76, $p = 0.645$, 95% CI [-4.131 , 6.70]). This small effect seems to be driven by differences in the EVR detection using the change of slope detection method (see methods). This method appears to be less sensitive to detect a smaller EVR, followed by a movement in the opposite direction, as seen in anti-reaches, compared to a larger EVR and movement in the same direction, as seen in pro-reaches.

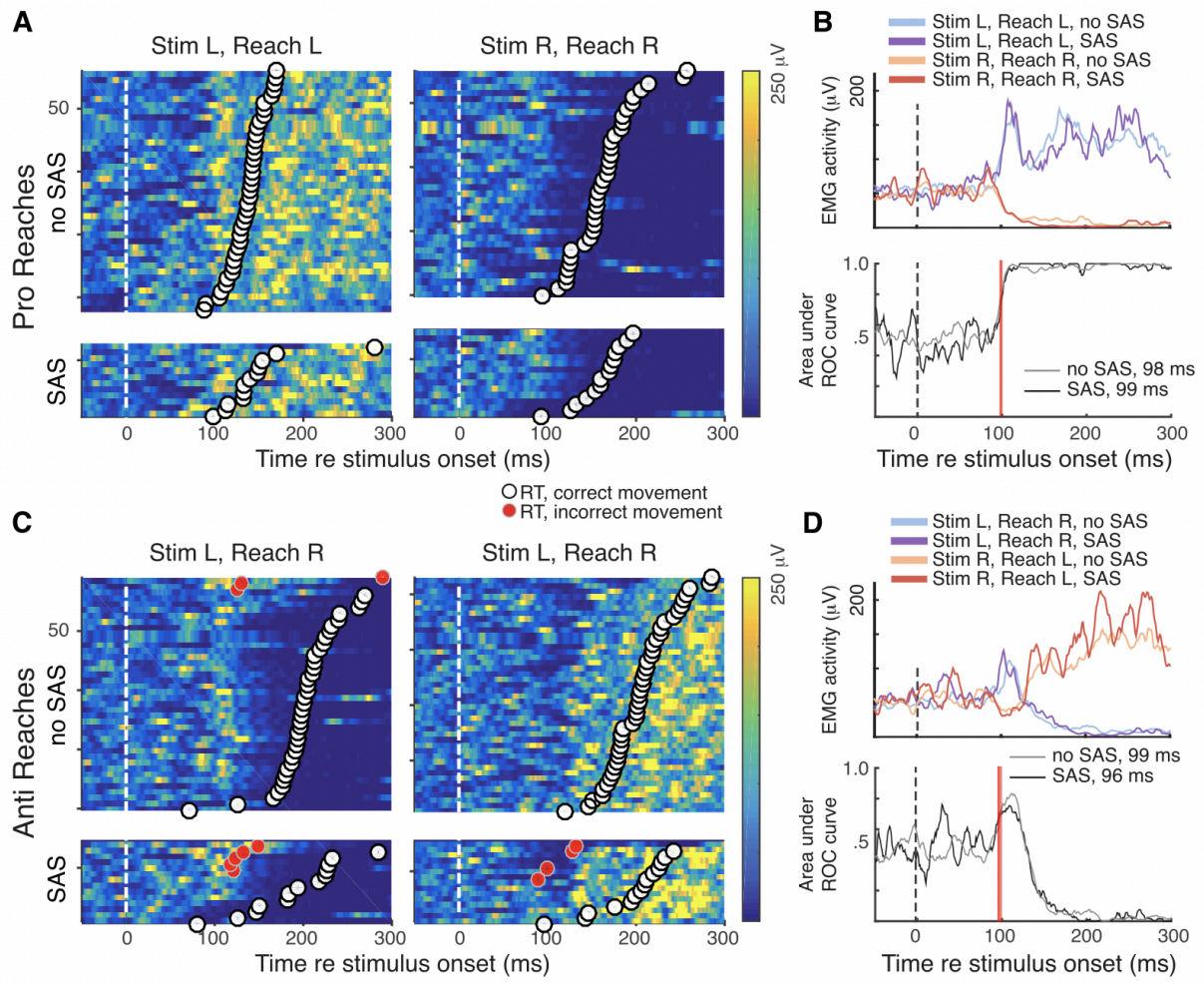

Figure 3. Representative EMG activity from the pectoralis muscle of an exemplar participant from Choice reaction task. EMG activity is shown in trial-by-trial heatmaps for pro-reach (**A**) and anti-reach trials (**C**). In each heat map, color conveys the magnitude of EMG activity aligned to stimulus emergence, with each row depicting an individual trial with trials ordered by the RT of the movement in the correct direction (white circles). Red circles on rows for anti-reach trials depict the RT of a wrong-way movement toward the emerging stimulus, which preceded the onset of the correctly-directed reach. Separate heat maps are depicted from trials with or without a SAS. **B, D**: Lines in the upper subplots depict the mean EMG activity for the four trial types. Lower subplots depict time-series ROC, calculated separately for trials with or without a SAS. Vertical red lines depict the time at which a change in time-series ROC was detected (values provided in each subplot).

Figure 4B shows the magnitude of PEC recruitment during the EVR window (80-120 ms), normalized relative to the maximum level of PEC recruitment aligned to reach onset averaged across all non-SAS left pro-reach trials. As expected for the EVR, PEC activity was significantly larger when targets were presented to the left than to the right (*side*, β = -30.32, SE = 2.50, p <0.001, 95% CI [-35.22, -25.41]), and more so in pro- than anti-reaches (*side x instruction*, β = 39.73, SE = 5.01, p <0.001, 95% CI [29.91, 49.54]). PEC activity was significantly larger with a SAS than without SAS (*SAS*, β = 14.38, SE = 2.50, p <0.001, 95% CI [9.47, 19.28]). This effect of the SAS depended on the side of target presentation (*SAS x side*, β = -14.96, SE =5.01, p =0.003, 95% CI [-24.77, -5.144]), but not on instruction (*SAS x instruction*; β = 1.00, SE = 5.01, p = 0.842, 95% CI [-8.81, 10.8161]). Post hoc

analyses revealed that the SAS significantly increased PEC recruitment in leftward targets ($p < 0.001$) but not in rightward targets ($p = 0.323$).

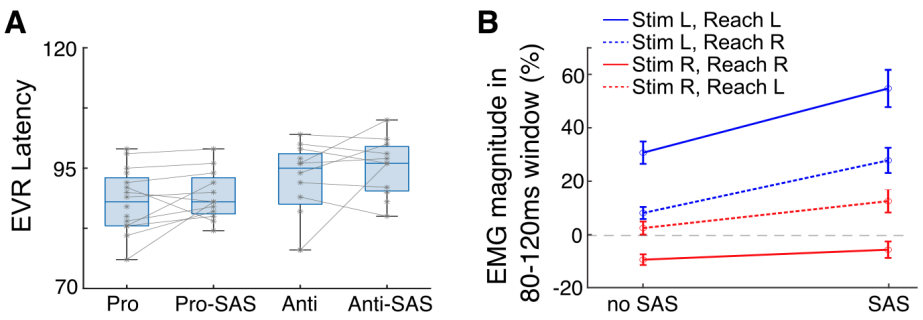

Figure 4. Quantification of the EVR in the Choice reaction task (Task A). Depiction of mean +/- standard error of the latency (**A**) and magnitude (**B**) of the EVR.

Relating EVR magnitude to movement RTs across SAS and non-SAS trials

Our task design in the Choice reaction task ensured that participants knew to generate a pro- or anti-reach on a given trial, but remained uncertain about whether the stimulus would emerge to the right or left. Despite this, participants generated pro-reaches with very short RTs (on average 142 ms or 154 ms with or without a SAS, respectively). When taking into account the electromechanical delay between the EMG signal and reach onset, this indicates that the forces arising from muscle recruitment during the EVR interval contributed to movement initiation. Prior research has also established a negative correlation between EMG recruitment in the EVR interval and the RT on pro-reach trials (Pruszynski et al., 2010; Gu et al., 2016). These considerations lead us to question the degree to which the shortened RTs on SAS trials were associated with concomitant increases in EVR magnitude. Our hypothesis of intersensory facilitation of the SAS and a subcortical visual signal predicts that RTs and EVR magnitudes are related by a uniform relationship, with SAS trials leading to shorter RTs on average simply because of larger EVRs. To put it another way, a trial with a given magnitude EVR should have the same RT, regardless of whether a SAS was presented or not.

To address this question, we conducted a within-participants analysis for leftward pro-reach trials, comparing the RTs on SAS and non-SAS trials that are matched for EVR magnitudes. For each participant, we binned the trials with respect to EVR magnitude (3 bins, bin width = 33%). Providing that there were sufficient SAS and non-SAS trials in a given bin (at least n = 1 of both), we derived the median RT for SAS and non-SAS trials in that bin. We then used a Wilcoxon signed-rank test to RTs across participants and bins (Fig. 5). RTs became faster with greater EVR magnitudes, but there were no significant differences between SAS and non-SAS trials (adjusted alpha = 0.05/ 3 = 0.0167; Bin 0-33, $p = 0.6221$; Bin 34-66, $p = 0.0582$; Bin 67-100, $p = 0.0967$).

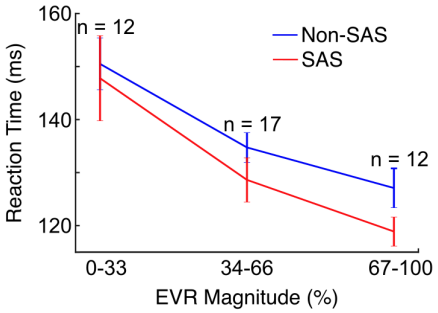

Figure 5. Negative relationship between RT and EVR magnitude, regardless of the presence of a SAS. For all subjects, we derived the median RT associated with a given EVR magnitude. Normalized EVRs were binned across 3 equal bins, and RTs and EVRs were tabulated separately for pro-left reaches with or without an accompanying SAS. See Results text for more details.

Generalized startle reflex activity in upper limb and neck muscles that precedes the EVR

While the finding of enhanced EVR magnitudes with SAS in leftward but not rightward targets (Fig. 4) argues against a generic effect on PEC recruitment in this time window of interest, we further explored whether the SAS elicited a reflexive startle response before the EVR. Here, we took advantage of our recordings not only from PEC, where activity is related to the reaching task, but also from our recordings of bilateral sternocleidomastoid (SCM). Although SCM recordings are commonly used to assess startle reflexes during StartReact experiments (for review see (Carlsen and Maslovat, 2019)), the typical time interval of such assessments largely overlap with the EVR and startle reflexes and therefore cannot be separated from potential stimulus-induced activity at the single trial level. We therefore explored the time course of averaged activity from PEC and bilateral SCM after stimulus emergence, pooling across pro- and anti-trials and side of stimulus emergence, but doing so separately for SAS and non-SAS trials. We normalized the average activity of these muscles to the activity in the 500 ms preceding stimulus presentation, and then subtracted the activity on non-SAS from SAS trials. This analysis produces a difference curve where any increase in EMG activity in the time after stimulus emergence is attributable to the presence of the SAS. As shown in Fig. 6, the presence of the SAS not only increased activity in the EVR interval (as expected, given the results in Fig. 4), but also increased both bilateral SCM and PEC activity in brief intervals before the EVR. To assess the significance of these results, we ran sample-wise signed-rank tests to identify where this excess activity was significantly different from 0 ($p < 0.05$) for at least 10 consecutive samples. In PEC we found significant SAS-induced activity for a brief interval between 30 and 50 ms after stimulus emergence, well before the EVR. In bilateral SCM, there was also brief and very early (starting at ~25 ms) increased EMG activity in SAS trials. After this response, we observed a later increase in EMG activity on SAS trials during the EVR interval only on left SCM, which began ~95 ms after stimulus emergence.

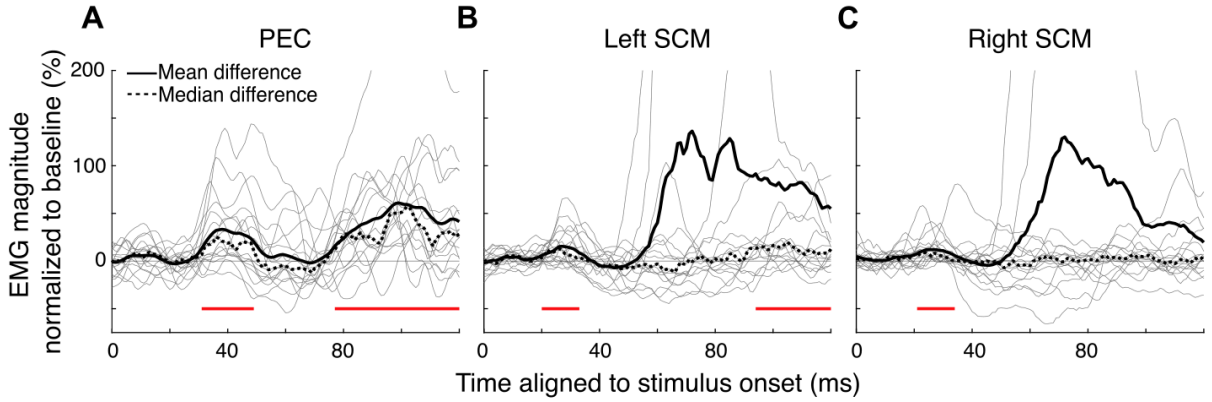

Figure 6. A SAS increases recruitment of left PEC and bilateral SCM activity before the EVR. Time-series of the difference in baseline-normalized EMG activity immediately after stimulus emergence due to the SAS, conducted separately for left-PEC (**A**), left-SCM (**B**), and right-SCM (**C**). In each subplot, thin lines show data from individual subjects, and red lines denote periods where significantly greater EMG activity was observed across our sample on SAS vs non-SAS trials.

Simple reaction task - performance, movement RTs, and EVR magnitudes

The StartReact phenomenon is most commonly observed on trials where subjects have foreknowledge of the requested response. In a separate block of trials, we therefore collected behavioral and EMG data from a Simple reaction task where stimuli always emerged to the left, to which participants responded with a left (pro-reach) or right (anti-reach) response, depending on the conveyed instruction. Compared to the Choice reaction task, we observed a large number of anticipatory responses (RTs < 80 ms; 36.9% vs 3.4% in Simple vs. Choice reaction task, respectively). Some subjects produced anticipatory responses more than half the time, hence we analyzed data only from the remaining 11 subjects that produced anticipatory responses on less than half of all trials.

We show data from a representative participant in Figure 7 (same participant as in Fig. 3). Behaviorally, the RTs on anti-trials are quite similar to those on pro-reach trials, and this participant did not generate wrong-way reaches toward the emerging stimulus on anti-reach trials (compare heatmaps and RTs in left columns of Figs. 3 and 7). Second, while prominent EMG recruitment during the EVR interval is apparent on pro-reach trials in the simple task (Fig. 7A,B), EMG recruitment during the EVR interval is absent on anti-reach trials (Fig. 7C,D). Thus, it appears that this participant fully prepared the motor program for the pro- or anti-reach before stimulus emergence. Finally, while the SAS further shortened RTs for both pro- and anti-reach trials, the SAS only augmented EMG activity during the EVR interval on pro-reach trials; we observed little to no increase in EMG activity in this interval following leftward stimulus emergence on anti-reach trials.

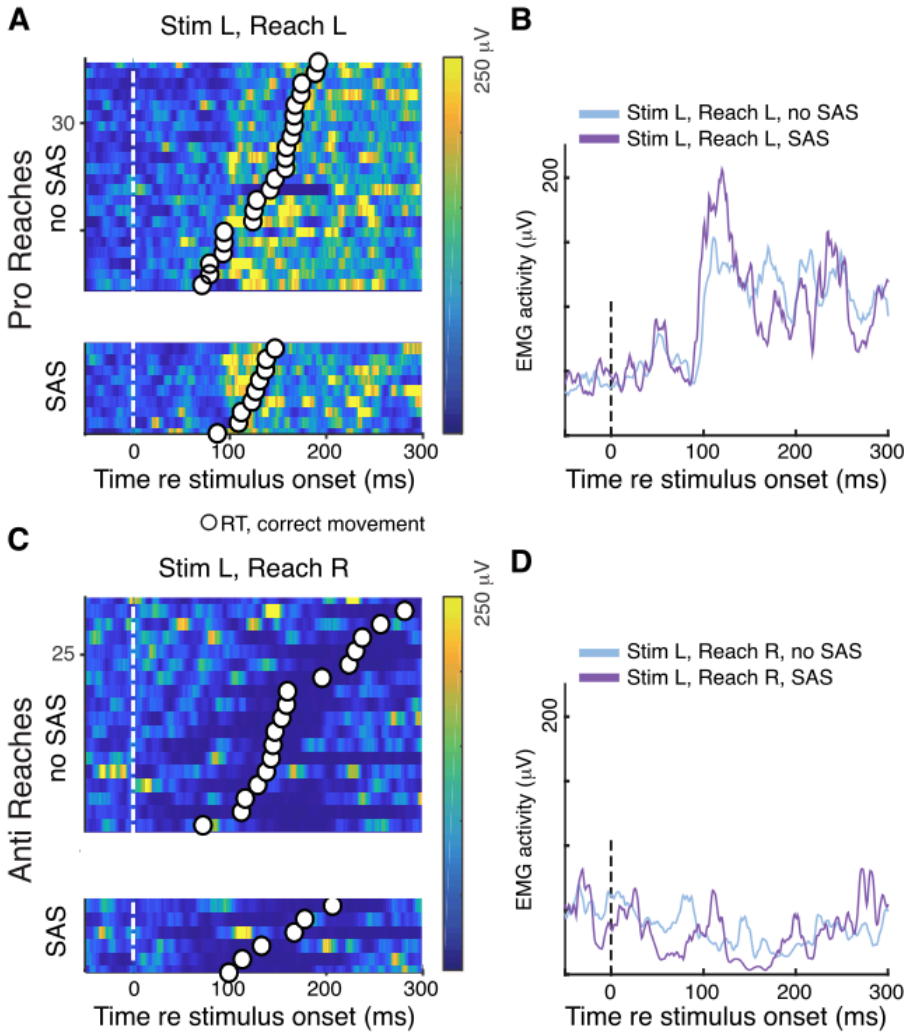

Figure 7. Representative EMG activity from the pectoralis muscle of an exemplar participant from Simple reaction task. Same participant and format as FIg. 3, excepting that a time-series ROC plot was not generated given the absence of trials with the stimulus emerging to the right.

We quantified the RTs and magnitude of EMG activity in the EVR interval across those 11 subjects that did not routinely anticipate stimulus emergence. The SAS significantly shortened RTs by 21 ms on average (Fig. 8A; SAS, β = -20.54, SE =3.32, p <0.001, 95% CI [-27.05, -14.0]), irrespective of the instruction (*SAS x instruction*, β = 1.98, SE =6.65, p = 0.767, 95% CI [-11.05, 15]) or the task (*SAS x task*, β = 10.58, SE =6.65, p =0.116, 95% CI [-2.44, 23.6]). There was an interaction effect between task and instruction (*task x instruction*, β = 48.06, SE =6.65, p <0.001, 95% CI [35.04, 61.1]); a post hoc analysis showed that, in contrast to the Choice reaction task, we observed no significant difference between the RTs of pro- vs anti-reach trials in the Simple reaction task (Fig. 8A; 141±7 ms in pro- vs 142±6ms in anti-reaches; p < 1.000). Further, RTs for both pro- and anti-reaches in the Simple reaction task were comparable to the RTs for pro-reaches in the Choice task (p = 1.000), whereas the choice anti-reaches showed significantly different RTs (Fig. 8A, p < 0.001).

In terms of EMG activity, PEC recruitment in the EVR interval across both tasks was significantly larger in pro- than in anti-reaches (*instruction*, β = -36.8, SE = 4.42, p < 0.001, 95% CI [-45.49, -28.174]). Yet,

this effect was dissimilar between tasks (*task x instruction;* β = 20.3, SE = 8.83, p = 0.025, 95% CI [2.97, 37.595]). While post-hoc tests showed that PEC recruitment was significantly different between pro- and anti-reaches in both tasks, the difference was greater in the Single than the Choice reaction task. Post hoc tests revealed differences between almost all conditions, including simple pro versus anti trials (p < 0.001) and choice pro versus anti-trials (p< 0.001). The only comparisons that did not show significant differences for the effect of task x instruction were simple and choice pro-reaches (p = 0.224), and simple pro-reach versus choice anti reach trials (p = 0.209). PEC recruitment was significantly larger in trials with SAS (*SAS*, β = 18.1, SE = 4.42, p < 0.001, 95% CI [9.46, 26.769]) and during the Choice task (*task*, β = 23.4, SE = 4.42, p < 0.001, 95% CI [14.74, 32.050]), with a significant interaction (*task x SAS;* β = 18.7 , SE = 8.83, p = 0.038, 95% CI [1.37, 35.994]). The SAS increased EVR magnitudes on all Choice task trial types (p> 0.001), but its pooled effect across Simple task trial types was neutral (p = 0.988). Finally, there was an interaction effect between SAS and instruction (*SAS x instruction*; β = -17.8 , SE = 8.83, p = 0.048, 95% CI [-35.12, -0.495]). The SAS had a potentiating effect on pro-reach trials when pooled across tasks (p > 0.001), while its pooled effect in anti-reaches across both tasks was neutral (p = 0.870). While this effect appears to be driven by lower PEC recruitment with SAS in the Simple task anti-reach trials (see the dashed cyan line in figure 8B), the three-way interaction did not reach significance (*SAS x instruction x task*; β = 28.4, SE = 17.67, p = 0.113, 95% CI [-6.26, 62.997]). In sum, in the Simple task anti-reaches (i.e. to the right), the SAS seems to expedite an RT that is comparable to pro-reaches, in parallel with lower PEC recruitment.

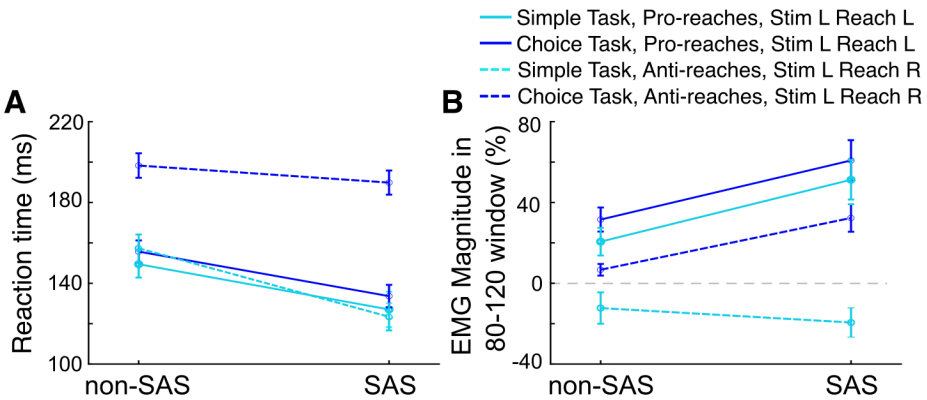

Figure 8. Quantification of behavior and EMG activity in Simple reaction task. Depiction of mean +/- standard error of RTs (**A**) and EMG magnitude in EVR interval (**B**). Light blue lines and symbols depict data from Simple reaction task . For comparison, dark blue lines and symbols depict data from Choice reaction task. The Choice reaction task data shown here are from the subset of 11 participants with sufficient data from the Simple reaction task, hence the subtle differences with Figs. 2 and 4.

Discussion

We examined the effect of a SAS on behavior and upper limb muscle activity as human participants made pro- or anti-reaches in an Emerging Target task. The task promoted reactive RTs and the generation of short-latency bursts of muscle activity termed EVRs, even on trials without a SAS. In separate blocks of trials, the side of stimulus emergence could be varied (a Choice reaction task where responses could not be fully prepared) or be fixed (a Simple reaction task permitting full response preparation). The SAS lowered RTs in both tasks (the StartReact effect), and increased the magnitude of EVRs without altering its timing. Our results affirm that the StartReact phenomenon

can be reliably evoked for reactive movements in Choice reaction tasks. We surmise that the subcortical visuomotor pathway that produces EVRs is sufficiently primed prior to stimulus emergence in the Emerging Target task. In such scenarios, the StartReact effect can arise from intersensory facilitation within the reticular formation between the SAS and visually-derived signals relayed along a subcortical visual pathway; advanced preparation of a specific motor response is not required.

Our RT results in a Choice reaction task (Fig. 2B) complement similar reports of a StartReact effect in the context of on-line lower limb corrections to displaced targets (Reynolds and Day, 2007; Queralt et al., 2008), demonstrating that this effect can be observed for reactive movements of the upper limb initiated from a stable posture. Given that a StartReact effect is generally not observed in Choice reaction tasks initiated from a stable posture (Carlsen et al., 2004, 2009; Forgaard et al., 2011; Maslovat et al., 2012; Marinovic et al., 2017)), what is distinct about the Emerging Target task? The Emerging Target task promotes a readiness to respond via strong top-down priming of a subcortical visual pathway due to implied motion and temporal certainty about the timing of stimulus emergence (Kozak et al., 2020; Contemori et al., 2021b). Consequently, pro-reach RTs with or without a SAS were essentially identical in both the Choice and Simple reaction tasks (Fig. 8). Similar facilitating effects of a SAS are also seen in launching interceptive actions (Tresilian and Plooy, 2006), and in promoting accurate responses in a forced RT paradigm (Heckman et al., 2023). All of these paradigms promote a degree of response urgency which may be an important factor in dictating reactive responses even without a SAS. As seen in the work by Heckman and colleagues (2023), a SAS in such scenarios can facilitate congruent movements directed toward a stimulus (pro-reaches in our case) or voluntary movements directed elsewhere (e.g., the RTs on correct anti-reach trials). Future studies of the StartReact phenomenon in clinical or neurophysiological settings may benefit from incorporating paradigms that promote a degree of response urgency. Conversely, presentation of a SAS may increase the probability of observing EVRs in stroke patients, given the facilitating effect of a SAS on upper limb movements in this population (Honeycutt and Perreault, 2012; Honeycutt et al., 2015; Marinovic et al., 2016).

Is it possible that subjects prepared these alternative motor programs in advance, which were released by the SAS? The primate brain can prepare alternative motor programs simultaneously (Cisek and Kalaska, 2005), and this idea could be directly tested by introducing more potential target locations. However, robust EVRs can be evoked even in the absence of any motor preparation and in scenarios where either limb could be moved (Kearsley et al., 2022; Selen et al., 2023), and a SAS facilitates accurate responses in conditions of multiple potential targets in forced RT paradigm (Heckman et al., 2023). Our data also show that a SAS did influence neck and upper limb muscle activity within 20-40ms, which we attribute to a non-specific acoustic startle reflex (Brown et al., 1991a, 1991b). However, this phase of recruitment was not direction specific even on PEC; direction specificity only emerged later, i.e. during the EVR interval, and even then the timing of the EVR was not influenced by the SAS. This absence of SAS effects on EVR discrimination time is consistent with the findings of Glover and Baker (2019). In the EVR interval, we also found that the SAS selectively increased PEC activity for leftward, but not rightward targets, regardless of whether participants were instructed to reach towards or away from the target. Thus, we saw no evidence of a “released” motor program. Our results speak to the SAS acting as an accessory stimulus that increases the excitation of the fast visuomotor network, such that it facilitates phases of muscle recruitment influenced by the emerging visual stimulus beyond the earliest startle reflexes. The fixed timing of the EVR reinforces

our supposition that the pathway underlying the EVR represents the shortest pathway capable of transforming visual inputs into target-directed reaching actions (Gu et al., 2018; Contemori et al., 2023).

Our recordings of upper limb muscle activity demonstrate a consistent relationship between the earlier phase of stimulus-directed recruitment, the EVR, and subsequent RT. In the Choice reaction task, the SAS enhanced EVR magnitude but not timing. Such enhancement correlated with reduced RTs (Fig. 2B), and the increased propensity for wrong-way errors on anti-reach trials (Fig. 2A). Importantly, these lower RTs as well as the increased wrong-way errors on anti-reaches were independent of target direction, which again speaks to the target-selective nature of EVR enhancement. These results affirm that the EVR, while brief in duration, leads to the production of relevant forces capable of initiating limb motion (Gu et al., 2016). Indeed, a trial-by-trial comparison of the relationship between EVR magnitude and RT shows that a given EVR relates well to a given RT, regardless of the presence or absence of a SAS (Fig. 5). While there are undoubtedly non-linearities in how muscles generate force, in the context of our experiment there appears a fairly straightforward explanation that the StartReact effect is largely due to the production of a larger EVR.

That being said, response preparation and notions of its involuntary 'release' with SAS still have an important role to play in the StartReact phenomenon. The impact of response preparation is most apparent in our experiment in the Simple reaction task, where (depending on instruction), left stimulus emergence requires a leftward pro-reach or a rightward anti-reach. Here, RTs on anti-reaches were ~50ms faster than in the Choice reaction task, and as fast as those on pro-reaches. Furthermore, the strong EVRs that are augmented by the SAS on pro-reach trials are fully absent on anti-reach trials, regardless of the presence or absence of the SAS (Figs. 7, 8). In the Simple reaction task, subjects had more than 2 seconds to consolidate the instruction to prepare for pro- or anti-reach trials, which apparently provides sufficient time on anti-reach trials to fully suppress the EVR to the leftward stimulus, which in this case acts as a signal to reach to the right. Such contextual suppression of the EVR resembles that observed in delayed reaching tasks (Pruszynski et al., 2010), and how EVRs from a given stimulus can be mapped onto different responses depending on task-relevant parameters (Gu et al., 2018; Contemori et al., 2023).

The reticular formation has been strongly implicated in both the StartReact effect (Valls-Solé et al., 1999; Nonnekes et al., 2015; Carlsen and Maslovat, 2019) and the phenomenon of EVRs (Corneil and Munoz, 2014; Contemori et al., 2023), hence it is a likely node for intersensory convergence between signals arising from the SAS and the emerging visual stimulus. Indeed, the reticular formation has the requisite efferent connections to the motor periphery to detail the task-appropriate motor commands that are hastened by the StartReact effect. Intersensory effects are also possible within the intermediate and deep layers of the superior colliculus, given its role in multisensory integration (Stein and Meredith, 1993) and inputs into startle circuitry (Fendt et al., 2001). Previous work examining multisensory integration in the SC of awake behaving monkeys has attributed the reductions in saccadic RT largely to changes in the timing and/or magnitude of saccade-related rather than visually-related signals (Frens and Van Opstal, 1998; Bell et al., 2005). However, such studies have used localizable acoustic stimuli with intensities <= 60 dB, hence the effect of a much louder SAS on visually-derived transients within the intermediate and deep layers of the primate SC is unknown.

Taken together, our results provide compelling evidence that the observed RT shortening with SAS in the presently studied Choice task could be attributed to intersensory facilitation of the fast

visuomotor network. EVR timing remained unaffected with SAS, and enhanced PEC recruitment was selective to left-sided target presentation, indicating that PEC recruitment was not triggered by the SAS, but by the emerging visual target. A limitation of this study is that we did not record EMG from the agonist muscles for rightward reaches (e.g. posterior deltoid). Yet, the results suggest that these recordings would mirror those from PEC, given the similar overall RTs as well as the similar SAS effects on RTs and wrong-way errors between leftward and rightward targets. Given our supposition of intersensory facilitation being the underlying mechanism of the observed RT shortening with SAS, why then have previous reports largely failed to observe the StartReact effect on Choice reaction tasks? A number of possible, and not mutually exclusive, explanations arise. First, a low level of response readiness in past tasks, perhaps due to the number of potential targets and/or uncertainty about the exact time of stimulus onset, engendered longer RTs which were generated after the SAS' influence had dissipated. Second, in the context of reaching movements, it is possible that the SAS did facilitate small or subthreshold signaling along a fast subcortical visuomotor pathway, but such signaling was not sufficient to produce forces to overcome the arm's inertia. This latter alternative could be tested by systematically manipulating stimulus properties or timing so that EVRs would or would not appear on trials with or without a SAS, respectively. Third, previous StartReact studies that did observe very fast RTs with SAS under Single but not Choice task conditions involved finger, wrist or elbow movements (Carlsen et al., 2004, 2009; Forgaard et al., 2011; Maslovat et al., 2012; Marinovic et al., 2017). As axial muscles are known to express stronger EVRs than distal muscles (Pruszynski et al., 2010), these movements may not equally benefit from SAS-induced facilitation of the fast visuomotor network. As such, and in agreement with the views expressed in recent review papers (Nonnekes et al., 2015; Marinovic and Tresilian, 2016; Carlsen and Maslovat, 2019), there may not be a single unifying mechanism underlying the StartReact phenomenon across paradigms and effectors.

FIGURE LEGENDS

Figure 1. Behavioral paradigm. At the start of each trial, participants acquired the central start position with their hand (grey circle), and fixated a small notch at the bottom of the barrier. The barrier color conveyed the instruction to reach toward (green barrier, a pro-reach) or away from (red barrier, an anti-reach) the stimulus (white circle) upon its emergence below the barrier. On 25% of trials, a starting acoustic stimulus (SAS; 119-120 dB) was presented at the time of stimulus emergence. In a block of Choice reaction task trials, the stimulus could emerge at either the left or right outlet with equal probability. In a block of Simple reaction task trials, the stimulus only emerged at the left outlet.

Figure 2. Behavioral results from Choice reaction task. Depiction of mean +/- standard error of error rates (**A**) and RTs (**B**). Errors are defined as anti-reach trials where participants initially moved incorrectly toward the emerging stimulus, and then corrected the movement in mid-flight to reach in the opposite direction. In **B**, the RTs of both the correct movement on anti-reach trials are shown (dashed blue and red lines), as are the RTs for the incorrect component of such error trials (cyan, pink dashed lines).

Figure 3. Representative EMG activity from the pectoralis muscle of an exemplar participant from Choice reaction task. EMG activity is shown in trial-by-trial heatmaps for pro-reach (**A**) and anti-reach trials (**C**). In each heat map, color conveys the magnitude of EMG activity aligned to stimulus emergence, with each row depicting an individual trial with trials ordered by the RT of the movement in the correct direction (white circles). Red circles on rows for anti-reach trials depict the RT of a wrong-way movement toward the emerging stimulus, which preceded the onset of the correctly-directed reach. Separate heat maps are depicted from trials with or without a SAS. **B, D**: Lines in the upper subplots depict the mean EMG activity for the four trial types. Lower subplots depict time-series ROC, calculated separately for trials with or without a SAS. Vertical red lines depict the time at which a change in time-series ROC was detected (values provided in each subplot).

Figure 4. Quantification of the EVR in the Choice reaction task (Task A). Depiction of mean +/- standard error of the latency (**A**) and magnitude (**B**) of the EVR.

Figure 5. Negative relationship between RT and EVR magnitude, regardless of the presence of a SAS. For all subjects, we derived the median RT associated with a given EVR magnitude. Normalized EVRs were binned across 3 equal bins, and RTs and EVRs were tabulated separately for pro-left reaches with or without an accompanying SAS. See Results text for more details.

Figure 6. A SAS increases recruitment of left PEC and bilateral SCM activity before the EVR. Time-series of the difference in baseline-normalized EMG activity immediately after stimulus emergence due to the SAS, conducted separately for left-PEC (**A**), left-SCM (**B**), and right-SCM (**C**). In each subplot, thin lines show data from individual subjects, and red lines denote periods where significantly greater EMG activity was observed across our sample on SAS vs non-SAS trials.

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