

# Rapid integration of face detection and task set in visually guided reaching

David Y. Mekhaieil<sup>1,2,3</sup> | Melvyn A. Goodale<sup>2,3,4</sup> | Brian D. Corneil<sup>2,3,4,5</sup> 

<sup>1</sup>Graduate Program in Neuroscience, Western University, London, Ontario, Canada

<sup>2</sup>Western Institute for Neuroscience, Western University, London, Ontario, Canada

<sup>3</sup>Department of Psychology, Western University, London, Ontario, Canada

<sup>4</sup>Department of Physiology and Pharmacology, Western University, London, Ontario, Canada

<sup>5</sup>Robarts Research Institute, London, Ontario, Canada

## Correspondence

Brian D. Corneil, Western University, London, Ontario, Canada.

Email: [bcorneil@uwo.ca](mailto:bcorneil@uwo.ca)

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## Abstract

The superior colliculus (SC) has been increasingly implicated in the rapid processing of evolutionarily relevant stimuli like faces, but the behavioural relevance of such processing is unclear. The SC has also been implicated in the generation of express visuomotor responses (EVR), which are very short-latency (~80 ms) bursts of muscle activity time-locked to visual target presentation. These observations led us to investigate the influence of faces on EVRs. We recorded upper limb muscle activity from healthy participants as they reached toward targets in the presence of a distractor. In some experiments, faces were used as stimuli. Across blocks of trials, we varied the instruction as to which stimulus served as the target or distractor. Doing so allowed us to assess the impact of instruction on muscle recruitment given identical visual stimuli. We found that responses were uniquely modulated in tasks involving high-contrast faces, promoting reaches toward or away from a face depending on instruction. Follow-up experiments confirmed that the phenomenon required highly salient repeated faces and was not observed to non-facial stimuli nor to faces expressing different affects. This study extends the hypothesis that the SC mediates the EVR by demonstrating that faces impact muscle recruitment at short latencies that precede cortical activity for face perception. Our results constitute direct evidence for the behavioural relevance of face detection in the brainstem, and also implicate a role for top-down cortical pre-setting of the EVR depending on task context.

## KEYWORDS

EMG, express visuomotor responses, human, superior colliculus, task set

**Abbreviations:** BF, Bayes factor; EMG, electromyography; EVR, express visuomotor response; MDES, minimum detectable effect size; RT, reaction times; SC, superior colliculus; TRSN, tecto-reticulo-spinal network.

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## 1 | INTRODUCTION

Orienting towards or away from objects and events in the world is so fundamental to an organism's survival that the ability to produce such movements has largely driven the evolution of sensory systems. When time is of the essence, ancient structures like the superior colliculus (SC) rapidly transform visual inputs into motor outputs, generating orienting reflexes by coordinating the rapid recruitment of muscles to facilitate low-latency gaze shifts (Corneil & Munoz, 2014; Gandhi & Katnani, 2011). A growing body of evidence suggests that the SC, via projections of the tecto-reticulo-spinal network (TRSN), can also influence the recruitment of limb muscles. In particular, it is thought that the SC and TRSN may mediate a reflex known as the express visuomotor response (EVR) in the muscles of the upper limbs that is temporally linked to the presentation of a visual stimulus. The EVR is short in latency (80–120 ms) and can be expressed as either an increase or decrease in muscle activation, depending on the location of the stimulus (Pruszyński et al., 2010). By modifying limb muscle activity, the EVR has been shown to contribute to the initiation of shorter latency reaches to suddenly appearing stimuli (Gu et al., 2016; Kozak et al., 2019).

Additional support for the hypothesis that EVRs are mediated by the SC and TRSN comes from the fact that low-spatial frequency and high-contrast stimuli, which are optimal for driving the magnocellular input to the SC, not only engender larger responses in movement-related layers of the SC and more frequent express saccades (Chen et al., 2018; Marino et al., 2012) but also evoke larger EVRs in the upper limbs (Kozak et al., 2019; Kozak & Corneil, 2021). In addition, priming and task set can affect the production of both express saccades (Meeter & Van der Stigchel, 2013) and EVRs (Contemori et al., 2021, 2023).

Recent work has expanded the understanding of the brainstem feature-detection system by showing that evolutionarily-relevant stimuli, like faces and snakes, evoke shorter latency orientation movements than other kinds of visual stimuli (Almeida et al., 2015; Bannerman et al., 2009, 2010; Martin et al., 2018). In addition, some neurons in the primate SC and pulvinar exhibit lower latencies (~50 ms) and larger bursts in response to faces than other visual stimuli (Almeida et al., 2015; Bogadhi & Hamed, 2023; Nguyen et al., 2013, 2014, 2016; Yu et al., 2024). These subcortical networks are thought to play a crucial role in the detection of faces and facial expressions in patients with lesions of the primary visual cortex (Celegnin et al., 2019). Taken together, these observations suggest that the SC responds to faces independently and well before face areas in the cerebral

cortex (Bentin et al., 1996; Collins & Olson, 2014; Decramer et al., 2021; Kato et al., 2004). Consistent with the fact that SC detects faces faster than other visual stimuli, faces evoke shorter-latency and more frequent express saccades (Salvia et al., 2020; VanRullen & Thorpe, 2001). Curiously, the saccadic preference for faces is most evident within saccadic choice paradigms, wherein participants look to an instructed target presented synchronously with a distractor (Crouzet & Thorpe, 2011). This suggests that express saccades to faces (and perhaps other visual stimuli) may be modulated by task set.

If EVRs in the upper limbs are also mediated by the SC and TRSN, then one might expect that they too will be affected by (1) the presentation of specific targets, such as faces, and (2) task set. In short, we predict larger EVRs in the muscles of the arm in instructed reaching tasks featuring faces, resulting in more vigorous muscle recruitment and thus more rapid reaching movements. Across five experiments, we employed various types of stimuli, including natural images of faces, high contrast cartoon faces, and other non-face images to test the influence of these image categories on the EVR.

Our results largely support our predictions, supporting the conjecture that face detectors in the SC/TRSN mediate the initiation of EVRs when face targets are presented. As with express saccades (Crouzet & Thorpe, 2011), the effect of faces was found only during choice conditions and not in single target conditions. In choice conditions, the EVR caused a larger increase in muscle activity when the instructed target was on the preferred side of the muscle and a larger decrease in muscle activity when the instructed target was on the non-preferred side of the muscle. Intriguingly, this demonstrates that top-down control, based on instruction or task set, can modify how the EVR directs movement towards or away from faces.

## 2 | MATERIALS AND METHODS

### 2.1 | Participants

Five experiments were conducted in this study. University students were recruited using the Psychology Research Participant Pool. All participants provided informed written consent and were free to withdraw from the study at any time. Participants were compensated financially or with research credits required for course completion. All procedures were approved by the Health and Science Research Ethics Board at the University of Western Ontario and followed the guidelines set by the Declaration of Helsinki. All participants had

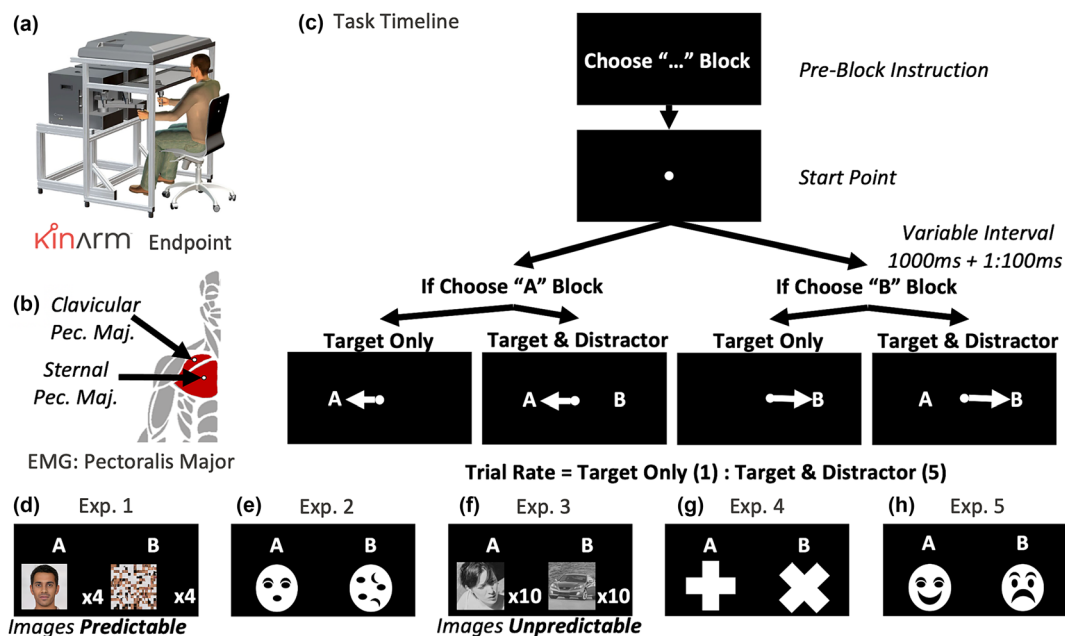
normal or corrected to normal vision and reported no neurological or motor disorders.

For experiment 1, data from a cohort of 20 participants were collected (female: eight, male: 12; mean age: 23 years, SD: 4.68; right-handed: 18, left-handed: two). Experiments 2 and 3 were completed in the same session by a second cohort of 20 participants (female: nine, male: 11; mean age: 18.3 years, SD: .86; right-handed: 16, left-handed: three, ambidextrous: one). Finally, experiments 4 and 5 were completed in the same session by a third cohort of 20 participants (female: nine, male: 11; mean age: 18.45 years, SD: .76; right-handed: 18, left-handed: two). No participant participated in more than one of the aforementioned three cohorts. These cohorts do not include data from six participants who were excluded: one for a resting tremor, one for failing to understand the task, and four for having a trial exclusion rate above 50%. We predicted a relatively small effect size; therefore, our sample size of 20 subjects was selected because it sits at the upper end of the standard sample size in EVR literature which typically included 15–20 subjects (Contemori et al., 2021, 2023; Gu et al., 2016; Kearsley et al., 2022; Selen et al., 2023). A post hoc sensitivity analysis was

conducted to determine the minimum detectable effect size (MDES) of the EMG frequentist analysis for all experiments. We found that the true effect size was always larger than the MDES, indicating that this sample size was appropriate to detect our effect of interest (see Supplementary Materials).

## 2.2 | Apparatus

The experiments were conducted using a Kinarm end-point robot (Figure 1(A); BKIN technologies, Kingston, Ontario, Canada). A Propixx projector (VPixx, Saint-Bruno, Quebec, Canada) integrated within the Kinarm platform enabled presentation of high-quality visual stimuli and ensured reliable event timing. A photodiode was employed to verify the exact time the stimuli appeared in each trial. Behavioural tasks were generated using Stateflow and Simulink within MATLAB (version R2021a, MathWorks Inc., Natick, MA, USA). The experimental paradigms were projected onto a horizontal surface which was approximately at shoulder level to the participants when seated.



**FIGURE 1** Experimental apparatus and task: (a) All data was collected while participants made planar reaches with their right arm in a Kinarm End-Point Lab. (b) Surface EMG activity was recorded from the sternal and clavicular heads of right pectoralis major muscle, which increases/decreases in activity prior to leftward/rightward reaches. (c) Participants were instructed to reach towards one of two targets (or target categories) at the beginning of each block. Participants initiated each trial by moving the Kinarm manipulandum to the start point. After a variable interval of time the target appeared to the right or left either on its own (target only; ~17% of all trials) or with a distractor on the opposite side (target and distractor; 83% of all trials). (d–h) Stimuli employed in each of the five experiments. Across blocks, each image or image category could serve as either the target or the distractor. In experiments 1 and 3, image categories were used (e.g., different faces could appear in conditions involving faces). In experiment 1, the target and distractor images changed *between blocks*, but remained predictable *within* a block of trials. In experiment 3, the target and distractor images were randomized *within* a block of trials, and hence were unpredictable. Stimuli in experiment 3, adapted from Crouzet and Thorpe (2011). EMG, electromyography.

All participants made reaches with their right arm, regardless of handedness. Surface electromyography (EMG; Delsys Inc. Bagnoli-8 system, Boston, MA, USA) recordings of the right pectoralis major muscle were acquired in two locations: the clavicular head and the sternal head of the muscle (Figure 1(b)), which were identified using palpation. EMG data were filtered using a high- and low-pass filter of 20 and 450 Hz, respectively, and then digitized at 1000 Hz onto the Kinarm system.

Participants completed the experiments using a manipulandum under the display surface to control a cursor (Figure 1(c)). An occluder obscured view of their hand and of the manipulandum. A constant force of 2 N towards the participant and 5 N towards the right was applied to the arm by the manipulandum throughout the experiments to induce baseline muscle activity in the right pectoralis. Kinematic data from the manipulandum were recorded at a rate of 1000 Hz by the Kinarm system. Eye movement data were not recorded.

## 2.3 | Experimental design

Five experiments were designed to test how EVR activity differed in response to (1) different types of visual stimuli and (2) task set based on block instruction delivered to the participant.

Since it is our hypothesis that the EVR is mediated by the SC, the experiments drew inspiration from studies investigating saccadic eye movements and the visual response properties in the SC (Crouzet & Thorpe, 2011; Nguyen et al., 2013, 2014, 2016; Salvia et al., 2020; VanRullen & Thorpe, 2001).

All experiments required the participant to make reaching movements towards a prescribed target or target category (Figure 1(d–h)). Participants initiated each trial by aligning the Kinarm manipulandum within a 2-cm diameter starting point for 500 ms. They were instructed to fixate their gaze on the start point until the reach target appeared. Following a variable time of 500–600 ms (hence, the total time at the start point was between 1000 to 1100 ms), the target appeared either to the left or to the right of the starting point. The temporal uncertainty was used to reduce the occurrence of anticipatory reaches. In 17% of trials, the target appeared on its own. In the remaining 83% of trials, a target and distractor appeared simultaneously. The ratio of target only trials to target and distractor trials was 1:5. The centre of the target and/or distractor was 10 cm away from the centre of the starting point, this translated to  $\sim 9.5$  degrees of visual angle from the centre of the starting point to the centre of the target or distractor. Participants then responded. The trial ended once the cursor contacted the target or the distractor.

Before each experiment, participants completed a practice session of 100 trials. Each experiment then consisted of 480 trials including 400 target and distractor trials and 80 target-only target trials. The experiments were broken up into eight blocks of 60 trials (50 target and distractor, 10 target only), after which the instructed target was alternated (e.g. a “choose face” block was followed by a “choose car” block). Following four experimental blocks, the participants were given a timed 5-min break. Within a given experiment, block order was alternated between participants. In experimental sessions where participants completed more than one experiment, the order of the experiments was likewise alternated between participants.

## 2.4 | Experimental stimuli

For experiment 1, we examined the EVR to natural looking images versus their scrambled counterparts. We used “Generated Photos” AI to generate faces of four individuals, two men and two women of varying ethnic backgrounds. To generate the scrambled counterpart, each image was broken up into a grid and the squares within were randomized. Within each block, only one of the four faces with its corresponding scrambled image were presented so that the target was predictable to the participant.

In experiment 2, we used a simplified version of experiment 1, using geometric shapes arranged to either resemble a face, or arranged randomly into an abstract figure. The use of geometric shapes in experiment 2 allows us to control for spatial frequency and luminance without reduction in image clarity. High contrast images of this type have been found to elicit higher neural activity in the SC of the monkey when compared to natural images of faces (Nguyen et al., 2013, 2014, 2016; Van Le et al., 2020).

In experiment 3, we selected images from the same visual database (Corel Photo Library) used by Thorpe and colleagues to investigate saccades (Crouzet et al., 2010; Crouzet & Thorpe, 2011). Images in this database were normalized for variations in luminance and spatial frequency. Ten images of faces and ten images of cars were selected. The images of faces selected included five men and five women of varying age and ethnicity. The pictures of faces and cars were made unpredictable through randomization, with each image appearing one or two times within a single experimental block either as a target or distractor. In alternating blocks, participants were instructed to reach either towards the face or the car.

In experiment 4, we investigated if the EVR differentiates between the same geometric shape in two different orientations (e.g., a “+” or “x”). In experiment 5, we

investigated if the EVR is influenced by geometric faces displaying *happy* or *sad* affect.

## 2.5 | Kinematic analysis

All analyses were completed using MATLAB (version R2021a, MathWorks Inc., Natick, Massachusetts, United States of America). On each trial, a white stimulus that was unseen by the participant appeared simultaneously with target and distractor onset and was detected by a diode. All kinematic and EMG data were aligned to diode onset.

Inclusion and exclusion criteria for trials was determined using the kinematic output from the Kinarm manipulandum. The second derivative of the horizontal position within the workspace was used to determine the horizontal acceleration of the participant's arm. The mean acceleration for the 100-ms preceding target onset to 50-ms following target onset for all trials was used to identify the baseline variation in acceleration for each participant. Movement onset was detected when hand acceleration increased beyond the 95% confidence interval of the baseline mean acceleration for the participant. A graphical user interface was used to confirm and adjust, if necessary, the onset and offset of movements.

Trials were labelled as "false start" and excluded if the participant initiated a movement from 100-ms preceding target onset to 120-ms following target onset. We excluded "too fast" trials where the reaction time (RT) was between 120 and 150 ms. Trials were labelled as "wrong way" and excluded if at any point following target onset the participant's hand moved towards the distractor. These two criteria ensured that EMG activity during the EVR epoch was not contaminated by voluntary movement related activity. Exclusion of "too fast" trials did not have any impact on the findings of the study since the mean RT across all experiments for target and distractor trials was greater than 200 ms.

An additional spatial analysis was conducted to ensure that muscle recruitment related to anticipation did not influence our analysis of the EVR. Since a participant's hand may drift outside of the starting position slowly, thus remaining below the acceleration threshold, their hand may leave the starting position without the preceding analysis registering a movement. Given that both the cursor and starting position had a radius of 1 cm, we also identified trials where the centre of the cursor was 2 cm or more from the middle of the starting point before the participant made their final movement towards the target. Such trials were labelled as "unstable" and were also excluded. The rate of "unstable" trials exceeded 50% for five participants in experiment 1, six

participants in experiments 2 and 3, and two participants in experiments 4 and 5. For these participants, we opted to retain the data from these subjects including the unstable trials. However, we re-ran all analyses after excluding all data from these participants and confirmed that doing so did not alter our main findings (results not shown).

## 2.6 | EMG filtering and normalization

Offline, EMG data were full-wave rectified and then filtered by a 7-point moving average filter.

EMG data were normalized on a trial-by-trial basis to the EMG activity counteracting the constant torque applied to the arm by dividing the EMG signal over the entire trial by the mean activity in the 100-ms preceding stimulus onset. Since results did not vary between the sternal and clavicular recordings, the two EMG recordings were then averaged.

## 2.7 | Analysis of the EVR

Previous work analysing the EVR typically contrasts trials where a stimulus appeared to the right or left. In the current study, we are aiming to determine whether the EVR on target-distractor trials is influenced by the features of the presented stimuli and by the block instruction to reach towards a specific stimulus. Thus, a key comparison will be to examine EMG activity when the exact same stimuli are presented to the retina. In planar reaching tasks, limb muscles are recruited in a direction-dependent manner (Selen et al., 2023). For right pectoralis major, it is maximally recruited for leftward movements, and recruitment decreases prior to rightward movements (recall that flexion of the right pectoralis muscle results in adduction of the right shoulder and therefore will be recruited for leftward, cross-body reaches). Therefore, we predict that the EVR on the pectoralis muscles should be larger when the block instruction requires that the participant reach to the stimulus on the left rather than the right.

Based on previous behavioural and neurophysiological studies, we expect that the influence of stimulus features and block instruction on the magnitude of the EVR to be relatively small within any given subject (Contemori et al., 2023; Kozak & Corneil, 2021). We therefore used group analysis methods which are more sensitive to small differences, relying on paired comparisons using both frequentist and Bayesian approaches.

For our frequentist approach, we conducted a time-wise paired *T*-test to analyse the effect of block instruction on mean muscle activity for each millisecond within

the EVR epoch (80–120 ms following stimulus onset). This was followed by a Benjamin and Hochberg false discovery rate correction ( $p\text{-crit} = .05$ ).

Bayesian statistics, although having a limited history of implementation in the literature within similar contexts, have many advantages. Unlike frequentist statistics with which we can only reject a null hypothesis or fail to reject it, Bayesian statistics allows us to quantify the level of certitude with which we believe a null hypothesis ( $M_0$ ) or alternative hypothesis ( $M_1$ ) is true. Additionally, sequential Bayesian statistics allow us to reiteratively sample participants until the “Bayes factor” (BF) or the ratio between the two-competing hypotheses remains stable within a given value range. Providing such stability is reached, the final statistical conclusion would not change with the addition or removal of a small number of participants. The visualization of Bayesian statistics is also a good test to see if a given result is consistent with iterative sampling. Finally, Bayesian statistics are non-parametric and therefore are a more flexible model for data analysis.

Bayesian analyses were conducted in Matlab R2021a using the function BayesFactor v.2.3.0 (Krekelberg, 2022). Our Bayesian analysis consisted of a one-sided paired  $T$ -test to compare the effects of block instruction on EMG magnitude. The model uses a multivariate Cauchy prior with a scale of  $\sqrt{2}/2$  ( $\sim .7$ ) to calculate the  $JZS$ -BF, as described by Jeffreys (1998) and Zellner and Siow (1979). The location of the instructed target was the independent variable, and the EMG magnitude was the dependent variable. Given EMG data for reaches to the left ( $EMG_{Left}$ ) and reaches to the right ( $EMG_{Right}$ ), the BF was calculated using two different models (our two hypotheses):

**Null hypothesis** ( $M_0$ ):

$$EMG_{Left} \leq EMG_{Right}$$

**Alternative hypothesis** ( $M_1$ ):

$$EMG_{Left} > EMG_{Right}$$

Given data ( $D$ ), the BF can be calculated as such using the posterior probabilities ( $Pr$ ) of both models. For the purpose of this study, we calculated the inverse of the standard  $B_{01}$  ( $B_{10}$ ), meaning that the BF is directly proportional to the probability of  $M_1$ .

$$BF = B_{10} = \frac{Pr(D|M_1)}{Pr(D|M_0)}$$

This analysis was run sequentially with the addition of each participant (from  $N = 1$  to  $N = 20$ ) for a time

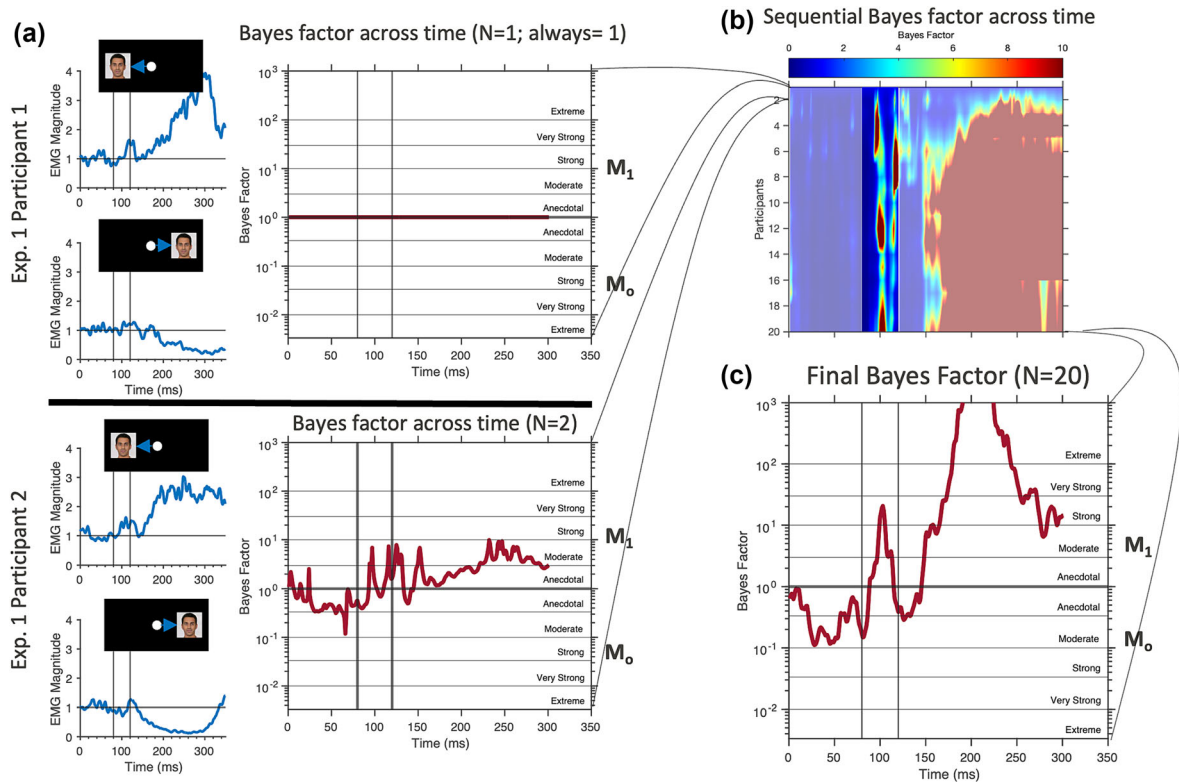
spanning from 500 ms before to 1000 ms after target onset. The validity of the final BF for each time point (including all participants) can be verified by looking at how the BF changed over time with the iterative inclusion of each participant.

To demonstrate this group Bayesian analyses, we present an analysis using the target only conditions for experiment 1 (Figure 2). The left most column (Figure 2(a)) shows the mean EMG for correct target-only face trials where the target was on the left or right for the first two participants, in the order of sampling. As previously discussed, one advantage of Bayesian analyses is that they can be run sequentially, therefore allowing us to visualize how the BF changes with iterative sampling and across each time point. The second column demonstrates the BF across time with the inclusion of the first participant only ( $N = 1$ ) and the first two participants ( $N = 2$ ). The boundaries in the y-axis describe the heuristic classification scheme for the BF indicating level of support for either  $M_0$  or  $M_1$ , from “anecdotal” to “extreme” (Jeffreys, 1998). These values are also visualized in the heatmap (Figure 2(b)), where the EVR epoch (80–120 ms) is bolded. The heatmap is scaled for a BF of 0 to 10 (blue to red), meaning that red value would indicate, at minimum, “strong” support for our alternative hypothesis.

To ensure the validity of the final BF, we should observe consistent values with sequential sampling (the addition of new participants). For instance, this is confirmed through the consistent red banding during the EVR epoch. Plotting the final BF across time with the inclusion of all participants ( $N = 20$ ) demonstrates that we observe moderate evidence for  $M_0$  before the EVR epoch. We then observe two BF peaks, the first during the EVR epoch indicating “strong” support for  $M_1$  and the second during the voluntary response epoch (150 ms+) indicating an “extreme” likelihood of  $M_1$ . The distinction between the two BF peaks is consistent with the difference observed during the EVR epoch not being driven by the voluntary motor response. These results are in line with our subjective observations of EMG activity during target only trials (Figure 2(a)), where there are distinct increases of activity during leftward reaches and decreases in activity during rightward reaches in both the EVR and voluntary movement epochs.

### 3 | RESULTS

Recordings in the primate SC show that presentation of face or face-like stimuli can influence the vigour of visual responses within <50 ms (Almeida et al., 2015;

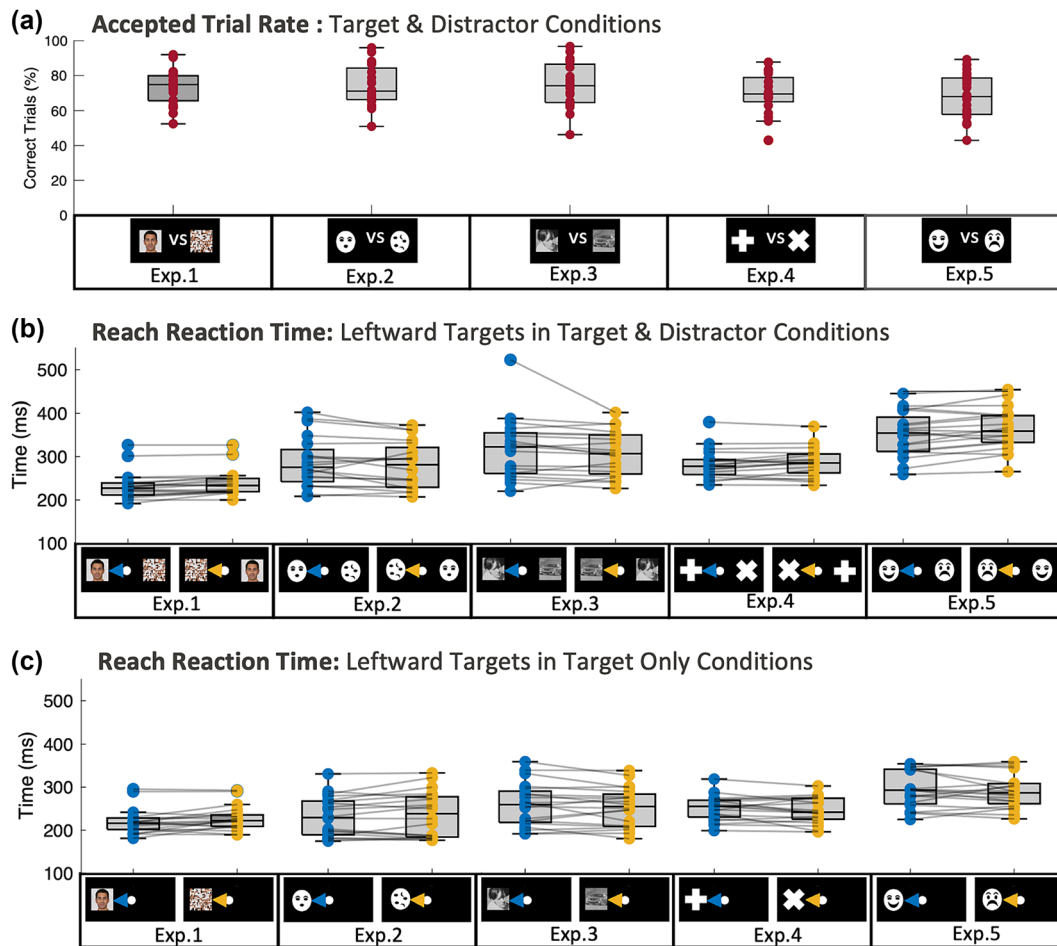


**FIGURE 2** Demonstration of sequential Bayesian analysis of EMG recruitment across time using target-only trials in experiment 1: (a) Blue traces in the left-most column show mean EMG activity for two participants for target-only trials to the left (upper subplots) or right (lower subplots). The red lines in the second column from the left show the Bayes factor through time. When data from only one subject is considered (upper plot), the Bayes factor is always equal to 1. Given the first participant's data as a posterior, with the inclusion of the second participant, the *BF* indicates a moderate effect of the conditions on the EMG activity during the EVR epoch, favouring  $M_1$  as expected since the right pectoralis major muscle is recruited for leftward reaches. (b) Such time courses are created for the sequential inclusion of each participant, which can be viewed by a heatmap where the colour displays the value of the Bayes factor as a function of time after stimulus presentation (x-axis) and the number of included participants (y-axis). A value of 10 ( $10^1$ ) or higher indicates a "strong" impact of target location; note how evidence for this occurs during the EVR epoch (80–120 ms), as indicated by the red banding in the bolded region. (c) The Bayes factor as a function of time when data from all 20 participants is included. Here, a Bayes factor between 10 and 30 during the EVR epoch indicates a "strong" likelihood of the alternative hypothesis; that muscle activity in the right pectoralis major is higher when a face is presented to the left vs to the right. The Bayes factor gets even higher ( $> 100$ , or  $10^2$ ) during subsequent phases of muscle recruitment ( $> 150$  ms after stimulus onset), which is expected given the recruitment of right pectoralis major for leftward reaches. BF, Bayes factor; EMG, electromyography; EVR, express visuomotor response.

Nguyen et al., 2014, 2016; Yu et al., 2024). Given that the tecto-reticulo-spinal pathway is hypothesized to mediate the EVR on the upper limb (Corneil & Munoz, 2014; Pruszynski et al., 2010), we investigated if presentation of face-or-face-like stimuli influence the magnitude of the EVR. We recorded surface EMG from the right pectoralis major muscle, which is active during leftward movements, during a reaching choice task. Across five experiments, human participants were instructed to reach toward a target defined by various features, often in the presence of the distractor presented on the opposite side. In different blocks, we interchanged the instructed target, allowing us to compare the influence of block instructions on the EVR given the exact same visual inputs.

### 3.1 | Consistent error rate across experiments

Across all five experiments,  $\sim 75\%$  of target and distractor trials met our acceptance criteria (Figure 3(a)). Of the trials that did not meet our acceptance criteria, we rejected  $\sim 2\%$  of all trials as anticipatory,  $\sim 1\%$  of all trials that moved all the way to distractor, and  $\sim 22\%$  of trials composed of multiple movement segments (e.g. the subject initially moved to the distractor and then moved to the target). Rejecting these trials ensured that we were examining trials where participants consolidated the block instruction to move toward a specific target feature and ensured that EMG activity related to anticipation did not influence muscle recruitment during the EVR window



**FIGURE 3** Analysis of performance: (a) Error rate for target-distractor conditions for experiments 1–5. Mean leftward reaction times for correct movements in each condition for each experiment for either target-distractor (b) or target-only (c) trials. Since the manipulandum was loaded to the right, we analyzed leftward reaches. We used repeated measures ANOVA to analyse the effects of target types and presence of a distractor on RT and error rate. Each dot and line connect data from a single participant. ANOVA, analysis of variance; RT, reaction time.

(80–120 ms after target onset). As will be discussed at the end of the results section, inclusion of 22% of trials where the participant first inappropriately moved to the distractor did not change the overall interpretation of our results.

We performed a two-way repeated measures ANOVA in each experiment to analyse the effect of target type and the presence of the distractor on error rate. The analysis showed that target type did not have a statistically significant effect on error rate in any experiment (all  $P > .458$ ), while the presence of the distractor resulted in a statistically significant increase in error rate across all experiments, when compared to target-only trials (all  $F_{1, 76} > 13.16$ ,  $P < .001$ ). There was no statistically significant interaction in any experiment (all  $F_{1, 76} < .90$ ,  $P > .345$ ).

### 3.2 | RT differences

Next, we examined the pattern of RTs across all experiments (Figure 3(b,c)), focusing on leftward reaches since we measured the recruitment of the right pectoralis major muscle. Within each experiment, we are specifically interested in whether RTs vary as a function of the block instruction, and by the presence or absence of a distractor. We therefore ran a two-way repeated measures ANOVAs to examine the effect of instructed target type and the presence or absence of the distractor.

Although we predicted that limb movements towards faces would be initiated more rapidly than towards the scrambled image, we did not observe any statistically significant effect of the instructed target on RT (all  $F_{1, 76} < 1.14$ ,  $P > .288$ ) in any experiment. It is worth noting,



however, that before correction for multiple comparisons, the RTs for leftward movements to faces in experiment 1 were significantly shorter than the leftward RTs for scrambled faces in both the target only ( $t_{19} = -2.10$ ,  $P < .05$ , pre-correction) and the target plus distractor conditions ( $t_{19} = -3.66$ ,  $P < .001$ , pre-correction). In the target and distractor condition of experiment 5, the RTs for leftward movements to happy faces were shorter than leftward movements to sad faces ( $t_{19} = -2.65$ ,  $P < .05$ , pre-correction). No other comparisons were significant before correction. Finally, the presence of the distractor did have a statistically significant effect on RT, delaying RTs in experiments 2–4 (all  $F_{1, 76} > 17.02$ ,  $P < .001$ ); this effect approaches significance in experiment 1 ( $F_{1, 76} = 3.65$ ,  $P = 0.06$ ). There was no statistically significant interaction in any of the experiments (all  $F_{1, 76} < .44$ ,  $P > .509$ ).

### 3.3 | The EVR persists on target-distractor trials

Recall that participants performed the task while their right arm was loaded with a constant force that increases the recruitment of right pectoralis major. In Figure 4(a), we show the data from a representative participant in experiment 1. As a consequence of the loading force, the EVR on target-only trials is easily identified as a brief increase or decrease in EMG activity  $\sim 100$  ms after target presentation to the left or right, respectively. Even on single trials, this initial phase of muscle recruitment is more aligned to target onset than movement onset.

The representative example in Figure 4(a) displays a prominent rebound of EMG activity following rightward target-only presentation, similar to what has been observed previously (Wood et al., 2015). The key features of the EVR observed on target only trials mirror those described previously (Contemori et al., 2021; Gu et al., 2016; Kearsley et al., 2022; Kozak et al., 2019, 2020; Kozak & Corneil, 2021; Pruszynski et al., 2010). The EVR is followed by a phase of voluntary muscle activity  $>150$  ms after target onset, in which an increase or decrease in muscle activity of the right pectoralis directs the arm to the left or right, respectively.

Figure 4(b) shows data from conditions where the target and distractor were presented simultaneously on opposite sides. Somewhat surprisingly given the presentation of diametrically opposite stimuli, we still observed a prominent band of recruitment in the EVR epoch (80–120 ms) on target-distractor trials, which was also clearly separable from the subsequent phase of reach related activity. Importantly, this first phase of recruitment was

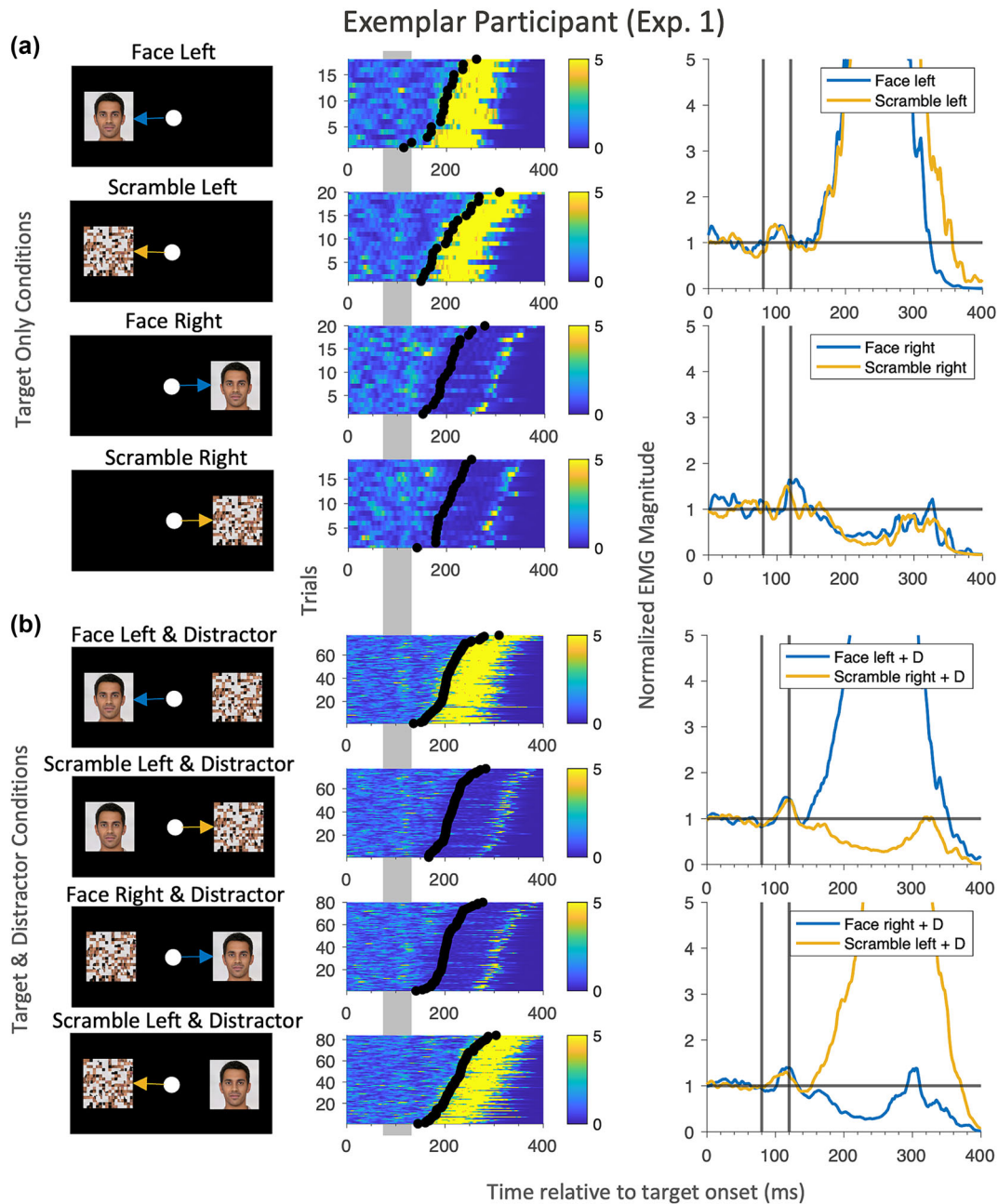
not obviously lateralized and was largely similar across all four possible configurations of stimuli and block instruction. This observation resembles a recent report of EVRs following the presentation of identical diametrically opposed visual stimuli (Selen et al., 2023). Given that the timing of such activity and the general profile of recruitment (e.g. an  $\sim 30$ -ms increase in activity more time-locked to stimulus than movement onset) are very similar to the EVR on target only trials (Figure 4), this shows that the EVR persisted in this participant on target-distractor trials. Similar patterns were observed in all participants, in all experiments.

### 3.4 | Task set modulates the EVR in face-related reaching tasks

Having established that the EVR persists in the target and distractor conditions, we analysed the effect of block instruction in these conditions. As shown in Figure 1, our experimental structure, which was inspired by the 2011 study of Crouzet and Thorpe, enables us to compare the EVR given the exact same visual images but different block instructions. Consider for example trials in experiment 1 where the “face” is presented on the left and the “scramble” is presented on the right; participants should reach leftward in the “choose face” block but rightward on “choose scramble” block. Comparing such trials isolates any effect of the block instruction on the EVR. Our hypothesis predicts larger EVR on the right pectoralis major muscle when the face target is to the left versus the right.

#### 3.4.1 | Group analysis: Experiment 1

We start with the group outcomes from experiment 1, which contrasted the EVR to an expected face versus a scrambled image of this face. For each participant, we quantified the magnitude of the EVR by integrating EMG activity in a window from 80 to 120 ms (Figure 5(a)), and plotted response magnitude to the exact same visual stimulus as a function of the block instruction. As shown in the first two rows of Figure 5(a), we observed significantly larger EVR across to a leftward face in the “choose face” block (i.e. when the participant reached to the left) than in the “choose scramble” block (i.e. when the participant reached to the right;  $t_{19} = 3.15$ ,  $P < 0.01$ ). An influence of block instruction was not seen when the scrambled image was present to the left (Figure 5(a)), as we observed comparable magnitude EVRs in both the “choose face” and “choose scramble” blocks ( $t_{19} = .25$ ,  $P = .803$ ).



**FIGURE 4** Exemplar participant in experiment 1: representation of muscle recruitment for (a) target-only conditions and (b) target and distractor conditions. Middle column shows data in a heatmap, where each row depicts single-trial normalized muscle recruitment in colour aligned to target onset (0 ms), ordered by RT (black circles). The EVR epoch is shaded in grey. Rightmost column shows normalized muscle activity with the EVR epoch (80–120 ms) demarcated by the vertical black lines. EVR, express visuomotor response; RT, reaction time.

The third and fourth rows of Figure 5 show the  $BF$  for a paired  $t$ -test plotted across time with sequential sampling (upper subplot) and the final  $BF$  ( $N = 20$ ) across time (lower subplot). As reflected by the red banding during the EVR epoch in the upper plot, there was a consistent effect of block instruction with sequential sampling (addition of participants to the analysis). The final  $BF$  peaks during the EVR epoch at 113 ms with a  $BF = 272$  indicating an “extreme” likelihood of the effect of block instruction on EVR expression when the face is presented

to the left. However, only “anecdotal” evidence of an effect was seen in the comparison where the scramble was presented to the left ( $BF = 1.17$ ,  $t = 98$  ms).

### 3.4.2 | Group analysis: Experiment 2

Serving as a follow-up to experiment 1, experiment 2 employed high-contrast face symbols, which elicit a stronger response in the SC as well as larger magnitude

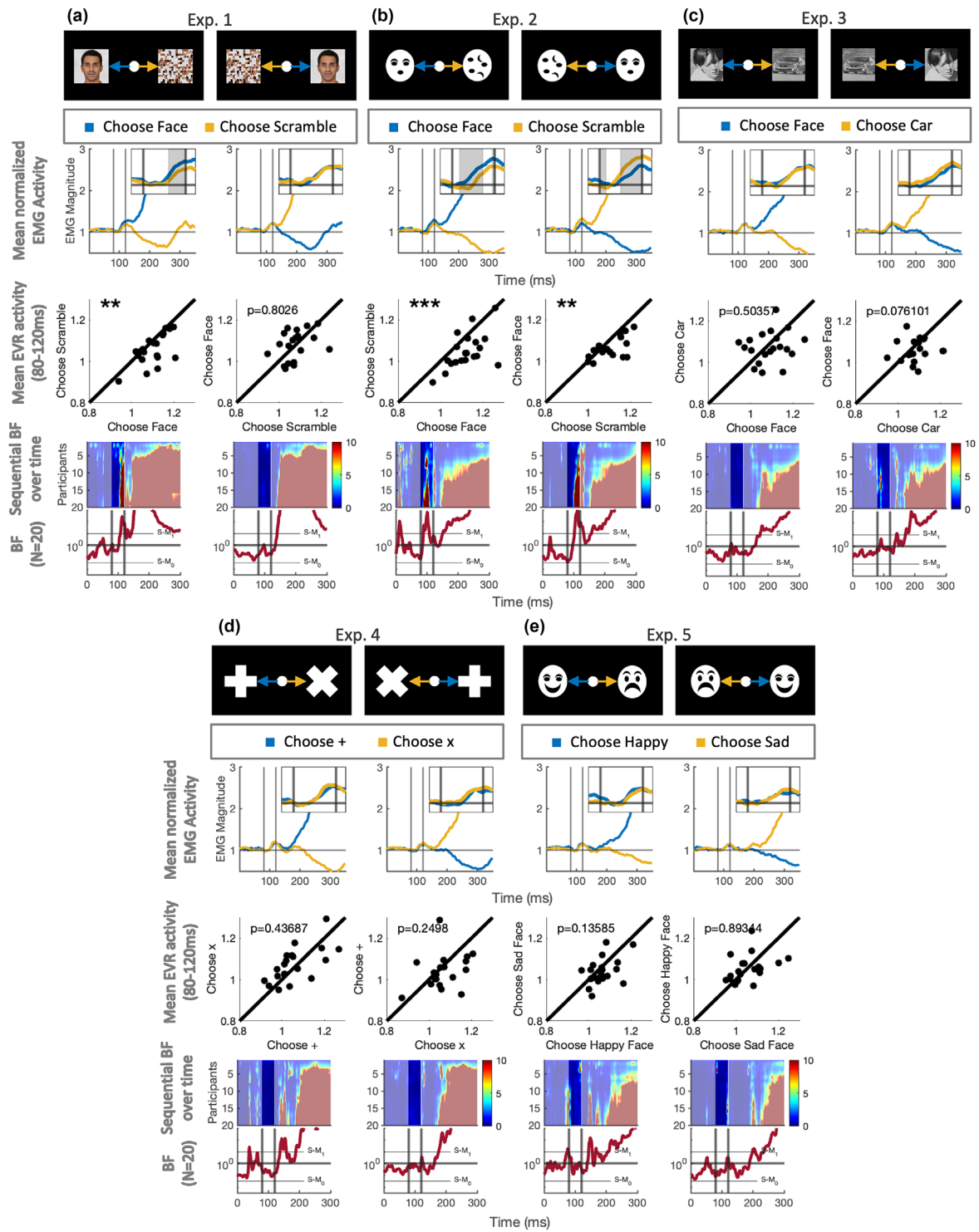


FIGURE 5 Legend on next page.

EVRs compared to low contrast images (Kozak & Corneil, 2021; Nguyen et al., 2014; Wood et al., 2015). We predicted that we would observe a larger face-related effect in experiment 2 than experiment 1. As can be seen in the upper two plots of Figure 5(b), our frequentist analysis finds a significant influence of block instruction given the same visual stimuli in “choose face” blocks (e.g. significant effects are seen when the instructed stimulus appears on the left;  $t_{19} = 4.30$ ,  $P < 0.001$ ). However, unlike experiment 1, we also observed a significant influence of block instruction in “choose scramble” blocks ( $t_{19} = 3.17$ ,  $P < 0.01$ ). Similarly, using the Bayesian analysis in the bottom two rows of Figure 5(b), red banding during the EVR epoch in the upper plot indicates a consistent effect of block instruction with iterative sampling. In the bottom plot, for both comparisons, the  $BF$  peaks during the EVR epoch above 100, indicating an “extreme” likelihood of an effect on block instruction on EVR expression (face left:  $BF = 636$ ,  $t = 101$  ms; scramble left:  $BF = 1328$ ,  $t = 112$  ms). Therefore, there was an “extreme” likelihood that block instruction resulted in a higher EMG magnitude when the participant is instructed to reach to the leftward image vs. instructed to reach to the rightward image, regardless of block instruction.

Could our results from experiments 1 and 2 simply be due to early voluntary muscle activity influencing muscle recruitment during the EVR epoch? Two aspects of our results argue against this. First, the vast majority of RTs on target-distractor trials are  $> 200$  ms; as with previous work, we excluded trials with RTs between 120 and 150 ms to ensure that voluntary muscle activity did not influence recruitment during the EVR epoch. Second, the timecourse of the  $BF$  through time does not simply increase monotonically. Instead, for both experiments 1 and 2, after the peak during the EVR epoch, the  $BF$

decreases to  $\sim 1$  at around 140 ms following stimulus onset. It then increases again around the time of voluntary movement onset (150 ms). Thus, the difference in EMG magnitude observed during the EVR epoch is distinct from that observed due to voluntary movement activity that proceeds it.

### 3.4.3 | Group analysis: Experiments 3

Experiments 1 and 2 used highly salient repeated targets. Experiment 3 aimed to test if the face effect would extend to non-repeated, less salient targets. In any given trial of experiment 3, the targets and distractor were unpredictable to the participant, whereby any one of 10 faces or 10 cars could be presented as target or distractor. Unlike experiments 1 and 2, there was no significant effect of block instruction on the EVR in the frequentist analysis. Similarly, the  $BF$  did not indicate a strong likelihood of an effect of block instruction or the null hypothesis ( $1/10 < BF < 10$ ).

### 3.4.4 | Group analysis: Experiments 4 and 5

In experiment 2, we saw an effect of block instruction when one image was a face and the other was a scrambled image. Perhaps the EVR would reflect a similar preference for any instructed target, independent of content, as long as the target is predictable (unlike in experiment 3), or perhaps the strong effects in experiment 2 reflect some aspect of facial affect. We therefore conducted experiments 4 and 5. In experiment 4, we used two highly salient abstract objects (+ vs. x), and in experiment 5, we used face symbols of different affect (happy vs. sad). No effect of block instruction was observed for experiments

**FIGURE 5** Group frequentist and Bayesian analyses for experiments 1–5: *The first row* for each experiment indicates the mean of mean normalized EMG activity for all participants in target and distractor conditions. Each column contains statistical comparisons of conditions where the exact same images were presented to the participant, but where the participant had received different block instructions preceding the trial (e.g. reach to the face vs. reach to the scramble in experiment 1). The EVR epoch (80–120 ms) is demarcated with two black lines. Grey shading in the EVR epoch signifies time points identified as significantly different, using a rolling paired two tailed  $t$ -test followed by a Benjamin Hochberg false discovery rate correction ( $p\text{-crit} = 0.05$ ). *The second row* shows a scatter plot of the mean muscle activity for each participant for each of the two conditions. Significant observations or  $P$ -values from a paired two-tailed  $t$ -test ( $*P < 0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$ ). *The third row* for each experiment shows a  $BF$  for a one-tailed  $t$ -test to identify time points at which block instruction impacted EMG magnitude. An increase in the  $BF$  above  $10^0$  (or 1) indicates higher likelihood of  $M_1$ ; that is, that the EMG magnitude was higher when the participant was instructed to reach towards the target that is on the left versus the target on the right. A  $BF$  lower than  $10^0$  indicates a higher likelihood of the null hypothesis. The  $BF$  changes over time relative to stimulus onset and with the addition of every sequential sample (participant). Red banding during the EVR epoch shows that the Bayes factor consistently indicates a “strong” likelihood of the  $M_1$ . *The fourth row* for each experiment shows the  $BF$  across time with the inclusion of all participants ( $N = 20$ ). The three horizontal lines indicate  $BF = 10^0$  (no evidence for  $M_1$  or  $M_0$ ) and “strong” evidence for  $M_1$  ( $BF = 10/1$ ) and  $M_0$  ( $BF = 1/10$ ) are indicated above and below  $10^0$ , respectively. BF, Bayes factor; EMG, electromyography; EVR, express visuomotor response.

4 and 5. No significant effect was found in our frequentist analysis, and the  $BF$  indicates that the likelihood that block instruction had any effect on muscle activity during the EVR epoch (80–120 ms) was “anecdotal” for either  $M_1$  or  $M_0$  (Figure 5(d,e);  $1/10 < BF < 10$ ).

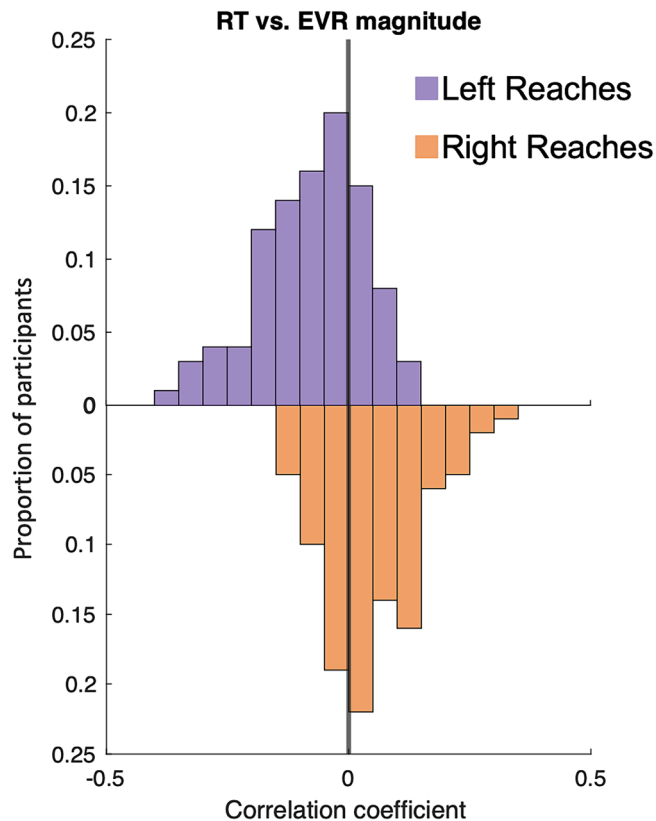
### 3.5 | EVRs facilitate lower latency voluntary responses

The EVR has been found in previous studies to correlate with RT, consistent with the EVR leading to the development of forces that aid arm movement initiation (Contemori et al., 2021; Kearsley et al., 2022; Kozak & Corneil, 2021). To contextualize our findings, we conducted a cross-experiment analysis of the correlation coefficient between RT and EMG magnitude during the EVR epoch (80–120 ms). We found that there was a significant within-subject negative correlation between RT and EVR magnitude on target and distractor trials when the instructed target was on the left ( $t_{99} = -6.86$ ,  $P < 0.001$ ) and a significant positive correlation when the instructed target was on the right ( $t_{99} = 5.18$ ,  $P < 0.001$ ), using a two-tailed one-sample  $t$ -test (Figure 6).

### 3.6 | Alternative group analysis

While we did observe an effect due to faces and instruction in experiments 1 and 2 with our first analysis, we were concerned that our trial exclusion criteria inadvertently biased the results. This possibility seems unlikely, since the analysis did not yield a similar effect in experiments 3–5, despite similar trial exclusion rates. To confirm the validity of our finding, however, we repeated all our analyses after adopting less conservative trial exclusion criteria, including trials where the participants moved part way toward the distractor before correctly reaching toward the target (these trials constituted 22% of all trials).

Despite the inclusion of these trials, we observe similar trends in our analysis. For experiments 1 and 2, the frequentist analysis indicates a significant effect of block instruction when the face is on the left and the scrambled image is on the right (Figure 7(a,b)). Our Bayesian analysis indicates that there is a “strong” likelihood of an effect of block instruction during the EVR epoch when the face was on the left in experiment 1 (face left:  $BF = 29$ ,  $t = 113$  ms; scramble left  $BF = 1.0$ ,  $t = 98$  ms) and a “very strong” and “moderate” likelihood of an effect of block instruction in both comparisons in experiment 2 (face left:  $BF = 38$ ,  $t = 101$  ms; scramble left:  $BF = 6$ ,

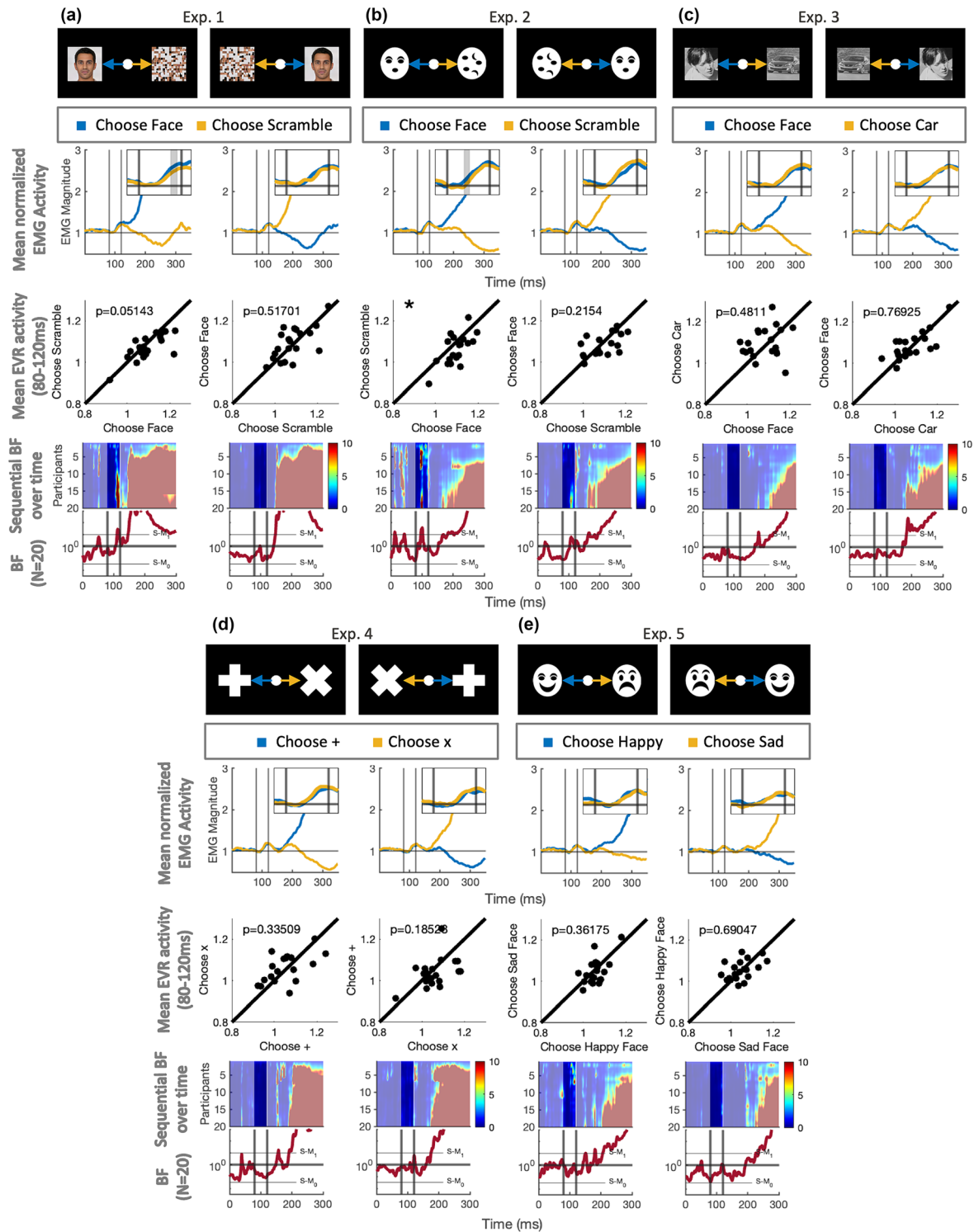


**FIGURE 6** Correlation of RT with EVR magnitude: Histogram of subject-wise Pearson’s correlations between RT and EVR magnitude of correct-trials for participants in all five experiments, split by the location of the instructed target. EVR, express visuomotor response; RT, reaction time.

$t = 108$  ms). As with our initial analysis, the alternative analysis yielded null findings in experiments 3–5 (Figure 7(c–e)).

## 4 | DISCUSSION

Our working hypothesis is that the EVR is evoked by visual input via the tecto-reticulo-spinal pathway. Our prediction of a face preference for the EVR was inspired by findings of a reported increase in the number of express saccades to faces versus other stimuli, such as vehicles (Crouzet et al., 2010; Crouzet & Thorpe, 2011), and enhanced visual responses to faces in the SC (Nguyen et al., 2014, 2016; Van Le et al., 2020; Yu et al., 2024). Across five experiments, we quantified the EVR in a task requiring participants to reach toward an instructed target in the presence of a distractor. Across blocks, instruction varied as to which stimulus was the target. We found that block instruction influenced the EVR when one target was a salient, repeated face (Figure 5(a,b)), in support of our hypothesis.



**FIGURE 7** Alternative group analyses for experiments 1–5: Group analysis as in Figure 5, including trials where the participants moved part-way towards the distractor.

#### 4.1 | EVRs are evoked by diametrically opposed stimuli

Our experimental findings with respect to task set relied on the EVR being present on trials in which both an

instructed target and a distractor were present. We presume that the EVR to the target stimulus in such tasks reflects how the TRSN integrates visually related activity evoked simultaneously in each SC. When stimuli are equally weighted with respect to activity across the SC,

as appears to be the case in experiments 3, 4, and 5, the EVR remains unaffected by the instructed target. In short, stimulus weighting in the SC and TRSN appears to be biased both by the nature of the stimuli and by the instruction on a particular block of trials. Put another way, one target (but not both) has to be an evolutionarily-relevant stimulus, such as a face, and this stimulus has to be predictable for an instruction bias to be evident.

We did not measure muscles that act as antagonists to the pectoralis muscle, and hence do not know if co-contraction is occurring during the EVR interval. Our loading of the pectoralis muscle meant that the EVR could consist of an increase or a decrease in recruitment. The correlations we observed (Figure 6) between the amplitude of the EVR and RT strongly suggest that the EVR resulted in forces that impacted subsequent reaching movements.

## 4.2 | Faces impact the EVR in a task-dependent manner

As discussed earlier, the main evidence for an influence of faces on the EVR comes from experiments 1 and 2, in which we found larger EVRs on target and distractor trials when faces were presented on the left in the choose face block than in the choose scramble block (experiment 1) and larger EVRs on target and distractor trials when the instructed target was presented on the left, regardless of whether the instructed target was an intact or scrambled face (experiment 2). This raises the possibility that the feature detector underlying the EVR may be capable of identifying a wide range of stimuli. Follow-up experiments demonstrated that the larger EVRs for the instructed target in experiments 1 and 2 could not be attributed to task difficulty nor could they be elicited by just any instructed object. Thus, we did not find an instructed target effect on the EVR with the repeatable, salient non-face objects used in experiment 4 (Figure 5(d)), despite similar RTs and error rates as those observed in experiments 1 and 2. In experiment 5 (Figure 5(e)), our observation of no influence of instructed facial affect (happy vs. sad) on the EVR resonates with recent studies showing that the SC by itself can distinguish between evolutionary relevant objects (faces) and abstract objects (scrambled images) but cannot easily distinguish between abstract objects or faces of expressing different affect, with the possible exception of fearfulness and threat (Soares et al., 2017; but see Webb et al., 2022). Presumably then, in experiment 5, the activity invoked in the left and right SC by happy and sad faces would be equivalent.

## 4.3 | The importance of stimulus salience and predictability

Although the presence of a face and instruction influenced EVR magnitude in experiments 1 and 2, no effect was observed in experiment 3 where faces were also present. In other words, we did not observe an effect of task set even though faces were sometimes the instructed target. We speculate that these results could have arisen because of stimulus salience and/or predictability resulting in an interaction between faces and task set. With respect to salience, several studies have shown that low-spatial frequency, high-contrast stimuli evoke larger magnitude EVRs, more express saccades, and stronger visual responses in the movement-related layers of the SC (Chen et al., 2018; Marino et al., 2012; Meeter & Van der Stigchel, 2013; Webb et al., 2022).

The stimuli used in experiment 3 were not nearly as salient as those in experiment 1 or 2. Moreover, in both experiments 1 and 2, the two images (intact face vs. scrambled face) did not change within blocks of trials, whereas in experiment 3, 20 different images of faces and cars were randomly presented, making the target and distractor on any one trial unpredictable. Thus, any task set in experiment 3 would have to be invoked at the category rather than the exemplar level, a computation that might be more difficult for the SC/TRSN circuitry (Nguyen et al., 2014). The effect of target predictability was also observed behaviourally: as reach RTs were longer for experiment 3 in the target and distractor conditions than they were in experiments 1 and 2 (Figure 3(b)). Future studies should systematically investigate how stimulus salience and predictability independently affect feature detection in the neural mechanisms giving rise to the EVR.

## 4.4 | Top-down and bottom-up effects on the EVR

The EVR is influenced by both bottom-up processes related to stimulus properties and top-down instructions (Contemori et al., 2023). This resembles the process of express saccade generation, wherein the magnitude of the express response depends on both the bottom-up visual response in the SC and baseline activity in the SC as established by task set (Munoz et al., 2000). Our current findings reinforce that the top-down signal modulates the bottom-up responses when faces are present; this modulation is necessary to explain results from experiment 2, where a larger EVR is evoked when the instructed stimulus appears on the left in both the “choose face” and “choose scramble” blocks. We surmise

that the instruction to move to the scrambled face is akin to responding in an anti-reach task (Gu et al., 2016), in which the EVR is muted.

We presume such a top-down influence in the setting of SC activity comes from ample projections from the frontal cortex, which is involved in the implementation and selection of task sets (Cameron et al., 2015; Johnston & Everling, 2006; Postle, 2005; Wallis et al., 2001) and basal ganglia, which codes for task urgency and reward expectation (Hikosaka et al., 2000; Kawagoe et al., 1998; Thura & Cisek, 2017; Yasuda & Hikosaka, 2015). It is unlikely that these areas produce the bottom-up effect since EVR latencies are shorter than visual response and face detection latencies in the primate prefrontal cortex (Blanke et al., 1999; Heekeren et al., 2006) and basal ganglia (Kunimatsu et al., 2023).

While visual response latencies in the SC are short enough to produce the EVR (Cecala et al., 2023), it is unclear if this arises from retinotectal projections to the superficial SC, as in mice (Cazemier et al., 2024), or from the retino-geniculo-striate pathway (White et al., 2017). Recent findings that SC face responses disappear after temporary lesions of the lateral geniculate nucleus (LGN; Yu et al., 2024) are not definitive, since such lesions abolish all bottom-up visual responses in the SC (Schiller et al., 1974). The loss of SC visual responses after LGN inactivation could arise from the loss of reticulo-geniculo-striate signalling and/or an increase in contralateral SC inhibition of the ipsilateral SC as seen in the Sprague effect (Goodale, 1973; Schiller et al., 1974; Sprague, 1966).

#### 4.5 | Evolutionary underpinning of rapid face-related orienting

Despite the physiological and behavioural correlates supporting our finding, a key question remains: what advantage does the EVR's ability to facilitate reaching towards or away from faces confer? A possible answer lies in literature on the SC and its role in reaching and full-body movement. The SC contains reach and grasp neurons, firing strongly when the hand touches an object in their receptive field (Kutz et al., 1997; Nagy et al., 2006; Stuphorn et al., 1999, 2000; Werner, 1993; Werner, Dannenberg, & Hoffmann, 1997). SC microstimulation can evoke varying degrees of full-body movement across a variety of species, including monkeys, cats, rodents, snakes, frogs, goldfish, and lampreys (Courjon et al., 2004; Cowie & Robinson, 1994; Dacey & Ulinski, 1986; Dean et al., 1986; Ewert & Arbib, 2013; Herrero et al., 1998; Saitoh et al., 2007; Schaefer, 1970; Syka & Radil-Weiss, 1971; Tehovnik & Yeomans, 1986).

Activity in the primate SC and mesencephalic reticular formation correlates with the EMG signals in the upper limbs (Stuphorn et al., 1999; Werner, Hoffmann, & Dannenberg, 1997). Recent studies in humans have reported that EVRs can be distributed bilaterally in reaching tasks (Kearsley et al., 2022) and lower limbs during visually guided stepping (Billen et al., 2023), consistent with the involvement of the reticulospinal system.

Our results indicate that early face detection in the SC may serve the ecological purpose of aiding rapid orienting of the gaze axis. To the best of our knowledge, the SC is the only region projecting directly to the reticular formation that can both rapidly identify a target (Nguyen et al., 2014, 2016; Van Le et al., 2020; Yu et al., 2024) and direct orienting movements (Bogadhi et al., 2021; Herman et al., 2018).

## 5 | CONCLUSION

We conclude that the sensorimotor pathway underlying the EVR can rapidly initiate reaching in response to faces in a task-dependent manner. This pathway does so at latencies far shorter than those associated with face detection in the cortex (Kato et al., 2004). Previous electrophysiological studies have shown a short latency response to faces in the primate SC (Nguyen et al., 2014, 2016; Yu et al., 2024). This evidence has been interpreted as support for the idea that the SC aids cortical face detection by tagging (Yu et al., 2024) or preferentially filtering (Nguyen et al., 2014, 2016) relevant spatial locations via ascending tecto-thalamo-cortical projections. Our results align with this work and link the rapid processing of faces in the SC to rapid recruitment of upper limb muscles.

#### AUTHOR CONTRIBUTIONS

Conceptualization — DYM, MAG, BDC; data curation — DYM; formal analysis — DYM; funding acquisition — MAG, BDC; investigation — DYM; methodology — DYM, MAG, BDC; project administration — MAG, BDC; resources — MAG, BDC; software — DYM; supervision — MAG, BDC; validation — MAG, BDC; visualization — DYM; original draft — DYM; review and editing — DYM, MAG, BDC.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ejn.16497>.

## DATA AVAILABILITY STATEMENT

Data sets and Matlab code for group analysis and figures can be found on figshare ([doi.org/10.6084/m9.figshare.25854739.v1](https://doi.org/10.6084/m9.figshare.25854739.v1)).

## ORCID

Brian D. Corneil  <https://orcid.org/0000-0002-4702-7089>

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