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The Express Sensorimotor Response Selects Visual Features Based On Instruction

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Abstract

In time-sensitive situations, *orienting reflexes* allow us to move rapidly in response to stimuli. The *express sensorimotor response (ESR)* is an orienting reflex presenting as a brief burst of muscle recruitment. Previous studies have identified commonalities between ESRs and *express saccades*, another orienting reflex.

In this study, we investigate if ESRs share in a characteristic of express saccades: preference for faces. In separate blocks, participants were instructed to reach toward one of two simultaneously appearing targets: a face and another image. Muscle activity in the pectoralis major muscle of the reaching arm was recorded using skin surface EMGs.

We found that the ESR, occurred in greater amplitude towards the instructed target, regardless of whether the instructed target was a face or not. While we found no evidence that ESRs preferer faces, our surprising finding demonstrates that ESRs can be modified by top-down modulation to identify stimulus features based on instruction.

Keywords: Express Sensorimotor Response, Express Saccades, Reaching, Superior Colliculus, Brainstem

Summary for Lay Audience

In time-sensitive situations, we rely on fast reflexes to respond in a short amount of time. This study investigates the *express sensorimotor response (ESR)*, a reflex that happens in the body muscles when something suddenly comes into our view. More specifically, we investigate if ESRs are more likely to happen if a person sees a face, since faces are more likely to cause other reflexes. To investigate, we instructed participants to reach toward one of two suddenly appearing images: a face and another image.

We found that an ESR occurred within 80ms in all situations. The ESR was stronger in the direction of the instructed target to direct the arm towards it, regardless of whether the instructed target was a face or not. Thus, while we found no evidence that the ESR prefers faces, we surprisingly found that the ESR can respond to a wider range of images than we expected.

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List of Abbreviations

ATL	Anterior Temporal Lobe
BG	Basal Ganglia
EMG	Electromyography
ESR	Express Sensorimotor Response
FFA	Fusiform Face Area
NHP	Non-Human Primate
OFA	Occipital Face Area
PFC	Prefrontal Cortex
SC	Superior Colliculus
SCd	Deep Superior Colliculus
SCi	Intermediate Superior Colliculus
SCs	Superficial Superior Colliculus
SNr	Substantia Nigra Pars Reticulata
V1	Primary Visual Cortex

1 Chapter 1: Introduction

1.1 Orienting

The ability to orient in space predates humans by more than 2 billion years. Being able to detect, identify, and move in response to stimuli in the world is so fundamental to an organism's survival that it has largely driven the evolution of our senses. In essence, our vision did not evolve simply to allow us to 'see' our environment, but to allow us to navigate, find food, avoid predators, and mate more successfully (Goodale & Humphrey, 1998). This evolutionary pressure also created systems that ensured the efficient functioning of these senses and use of the acquired information by integrating sensory systems with motor systems. For instance, the oculomotor system has evolved to optimize image acquisition by the retina, ensuring that the eyes orient to keep targets of interest in the line of sight through the integration of information from many sources such as visual, proprioceptive, motor inputs (Corneil & Munoz, 2014).

In humans and other mammals, orienting is mediated by several sophisticated mechanisms which take in sensory information and move the body accordingly to achieve specific goals or avoid harm. The initiation of movement often involves the convergence of multiple inputs via the spinal cord or brainstem to the muscles, with no one region holding a monopoly on the process. Broadly speaking orienting can be initiated on three levels: in the cerebral cortex, subcortical structures, and the spinal cord. Cortically meditated orienting involves high-order high-latency (150ms +) processing by multiple senses, allowing for the execution of complex and contextually appropriate movements. Cortical orienting is typically voluntary, requiring volitional initiation of movement by the motor cortex via the corticospinal tract (Hatsopoulos & Suminski, 2011). Cortical orienting would include behaviour such as picking up a cup or kicking a ball. On the other end of the spectrum, spinal orienting occurs reflexively and with incredibly low latency (30ms - 60ms), allowing for physical responses without sensory information needing to travel to the brain. Spinal reflexes are critical for the avoidance of painful stimuli and the efficient execution of cortical commands by making rapid adjustments in response to perturbations during movement (Forgaard et al., 2015; Skljarevski & Ramadan, 2002; Weiler et al., 2021). An example of a spinal reflex is the withdrawal reflex observed when one steps on a sharp object like a nail, retracting the leg in contact with the painful stimulus and extending the other leg. While the aforementioned modes of orienting serve important roles in helping us interact with the world, they are not sufficient for all situations. Cortical orienting is too slow, limiting its contribution to movements in response to sudden stimuli. On the other hand, spinal orienting is executed with a scarce amount of information since it lacks multisensory integration, depending largely on somatosensory input. Subcortical orienting bridges this gap, allowing for low-latency orienting (80-120ms) which takes into account low-level computations of sensory inputs and task sets, such as instructions needed to understand, plan for, and complete a given behavioural task. (Arber & Costa, 2022; Gomi, 2008; Scott, 2016).

1.1.1 The Hub of Subcortical Orienting: The Superior Colliculus

The subcortical hub for orienting movements is a pair of nuclei in the brainstem known as the superior colliculi (SC). While the SC has been very thoroughly studied as it relates to saccadic eye movements, the exact role of the SC in the initiation of subcortical orienting remains in question. This is because the SC sits at a crossroads between several neural systems. Firstly, the SC receives sensory inputs from multiple sources; visual information directly from the retina via the optic nerve as well as indirectly from the primary visual cortex (V1), somatotopic information from the spinal trigeminal nucleus, and auditory information from the inferior colliculus (Kustov & Robinson, 1996). Secondly, the SC is tightly integrated with several other subcortical brain structures including various regions of the striatum and the thalamus. Finally, contained within the SC are several different regions which interact to produce the output initiating the orienting response (Gandhi & Katnani, 2011; May, 2006). The way the SC may be translating visual and top-down input into reflexive-orienting commands is not fully understood. There is sufficient evidence, however, to construct a general model of the functional organization of the SC.

Broadly speaking the SC is organized along three different axes: deep to superficial, lateral to medial, and rostral to caudal. Inputs and outputs in the superior colliculus vary along these axes. This is in addition to the variation of connections across ipsi- and contra-lateral brain structures (May, 2006; Oliveira & Yonehara, 2018). In the superficial to deep axis, the SC is divided into seven different laminar layers, which are conventionally grouped into three subgroups: three superficial layers (SCs), two intermediate layers (SCi), and two deep layers (SCd) (May, 2006). The SCs contains a retinotopic map made up of visual neurons that fire in response to visual stimuli in the visual field. This retinotopic map is derived from visual input received both directly from the retina and also indirectly through cortical input from the primary visual cortex (V1) and thalamic input from the lateral geniculate nucleus (Ito & Feldheim, 2018). The second subregion of the SC, the SCi, contains a topographic map which codes for “spatial motor error.” This map allows for the correction of the activation across the SC layers to accommodate changes in the visual perspective following impending saccadic eye movements (Kojima & Soetedjo, 2017). This map is organized along the rostral to caudal axis to code for saccadic amplitude and along the medial to lateral axis to code for saccade direction. The SCi contains inhibitory GABAergic interneurons which can suppress activity in the SCs and ultimately suppress saccadic activity (Basso et al., 2021; Phongphanphanee et al., 2011). Additionally, the SCi can enhance activity in the SCs through excitatory interneurons (Ma et al., 1990). Critically, the SCi activity input from the substantia nigra pars reticulata (SNr) (Basso & May, 2017; Benavidez et al., 2021; Hikosaka & Wurtz, 1985; Liu & Basso, 2008). The SCi also receives regulatory inputs from the cerebellum (Roldan & Reinoso-Suarez, 1981; Westby et al., 1994). The third subregion of the SC, the SCd contains an auditory/somatosensory map which is made up of input from auditory, somatosensory, and association areas in the cerebral cortex. Together, the SCi and SCd serve as the output hub of the SC projecting to the reticular formation via the predorsal bundle to initiate orienting reflexes like saccades and avoidance behaviour that are coordinated across the whole body (Gharaei et al., 2020).

In addition to the laminar organization mentioned above, studies in the mouse SC indicate that the motor map is subdivided into regions, not unlike the homunculus in the motor cortex. The mouse SC has a columnar organization in the medial to lateral axis. This organization is seen most prominently in the intermediate layer of the SCi and SCd (Chevalier and Mana, 2000). With respect to cortical inputs from the primary motor cortex, regions responsible for cephalic motor control (nose, mouth, upper limb) project to more medial regions of the SC with regions responsible for more caudal regions (trunk, lower limb) projecting to more lateral regions of the SC. This is similarly mirrored with inputs from the premotor cortex (Oliveira & Yonehara, 2018).

The laminar organization of the SC forms the basis for the execution of saccades, among other subcortical orienting responses. The topographic layers (retinotopic, auditory, somatosensory, etc.) are overlaid and aligned to facilitate the multisensory computation underlying the initiation of orienting responses toward relevant stimuli (May, 2006). More specifically, the SC is believed to encode the horizontal and vertical components of gaze before three-dimensional organization of orienting reflexes is organized by downstream control systems (Klier et al., 2003). For instance, the appearance of a stimulus in the visual field results in activation of the corresponding population of neurons in SCs retinotopic map and a simultaneous global inhibition of other non-target regions of the map. Absent any inhibition, the visual burst in the SCs ultimately drives a secondary motor burst in the SCd and initiates a saccade toward the stimulus (Mays & Sparks, 1980; Sparks et al., 2000).

The hypothesis underlying the empirical work in this thesis is primarily underpinned by findings relating to the role of the SC in the initiation of orienting responses. Below is a brief overview of the literature on a specific orienting response: express saccades. Additionally, there is a discussion of the unique influence of categories of evolutionarily relevant visual stimuli on the frequency of express saccades, as well as the neuronal correlates of this phenomenon. The hypothesized role of subcortical structures in orienting is discussed in the next section, more specifically in reaching and mediating another orienting response, the express sensorimotor response (ESR), which can accompany reaching. Finally, the current topic of study is addressed:

exploring if the ESR also exhibits the preference observed in express saccades of evolutionarily relevant stimuli, namely faces.

1.2 Express Saccades

Saccades have been classically segregated into two categories: normal saccades (latency +120ms in humans) and express saccades (latency 80-120ms in humans). Express saccades are relatively rare compared to normal saccades. The sub-categorization of saccades into these two categories in humans has been controversial, with some studies suggesting that there is a bimodal distribution in saccadic reaction time, while others suggest that this distribution does not exist or is a consequence of anticipatory saccadic activity (Fischer et al., 1993; Kingstone & Klein, 1993). In non-human primates (NHP), however, it is well established that saccadic reaction time resembles a bimodal distribution, supporting the hypothesis that express saccades are a unique subcategory of saccade (Coe et al., 2019). NHP electrophysiology studies show that in the case of normal saccades there is a delay between the offset of the visual burst and the onset of the motor burst in the SC (figure 1). In certain circumstances, however, the visual burst in the SCs, in addition to pre-sensory activity, immediately drives a motor burst in the SCd resulting in the initiation of express saccades which occur ~100ms following stimulus onset (Dorris & Munoz, 1998; Edelman & Keller, 1996; Sparks et al., 2000).

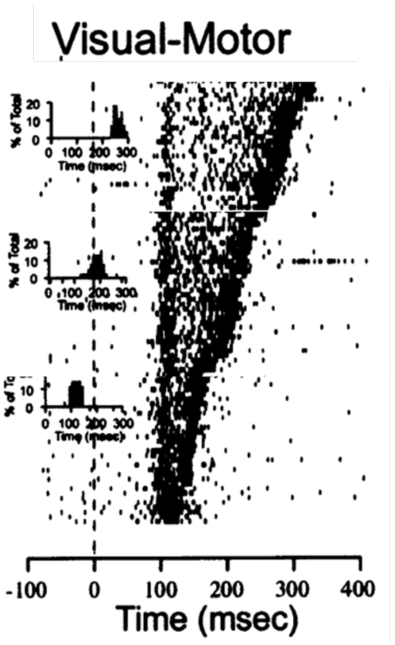


Figure 1. *Raster plots of neuronal activity of a visuomotor neuron in the SC. The bottom of the panel illustrates when the express saccades occur, namely when the visual burst leads directly to the initiation of the motor activity. Adapted from Sparks et al., 2000.*

In humans, saccadic reaction time resembles a normal distribution in most individuals, with only a small subset of individuals reflecting this bimodality. Most people, however, can still perform rapid saccadic eye movements (Fischer et al., 1993). Therefore, when assessing the impact of various conditions on the behaviour of express saccades in humans, the analysis relies not on identifying a difference in mean express saccade reaction time, but rather on identifying differences in the tail end of the distribution on the left. Using this approach, the behaviour of express saccades has been extensively studied. These findings have served as behavioural indicators of the theoretical computational capabilities of the SC and related brain structures. For instance, increased activity in the SC in response to lower spatial frequency images is reflected in the preference of express saccades for these stimuli (Chen et al., 2018; Kozak et al., 2020; Vuilleumier et al., 2003). This is also evident in how increased reward expectation results in more express saccades and higher activity in the SC (Bentin et al., 1996; Rezvani & Corneil, 2008). Of particular relevance to this study are the findings showing a preference of express saccades for faces and the correlated findings on face-sensitive neurons in the brainstem.

1.2.1 The Importance of Faces

An extensive body of literature has established that the “face,” as a visual stimulus, holds a unique importance. Even newborn infants will instinctually look and fixate on faces just moments following their birth (Johnson et al., 1991). Detecting faces has been hypothesized to hold an evolutionary significance since spotting others allows us to navigate social situations. Several findings also indicate faces are a uniquely important stimulus in the evocation of express saccades. Faces in particular can be detected much faster than other stimuli, at a rate of up to 6.5 faces per second using continuous saccades (Martin et al., 2018). Additionally, when compared to pictures of animals or inanimate objects, faces evoke more accurate express saccades (Crouzet & Thorpe, 2011; Salvia et al., 2020; Vanrullen & Thorpe, 2001).

Of particular importance to the methods employed in the current study is the work of Crouzet and Thorpe (2011), in which they identified the preference of express saccades for faces by employing a saccadic choice task. Participants were presented with two simultaneous images, one image of a face and the other of a vehicle. The images were placed randomly with one to the left and the other to the right of a central fixation point. In alternating blocks, participants were instructed to look toward the face or car. They found that the mean saccadic reaction time in both tasks did not differ. Additionally, they found that participants conducted more express saccades toward the faces than toward vehicles. They also found that participants could more reliably make a saccade towards pictures of faces (100-110ms) earlier than they could towards pictures of cars (140-150ms). This was defined as the participants making significantly more correct responses than incorrect ones starting at this given time point for each task. One caveat to this study is that the analysis conducted did not take into account the co-variance within participants. Rather, all the participants' saccadic reaction times were pooled and then analyzed as one distribution, potentially meaning that the finding may be driven by a minority of participants. Moreover, no multiple comparisons corrections were conducted to account for the false discovery rate of the chi-square tests employed to identify differences between the correct and error responses within each 10ms bin. This may indicate that this finding is false.

Face detection in the brain can broadly be broken down into two connected systems, one cortical and the other subcortical. The primary cortical region associated with the identification of faces is the fusiform face area (FFA) (Bentin et al., 1996). However, the FFA is only one region associated with face detection in the ventral visual stream, starting at the primary visual cortex in the occipital lobe and terminating in the inferior temporal lobe. The occipital face area (OFA) is located upstream of the FFA, in the inferior occipital gyrus. The OFA is responsible for low-level analysis of faces starting as early as 100ms following stimulus presentation. More specifically the OFA codes for the spatial frequency content and location of the face (de Vries & Baldauf, 2019). The OFA does not code for identity; therefore, changes in image quality and facial expression can impact activity in this region (Rotshtein et al., 2005). Conversely, the FFA involves more holistic processing of faces at a latency of ~130ms, with activity coding for facial identity as a function of the shape and relative spacing of visual features as well as viewing angle (Bentin et al., 1996; Collins & Olson, 2014). Since activity in the FFA is mainly associated with identity, it is not impacted by the location and size of the face in the visual field. Changes in facial expression, however, do result in a small but consistent amount of variation in activity in the FFA, indicating that the region is also involved in the processing of facial expressions (Ganel et al., 2005). The final node responsible for face processing is located deep within the ventral anterior temporal lobe (ATL). The ATL plays a central role in the face processing network, serving as an interface between regions responsible for face perception (OFA and FFA) and those responsible for face memory (amygdala and hippocampus). For this reason, the ATL is important for the semantic memory of faces, such as the retrieval of biographical information relating to a face or the feeling of familiarity when re-encountering known persons (Collins & Olson, 2014). Collectively, the OFA, FFA, and ATL form the core system of face processing in the cerebral cortex.

While these aforementioned regions certainly play a role in the recognition of faces, they may not be the primary drivers of the express saccade's preference for faces. Indeed, given the latency of express saccades (starting ~80ms), the feature detectors directly mediating express saccade preference for faces are unlikely to be located in the cerebral cortex. It is well established that subcortical systems may independently initiate saccades towards faces. Rapid saccadic eye movements are not impeded when the primary visual cortex (V1) is damaged, as has been demonstrated in blindsight (Kinoshita et al., 2019; Ro et al., 2004). These individuals can also respond differentially to different faces and emotions, implying that there must be extracortical areas which could play a role in the visual reactions to faces (Celeghin et al., 2020). These observations in patients with blindsight, although tested in relation to normal saccades, may also apply to express saccades.

Recent work has expanded the understanding of the subcortical face-detection system. Neurons within the monkey SC and pulvinar exhibit lower latency and larger bursts in response to faces as early as ~50ms following stimulus onset. Additionally, high-contrast face-like symbols evoked stronger bursts than natural faces, potentially indicating that the feature detectors in the SC responsible for saccadic preference towards faces is dependent on low spatial frequency information (Nguyen et al., 2014, 2020). This is corroborated by findings demonstrating that express saccades are more likely to be evoked by lower spatial frequencies and that both the SC and the pulvinar exhibit stronger bursts in response to lower spatial frequencies (Chen et al., 2018; Villeneuve et al., 2005). Furthermore, the SC has been found to be crucial, along with the amygdala, in the evaluation of faces by patients with Blindsight (Celeghin et al., 2020). Collectively, these findings imply that facial stimuli can be identified within early-level processing in the SC, circumventing V1, and initiating saccades towards these targets.

1.2.3 Feature Detection Beyond the Face

One recent study by Bogadhi and Hafed (2022) suggests that the SC may have neurons specifically tuned to respond not only to faces but to a wider range of stimulus categories. In this study, macaques were presented with images of objects within seven different object type categories while electrophysiology recordings of the SC were obtained. The researchers found that some neurons reliably fired in greater magnitude to specific categories of objects. For example, a similar number of neurons showed a preference towards evolutionarily relevant objects like monkey faces and snakes and in response to modern artificial objects. This finding expands the claims regarding feature detection by the SC and is in line with findings that the SC plays a role in the detection of snakes (Almeida et al., 2015). While the Bogadhi and Hafed (2022) findings may imply that the SC possesses substantially more capabilities than previously identified, a deficiency in the methodology of the behavioural paradigm makes conclusions uncertain. Instead of testing the behaviour of each neuron on *several* images from within a given category, only *one* image from each category was used to test the activity of any given neuron. Therefore, it may be incorrect to assume that the preferential activation of any neuron towards a single image from within a category could be generalized to the entire category. Rather, it is possible that something other than the content of the image, such as the location of lines or luminance distribution, may be resulting in the preferential activation of the recorded neuron.

Taken in the context of the mounting evidence that the SC plays a role in upper limb movement, the SC's preferential visual burst in response to face-like targets may also be reflected in more rapid muscle recruitment during reflexive reaching movements. Additionally, if findings regarding the SC's abilities to identify a wide range of objects are sound, reflexive reaching movements may be faster toward any instructed target.

1.3 Reaching

Visually guided reaching has been classically thought of as purely under the purview of the corticospinal system. Similarly, initial theories concerning the function of the SC limited its role to the initiation of eye movements (Wurtz & Goldberg, 1972). Later studies, however, demonstrated that while the dorsal visual stream in the cerebral cortex is primarily responsible for the control of visually guided reaching, the SC plays a role in expediting orienting motor behaviour. Activity in the SC does not simply reflect eye movements, but gaze shifts, which often include movements of the head as well as eye movements (Corneil et al., 2002; Freeman et al., 1996). This observation puts into context the sheer breadth of cortico-tectal and cortical-striatal inputs that have been identified, as the SC must integrate motor, proprioceptive, and visual information in order to properly mediate shifts in gaze. As previously mentioned, the SC receives extensive inputs from the cerebral cortex, including the motor and premotor cortex, with those inputs forming the basis for a somatosensory map in the SCd. A subset of neurons in the SCd of NHPs produce action potentials in correlation with upper limb movements and do not display saccade-related activity (Werner & Sabine, 1997). Furthermore, the neurons in the SCi of NHPs which project to the eye and ocular muscles have been found to project to the head, neck, and shoulder muscles via the spinal cord. Additionally, stimulation of the SC in cats results in muscle activity in the upper and lower limbs and trunk (Courjon et al., 2004; Syka & Radil-Weiss, 1971).

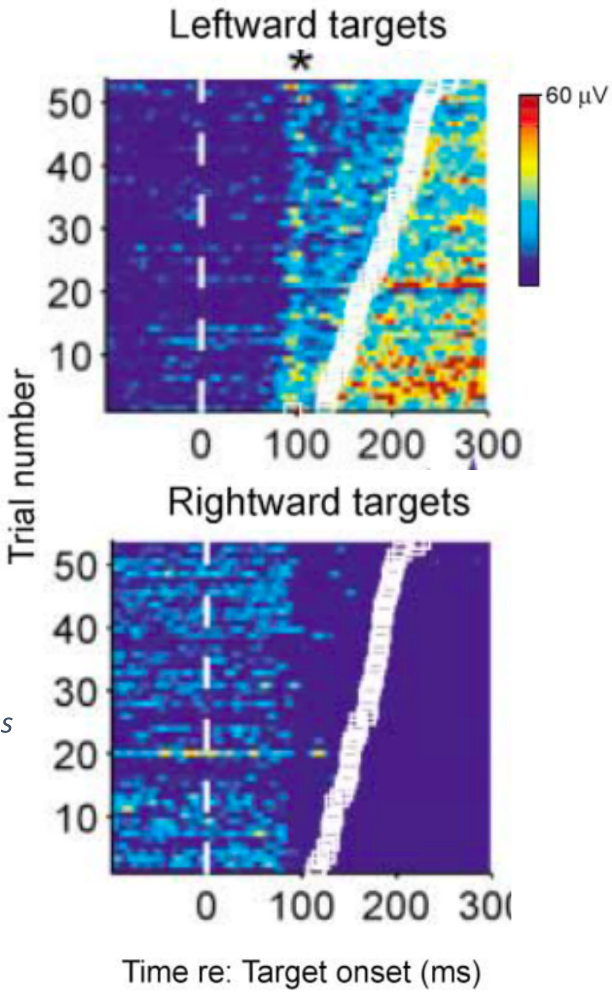
These findings support a model of subcortical orienting, where the SC is involved in coordinating muscles throughout the body. This model would satisfy the practical requirements for orienting in evolutionarily quadruped animals, such as our primate ancestors, in which activation of muscles in the forelimbs, hindlimbs, and trunk are required for orienting movements of the entire body. This would allow for orienting to be executed more rapidly than through the cerebral cortex, decreasing reaction time latencies. Recently, studies in humans and NHPs have corroborated this model, identifying low latency (~80ms) muscle recruitment in the neck, shoulder, and lower limbs driven by visual stimuli (Fautrelle et al., 2010; Kozak et al., 2019; Pruszynski et al., 2010).

Given these findings, further investigation is required to identify what specific role the SC plays in the computations underlying rapid initiation of orientation, more specifically reaching behaviour. Since the SC has been shown to express computational capabilities which induce preferential expression of saccades, another biomarker of these computations may be found in the expression of rapid subcortical reflexes in the upper limb during reaching movements.

1.4 The Express Sensorimotor Response (ESR)

Like other orienting movements, reaching is mediated in part by the cerebral cortex and in part by subcortical structures. The cerebral cortex mediates voluntary movements which begin at a latency of approximately 150ms. Subcortical structures are thought to be responsible for the initiation of the express sensorimotor response (ESR), which is a burst of muscle recruitment occurring 80-120ms following a visual stimulus (Corneil et al., 2004; Pruszynski et al., 2008). As seen in the top graph of figure 2, the ESR can be expressed as either an increase or decrease in muscle activation. This is dependent on whether the orienting movement of a body segment towards the stimulus requires for the activation or deactivation of the muscle. By modifying muscle activation before voluntary movement begins, the ESR drives shorter latency limb movements, allowing for quicker responses to sudden stimuli (Gu et al., 2016; Kozak et al., 2019).

__Figure 2.__ ESR in monkey neck EMG during orienting task. Heat plots reflect activity in the left obliquus capitis inferior, which is responsible for moving the neck to the left. Trials are ordered by reaction time, denoted by white dots. The ESR is denoted by an asterisk, ~80-120ms following stimulus onset at 0ms. When the target is on the left (top plot), the ESR presents as an increase in activation. When the target is on the right (bottom plot), the ESR presents as a decrease in activity. The ESR is aligned to stimulus onset, not to the reaction time. Adapted from Corneil et al., 2004.



What we now term the ESR, was first identified in humans in the neck muscles by Corneil et al. in 2004. As more was discovered about the ESR, it underwent several name changes. Indeed, the evolution of the terminology employed to describe the ESR can serve as a useful chronology of the discoveries made concerning its abilities. The term we have arrived at, “express sensorimotor response” or “ESR,” is employed in this thesis as it accurately encapsulates the known characteristics of this reflex without implying any limitations concerning its location or latency. Alternatively, the ESR has been described as “stimulus-locked.” However, not only has it been demonstrated that the latency of the ESR changes depending on stimulus features, it also appears that the ESR can be delayed to coincide with a go signal rather than the appearance of a stimulus (Wood et al., 2015). In some literature, the ESR has also been described as a visuomotor response (Contemori et al., 2021). However, since the ESR is hypothesized to be initiated through a common mechanism along with saccadic reflexes and saccades can be initiated through auditory inputs, the ESR may also be induced through other sensory inputs (Yao & Peck, 1997). Thus, although the ESR appears to be primarily driven by visual inputs, it may also be elicited through other senses, most notably through audition. Most recently the term “Express Arm Response” was employed. This term, however, limits the ESR expression to the upper limb (Kearsley et al., 2022) and the ESR has also been identified in the neck and may also exist in the lower limb. Further, since orienting requires the recruitment of many muscles, including hands or feet as well as core muscles, the ESR may indeed be expressed in many muscles of the body.

Since its identification, circumstantial evidence has been mounting that the ESR is mediated through the same brainstem orienting circuitry responsible for the initiation of express saccades. Given the short latency of the ESR (beginning ~80ms) and the length of time required for the visual signal to travel from the eye to the brain and then to the arm muscles to produce the ESR, it is unlikely that these signals are emanating from the cerebral cortex. Indeed, the latency of the ESR is correlated with the latency of both express saccades and the activity in the SC (as seen in figures 1-2), implying that the SC is a likely source of the ESR.

1.4.1 Factors Impacting the ESR

Much like express saccades, the ESR can be impacted by the quality of the visual stimulus. Thus, like express saccades, the ESR occurs earlier and with greater magnitude in response to low spatial frequency and/or high contrast stimuli (Kozak et al., 2019; Kozak &

Corneil, 2021, Chen et al. 2018, Marino et al., 2012). Further, the use of priming, such as endogenous or exogenous cues, results in stronger expression of the ESR and in more frequent express saccades (Contemori et al., 2021; Kozak et al., 2020; Meeter & Van der Stigchel, 2013).

Most relevant to our study, both express saccades and the ESR are impacted by the task set. Express saccades can occur more towards a given target if the participant is instructed to look towards a specific target in a choice task (Crouzet & Thorpe, 2011). Additionally, express saccades are less frequent when the participant is asked to look away from a single target (Coe & Munoz, 2017). Similarly, the magnitude, but not the directionality of the ESR is impacted by the task set. Gu and colleagues (2016) found that when participants are instructed to reach away from an appearing target that the magnitude of the ESR is reduced, but its directionality is maintained to direct the arm towards the target. Collectively this evidence indicates that the ESR may be impacted by top-down control and that its main purpose is modulating the direction of the orienting movements towards targets.

1.5 The Current Study

Given the demonstrated relationship between the SC and orienting reflexes in the eye, neck muscles, and perhaps the arm muscles, in this study, we investigated if the ESR in the upper arm muscles is enhanced by faces, in the same manner as express saccades.

We hypothesize that the SC has rudimentary feature detectors uniquely sensitive to faces. If our hypothesis is correct reaches toward faces will result in increased expression of the ESR, as well as a lower latency reaching time. Given the short latency of the ESR in the arm muscles (80-120ms) and the latency with which faces are detected in the cerebral cortex (~100ms), it is unlikely that the ESR exhibit a preference for faces through sensory processing in the cerebral cortex (de Vries & Baldauf, 2019; Pruszynski et al., 2008). If the ESR and motor responses are enhanced by the presentation of faces, this would imply that there are templates in the early visual processing system in the brainstem which can detect certain types of evolutionarily relevant visual stimuli and mount an orienting response in the arm. If this hypothesis were supported it would broaden the orienting response account, implying not only that the SC preferentially responds to specific categories of stimuli, but also that it can initiate preferential rapid orientations toward these stimuli by engaging movements of the arm.

In the current study, our paradigm failed to induce a sizable number of express saccades. Therefore, it may not be an ideal replication of the Crouzet and Thorpe (2011) study. Given the failure to replicate, this study should not be viewed as perfectly analogous to previous work related to express saccadic preferences for faces. Rather, the findings should be interpreted in the context of a motor task looking at variations in ESR express based on differences in stimulus and/or instruction.

Our findings do not support our original hypothesis and instead point to a more elaborate mechanism underlying the ESR. Our findings imply that the ESR can display a preference for targets other than faces, corroborating findings that neurons in the SC can respond preferentially to a wide range of image categories (Bogadhi & Hafed, 2022). Additionally, we found that the ESR only reflected this preference when the target was consistent. These results indicate that there are feature detectors in the brainstem responsible for selecting targets and initiating an ESR in the direction of the selected target. Further, and most intriguingly, these feature detectors may be modified by top-down cortical control to select for specific targets based on instruction or goal.

2 Chapter 2: Methods

2.1 Participants

Two experiments were conducted in this study. Each experiment was conducted both as a reaching task and as a saccadic task. Undergraduate students were recruited to participate in the reaching study through the psychology research participation pool system. Informed consent was obtained, and participants could withdraw from the study at any point. Participants were compensated with research credits required for course completion. The experiment complied with the regulations of the Health Science Research Ethics Board at The University of Western Ontario. All participants reported that they had no visual, neurological, or motor disorders. Upon completion of the data analysis, one participant's reaching data was excluded due to the presence of a resting tremor.

In total, 19 participants (female: 8, male: 11; mean age: 18.35, SD: .89) were included in the reaching tasks of both experiments. Fifteen were right-handed, three were left-handed, and one was ambidextrous. Additionally, 22 participants (female: 8, male: 14; mean age: 18.5, SD: 1.19) completed the saccadic portion of experiment 1 and 11 participants (female: 5, male: 6; mean age: 18.73, SD: 1.56) completed the saccadic portion of experiments 2.

2.2 Apparatus

The experiments were conducted using a Kinarm Endpoint Robot (BKIN technologies, Kingston, ON, Canada). A Propixx projector (VPixx, Saint-Bruno, QC, Canada) was employed within the Kinarm to generate high-quality visual stimuli and reliable event timing. The display was projected onto a horizontal surface. Participants completed the task using a manipulandum under the display surface to control a cursor. All participants conducted the task using their right arm independent of their handedness. A constant force of 2N towards the participants and 5N towards the right was applied to the arm from the manipulandum throughout the experiment to induce baseline activity in the right pectoralis muscle.

Surface electromyography (EMG; Delsys Inc. Bagnoli-8 system, Boston, Massachusetts, United States of America) recordings of the right pectoralis major muscle were acquired in two locations: the clavicular head and the sternal head of the muscle. Additionally, a photodiode was employed to identify the exact time the stimuli appeared in each trial. EMG and photodiode recordings were filtered using a high and low pass filter of 20 and 450 Hz, respectively, and then digitized at 1000 Hz by the Delsys Bagnoli system. An Eyelink 1000 plus eye tracker (SR Research Ltd., Ottawa, On, Canada) was employed to monitor eye movements during the task. Kinematic and eye movement data was recorded at a rate of 1000Hz by the Kinarm system. The task was generated using Stateflow and Simulink within MATLAB (version R2016a, MathWorks Inc., Natick, Massachusetts, United States of America).

2.3 Behavioural Task

In the Crouzet and Thorpe (2011) paradigm, which first identified that express saccades occur more frequently in response to faces, participants were asked to select between two simultaneously appearing targets. The visual stimuli were presented to the left and right of fixation, one the image of a face, the other of a car. They were instructed to look at the face in one block and the car in another. The researchers found that express saccades occurred more often in response to faces than to vehicles. Additionally, participants made fewer errors when they were attempting to look at the faces.

We adapted the aforementioned study into a reaching task to test the effect of faces on the ESR. **In experiment 1**, we employed the same stimulus bank employed in the Crouzet and Thorpe (2011) study within our paradigm, containing images of faces and cars. **In experiment 2**, we used the same experimental timeline, but instead presented a high contrast face and its scrambled counterpart. The latter stimuli resembled those used in the study by Nguyen et al. (2014, 2020), in which high contrast face-like symbols were found to elicit stronger activation in face sensitive neurons in the monkey superior colliculus and pulvinar.

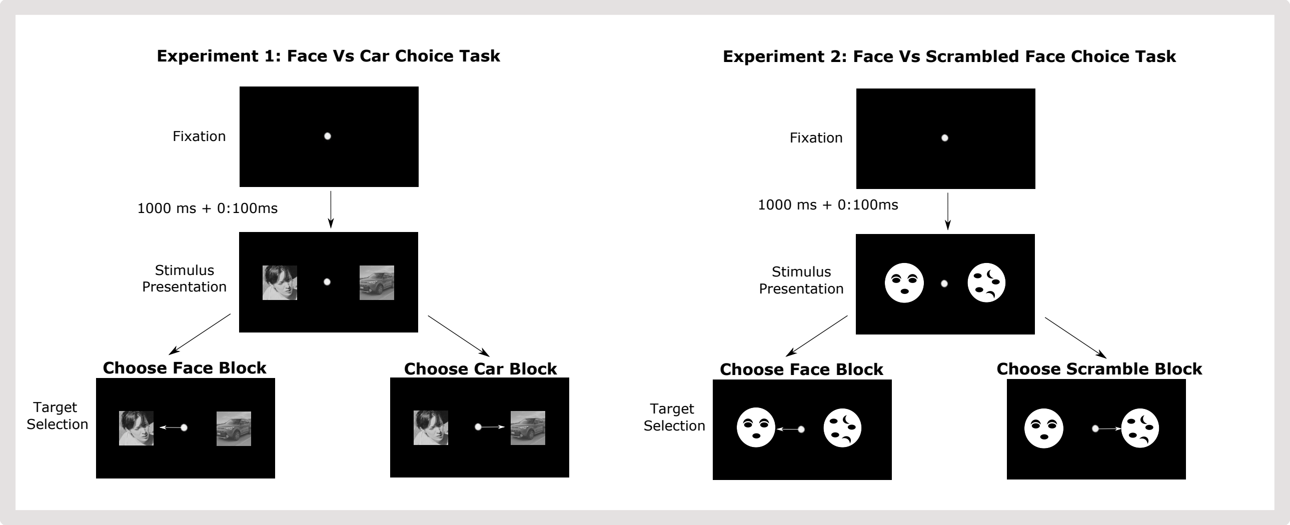


Figure 3. *Task Timelines. In the reach task, in both experiments, participants began a trial by fixating on a fixation point with the manipulandum centred. Targets appeared 1000ms following fixation, with an additional randomized time between 0 and 100ms to prevent temporal predictability. Once the targets appeared, participants moved toward the instructed target. In the saccadic task, the timeline was identical, with the only difference being that visual fixation point dictated the initiation of the trial rather than fixating with the manipulandum. Additionally, the fixation point disappeared 500ms before the onset of the targets.*

Participants were introduced to the tasks by viewing a video for the reaching and eye tasks. Additionally, before completing the task, participants completed 100 trials of reaching and 100 trials of saccadic movement to familiarize them with the tasks and stimulus types.

Figure 3 shows the timelines for the two experiments conducted in this study. **In experiment 1**, participants looked or reached towards the face in the 'choose face' block and the car in the 'choose car' block. Ten images of faces and ten pictures of cars were randomly interleaved. **In experiment 2**, participants looked or reached towards the face in the choose face block and the scrambled face in the choose scrambled block. Participants completed both experiments once as a look and reach task and as an eye movement only task. ***The reaching tasks*** were composed of 480 trials with the instruction changing every 60 trials. A subset of the trials (80) included only single targets. ***The saccade tasks*** were composed of 240 trials with the instruction changing every 60 trials. A subset of the trials (40) included only single targets. Participants were given a three-minute break following every 240 trials in both the reaching and saccadic tasks. The order in which each participant completed experiments 1 and 2 was alternated between participants. Additionally, the order of instruction blocks (Ex. chose face Vs chose car) was alternated between participants within each experiment.

2.4 EMG Filtering & Analysis

EMG data was full-wave rectified and then filtered through a second order low and high Butterworth filter (20Hz, 450Hz). The signal was then normalized as a proportion of baseline activity in response to a constant torque, on a trial-by-trial basis. This was accomplished by dividing the muscle magnitude by the mean activity in the 100ms preceding the stimulus onset. This was then followed by a 7-point moving average filter. The two EMG recordings (sternal and clavicular heads of pectoralis major) were then averaged. EMG recordings were normalized along the time axis to a stimulus onset time denoted as the point when the photodiode was triggered. Kinematic data were used to eliminate any error trials, where the participant moved before stimulus onset, moved in the wrong direction, or missed the target. Trials were categorized as correct, wrong way, and rejected. The correct trials were reaches where the participant made a continuous movement in the correct direction until they reached the target. The wrong way trials were reaches where at any point before the target or distractor was reached, the participant moved in the wrong direction. Rejected trials were reaches where the participant moved before stimulus onset or 80 milliseconds following stimulus onset or where the participant made an inconsistent movement.

A timewise paired T-test was conducted to analyse the effect of instruction on muscle activity within the ESR epoch; 80-120ms following stimulus onset. This was followed by a Benjamin and Hochberg false discovery rate analysis (p-crit=0.05).

2.5 Eye Movement Filtering & Analysis

Eye movement data was filtered using a low pass third order Butterworth filter of 45 Hz. Trials were excluded if a blink was detected 200ms before stimulus onset or before a saccade occurred. Saccadic reaction time was defined as the point when movement reached a velocity of 30 degrees per second. Since our study focused on express saccades, saccades occurring earlier than 70ms were excluded. Participants exceeding a 50% error or blink rate (2 participants) were excluded. In experiment 1, data sets from 22 participants were successfully collected for the saccadic task. In experiment 2, data sets from 11 participants were successfully collected for the saccadic task.

Reaction times for correct saccades were binned within 10ms bins for both potential targets (Ex. Face Vs Car). A paired T-test was conducted to identify if either target elicited a higher rate of express saccades. A Benjamin and Hochberg false discovery rate analysis was also conducted (p-crit=0.05).

3 Chapter 3: Results

3.1 Experiment 1: Face Vs Car

3.1.1 Experiment 1: Error Rate

As a measure of the participant's understanding of the task, we analyzed the error rate. Trials were categorized as correct, wrong way, and rejected. Of the non-rejected trials, on average, participants moved directly to the instructed target on ~80% of all trials and moved incorrectly to the distractor on ~20% of all trials. The rates of correct and wrong-way responses did not differ significantly across condition types using a one-way repeated measures ANOVA (F (3,72) =.189, p=.903). These results suggest that image categories and the direction of the stimulus had no impact on the participant's ability to successfully reach towards the targets.

3.1.2 Experiment 1: EMG

To contextualize the EMG results it is important to note what an increase or decrease in muscle activity means. Given that all participants were performing the task with the right arm and the muscle being recorded was the right pectoralis major muscle, an increase in muscle activity from baseline preceded movement to the left and a decrease from baseline preceded movement to the right. Recalling that the participants completed the task by moving the manipulandum loaded with a constant base force, the data are presented as a proportion of this baseline activity. This normalization allowed for the control of variation in within-participant variance of recording conditions, such as the strength of the electrode attachment across the session and the baseline recruitment of the muscle.

In figure 4, we show the data from a representative participant. The first 4 rows show the data for a single target condition. Although subtle, especially given the low trial count, the ESR is visible as an increase in muscle activity around 80ms in the first two rows when the target was located on the left. This is followed by an increase in muscle activity starting at ~150ms, in which the right pectoralis begins to move the right arm to the left. Similarly, the ESR is expressed as a decrease in muscle activity around 80ms in rows 3 and 4 when the targets were on the right. This is followed by a decrease in muscle activity as the right arm is directed to the right. The second section shows data from the double target conditions. Since there is a target to the left and right of the arm the ESR is not expressed in the same way. Firstly, it is lower in magnitude compared to the single target condition. Secondly, the ESR varies minimally when the instructed target is on either side of the starting point.

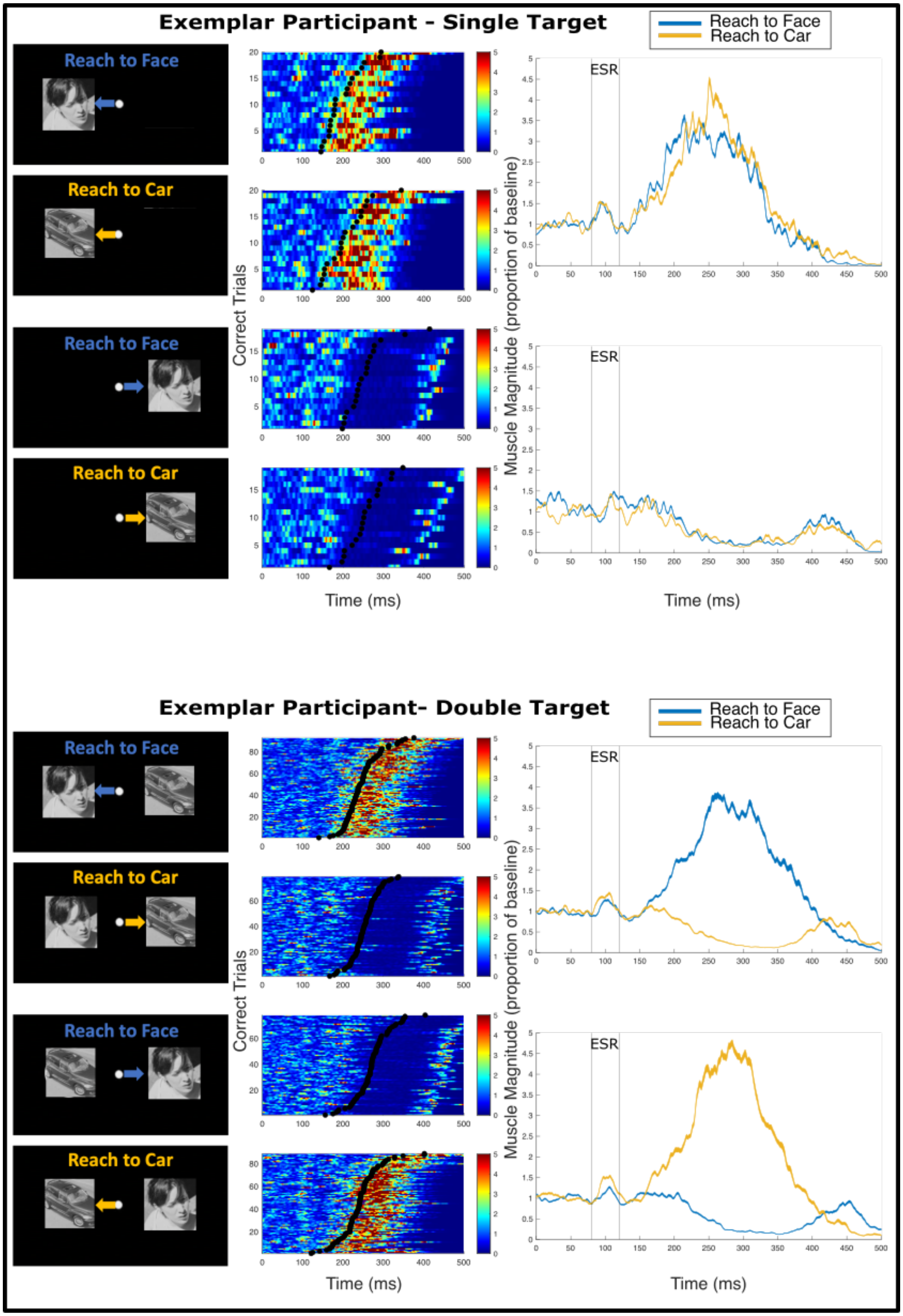

Exemplar Participant - Single Target
Reach to Face
Reach to Car
Reach to Face
Reach to Car
Reach to Face
Reach to Car
Correct Trials
Muscle Magnitude (proportion of baseline)
ESR
ESR
Time (ms)
Time (ms)
Exemplar Participant- Double Target
Reach to Face
Reach to Car
Reach to Face
Reach to Car
Reach to Face
Reach to Car
Correct Trials
Muscle Magnitude (proportion of baseline)
ESR
ESR
Time (ms)
Time (ms)

Figure 4. *Experiment 1: EMG data for exemplar participant. EMG data is normalized to baseline on a trial-by-trial basis. Trials in the heat plots are organized by reaction time which is denoted by black dots. Line plot shows the mean EMG activity and standard error of the mean for the first 500ms following stimulus onset for correct trials in each condition.*

The main prediction of this experiment is that as with express saccades, the ESR will display a preference to faces, reflecting a common subcortical origin for both reflexes. To test this prediction, three statistical comparisons of the EMG magnitude during the ESR epoch (80-120) were conducted. The statistical test used in these comparisons was a rolling time-wise paired T-test between the mean EMG magnitude across participants. To correct for multiple comparisons a Benjamin and Hochberg false discovery rate test with a critical p = 0.05 was used.

The first comparison was to identify any effect of target type on the ESR when a single target was presented (face or car) to the participant (figure 5). This comparison is modeled on the finding that saccades occur faster in response to faces than other categories of visual stimuli (Bannerman et al., 2009). In the context of the ESR, this comparison serves as a measure of whether the subcortical system responsible for the ESR has a bias towards faces. If true, we might expect that the faces would induce lower latency ESRs compared to the cars. Also, faces might induce a larger magnitude ESR than cars when the target is on the left or a smaller magnitude when the targets are on the right. We did not find any time points during the ESR epoch where the EMG magnitude was significantly different. Therefore, the stimulus type does not appear to impact ESR expression in a single stimulus condition.

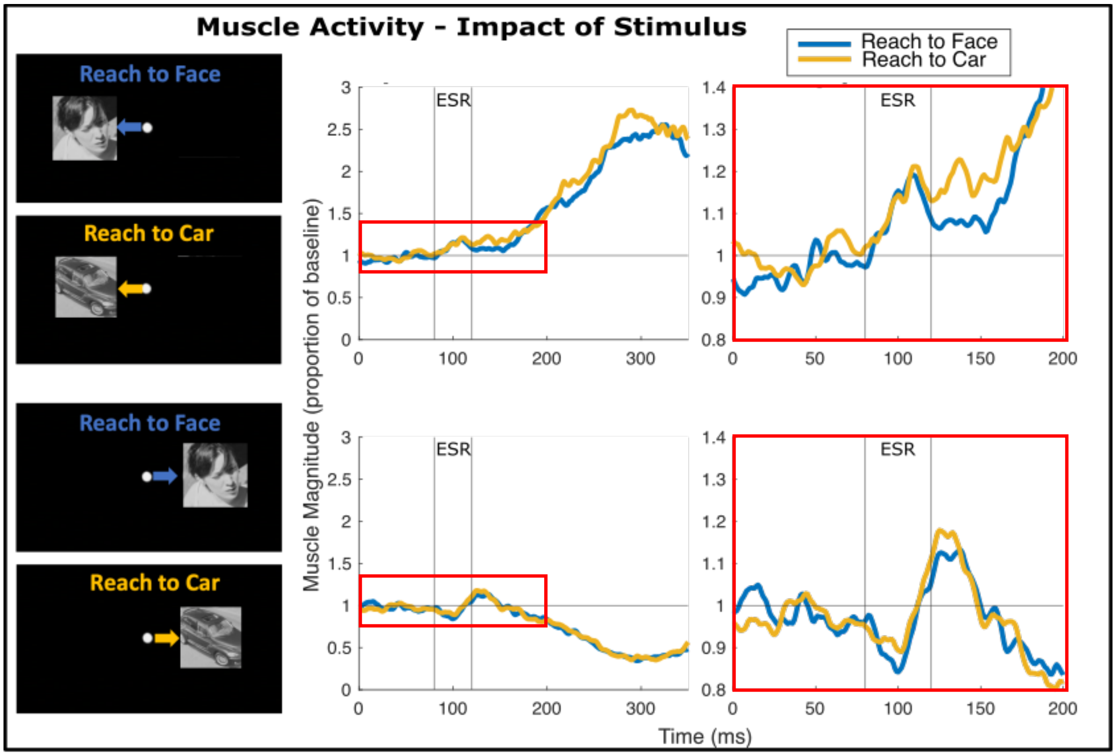


Figure 5. *Experiment 1: Impact of Stimulus on ESR. The first column shows mean muscle activity for correct trials across participants for the first 350ms following stimulus onset (0ms), including both the ESR (80-120ms) and voluntary activity (150ms +) (n=19). The second column focuses in on the ESR. At no point was a statistical difference in muscle activity identified within the ESR epoch, denoted by the vertical black lines.*

The second comparison was aimed at identifying any effect of *instruction* on the ESR during trials where the participants are presented with two targets and have a *choice* between the face and car in a two-target condition (figure 6). This comparison was modelled after the saccadic choice task completed by Crouzet and Thorpe where they asked participants to look towards faces in one block and towards cars in another. They found that participants initiated more express saccades towards faces than towards cars based on the instructions. Also, they found that participants were more likely to make errors towards the face when instructed to look towards the car. In the context of the ESR, this comparison would serve to identify if there was any effect of the instruction. Since the same exact images were falling on the retina, any variation in the ESR could be attributed to the task set as determined by the instruction given to the participant for that given block (look towards the face or look towards the car). If this were the case, we would expect the ESR to deviate more from baseline in the direction of the instructed target (higher than baseline if the target is to the left and lower if the target is to the right). Further, given that participants made more error saccades in the direction of faces in the Crouzet and Thorpe study, an alternative outcome could be that the ESR will deviate from baseline in the direction of the face, independent of the instructions. In this analysis, we did not find any point within the ESR epoch at which the instruction affected the magnitude of muscle activity.

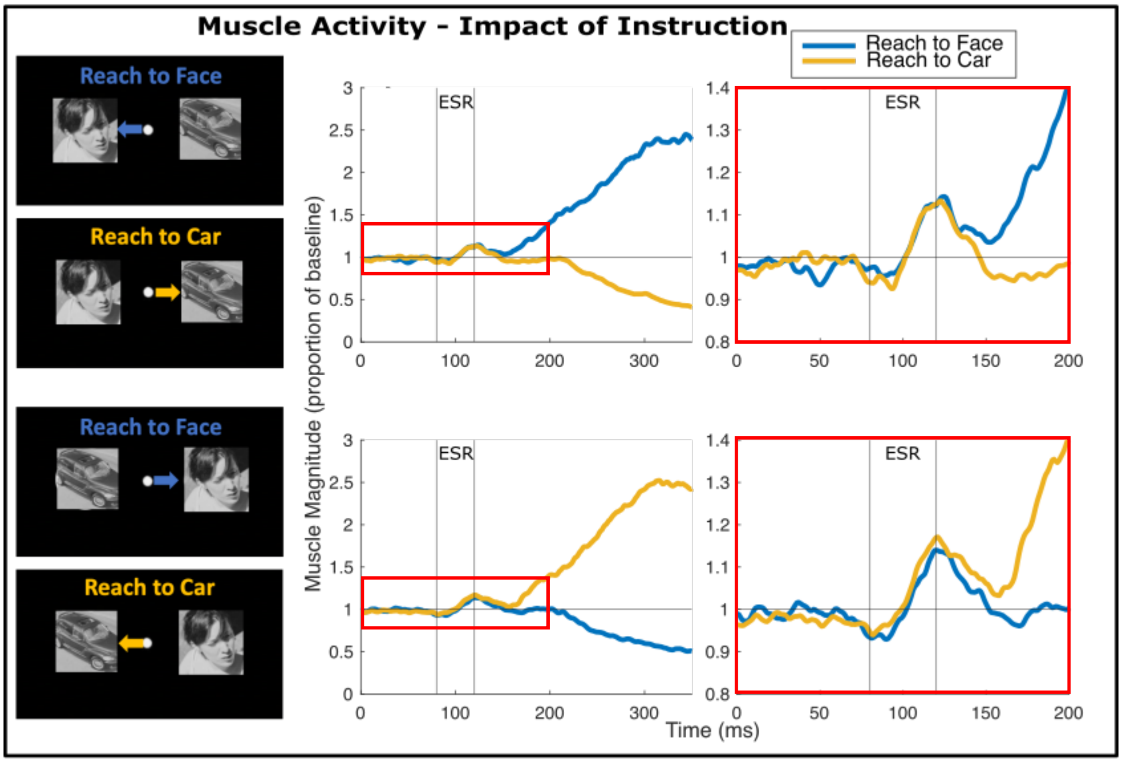


Figure 6. *Experiment 1: Impact of Instruction on ESR. Mean muscle activity for correct trials across participants (n=19). At no point was a statistical difference in muscle activity identified within the ESR epoch, denoted by the vertical black lines.*

One possible reason why we found no difference in the previous two comparisons may be that the stimulus was not optimal at eliciting the ESR. Therefore, to test that, we conducted a third comparison between the single target and double target trials (figure 7). Previous studies have established that the ESR is spatially locked to the stimulus in a single stimulus condition, meaning that the ESR will affect the muscle activity in a manner to support arm movement towards the stimulus. Since the ESR can be expressed as either an increase or decrease in activity from baseline, the ESR in the double target conditions can be interpreted as a competition between two different ESRs, one driving the right arm to the left by inducing more muscle activity in the right pec and the other driving the right arm to the right by inducing less muscle activity in the right pectoralis muscle. This interpretation is supported by the shape of the ESR in the two-target condition, where the mean EMG magnitude across participants decreases and then increases with respect to baseline activity. Given this finding, if these stimuli were optimal at eliciting the ESR, the magnitude of muscle activity across the ESR epoch should be significantly different when a single stimulus is presented than when a distractor is present in the two-target condition. In this comparison, we found that although ESR activity trended in the direction, which would imply a stronger expression of the ESR in the direction of the target when no distractor was present, higher when the target was to the left and lower when it was to the right, there was only a minimal significant difference in magnitude. This implies that the ESR in this experiment was not specific to the target (face vs. car) and these stimuli may not be optimal for testing the effect of faces on the ESR.

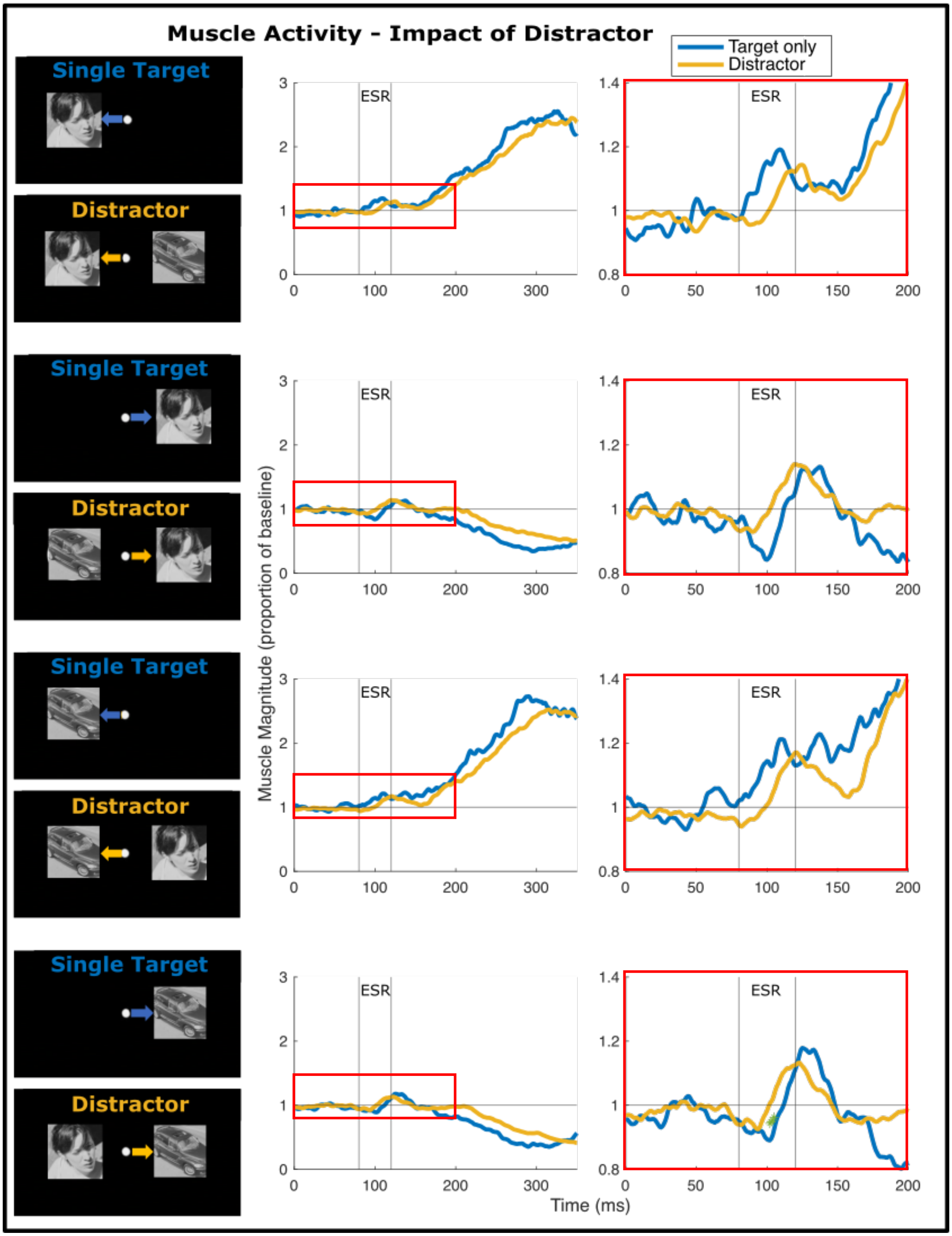

Muscle Activity - Impact of Distractor
Target only
Distractor
Single Target
Distractor
Single Target
Distractor
Single Target
Distractor
Single Target
Distractor
ESR
Muscle Magnitude (proportion of baseline)
Time (ms)
0
1
2
3
0.8
1
1.2
1.4
0
100
200
300
0
50
100
150
200

Figure 7. *Experiment 1: Impact of Distractor on ESR. Mean muscle activity for correct trials across participants (n=19). Green asterisks denote time points where a significant difference was identified using paired timewise rolling T-tests followed by a false discovery rate correction.*

3.1.3 Experiment 1: Kinematic Reaction Time

Since a hypothesized purpose of the ESR is that it facilitates more rapid limb movement, an analysis of reach reaction time was conducted in order to identify any effect of the stimuli on movement kinematics (figure 8). We predicted that limb movements towards faces would be initiated more rapidly than towards cars. Although we did not find an effect of the stimuli on the ESR, a paired T-test followed by a false discovery rate correction found a significant difference between some conditions in the choice task. The mean reaction time for correct reaches towards faces on the right is significantly longer than reaches towards cars on the left and right. This finding is counter to our prediction that face will elicit a shorter latency motor response.

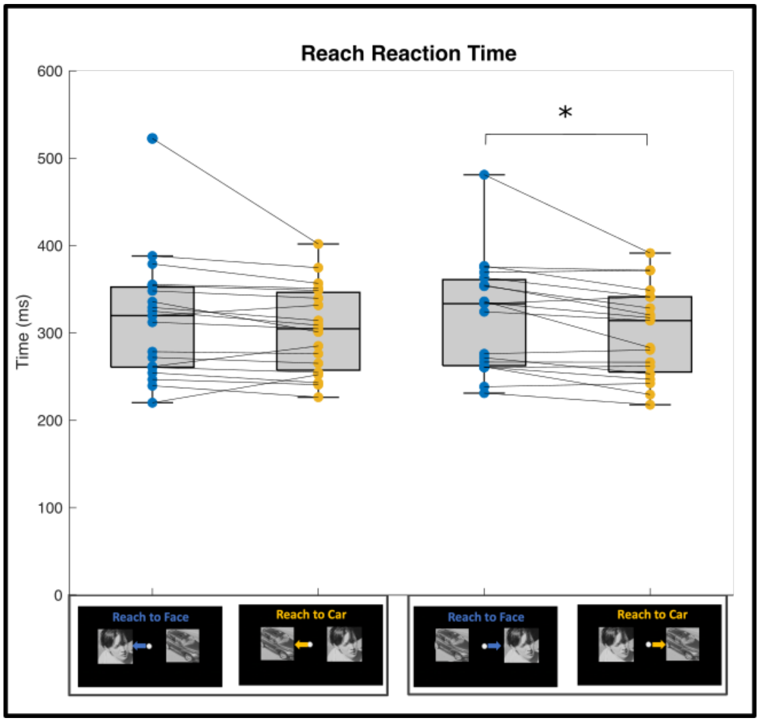


Figure 8. *Experiment 1: Mean Reach Reaction Time. (n=19). Asterisks denote significant difference identified using paired T-test.*

3.1.4 Experiment 1: Saccadic Reaction Time

The final analyses in experiment 1 were aimed at identifying if the findings relating to the preference of express saccades for faces was replicated within our experimental paradigm. We, therefore, repeated the experiment, requiring only that participants looked to the instructed stimulus with a saccadic eye movement. An analysis of the mean saccadic reaction time across participants found no impact of condition. Figure 9 shows the mean frequency distributions of the saccades across time (10ms bins) for 22 participants. A rolling paired T-test comparing the percent likelihood that a saccade will occur within a given time bin found no difference between the distributions of saccades towards faces or cars. Additionally, the number of express saccades detected was low, indicating that this task may not have been appropriate for measuring express saccades. The lack of difference in saccadic reaction time is consistent with the lack of difference in ESR if indeed they are both mediated through the subcortical orienting circuit.

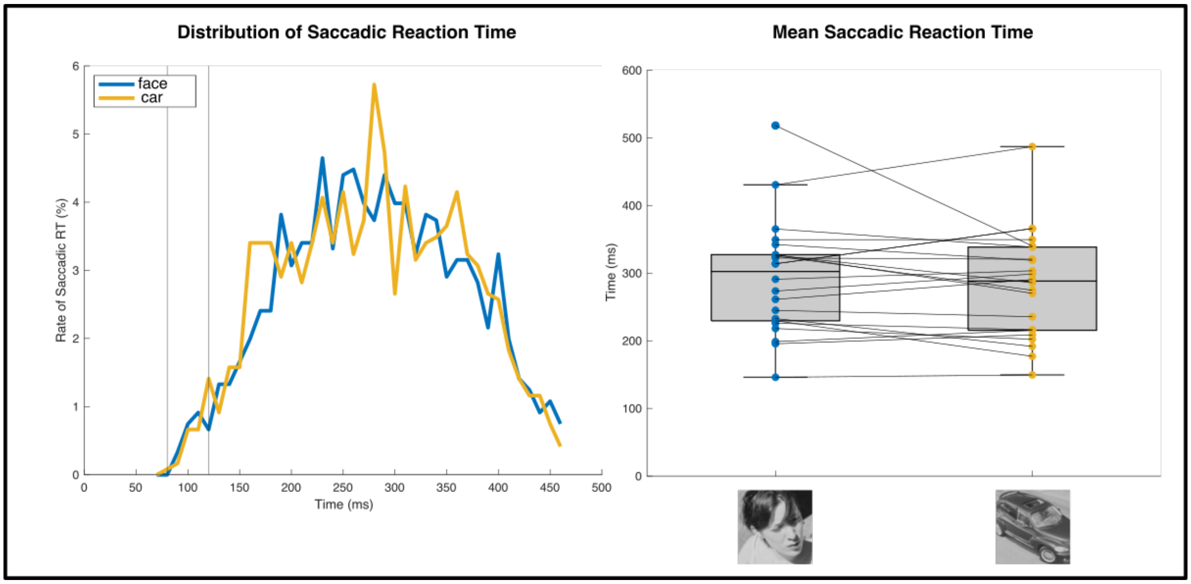


Figure 9. *Experiment 1: Saccadic Reaction Time. (n=22) Vertical black lines demark express saccade epoque (80-120ms). Paired T-tests were conducted to identify any effects of instruction within 10ms bins. This was followed with a false discovery rate analysis. No significant differences were identified. A paired T-test of the mean reaction time also found no significant difference.*

3.2 Experiment 2: Face Vs Scrambled Face

Experiment 1 used the same stimuli as the Crouzet and Thorpe (2011) study, and yet failed to find any significant influence of faces on either ESRs or express saccades. Experiment 2 was meant to serve as a simplified version of experiment 1. The only difference between the two experiments were the stimuli used. Unlike experiment 1 which employed a collection of 20 greyscale pictures (10 of faces and 10 of cars), experiment 2 employed one black-and-white high-contrast face-like symbol with its scrambled counterpart. The face-like symbols were modelled after those used by Nguyen et al (2014) who found that high-contrast face-like symbols elicited a stronger and earlier response in monkey SC and Pulvinar than natural faces. The images in experiment 1 were normalized for spatial frequency and luminance which reduced the contrast and sharpness. In experiment 2, scrambling the elements of the face-like symbol controlled for luminance and spatial frequency without impacting the clarity of the images. We predict that ESR expression will be stronger in response to the high contrast stimuli used in this experiment. All the analyses used for the first experiment were repeated for the second.

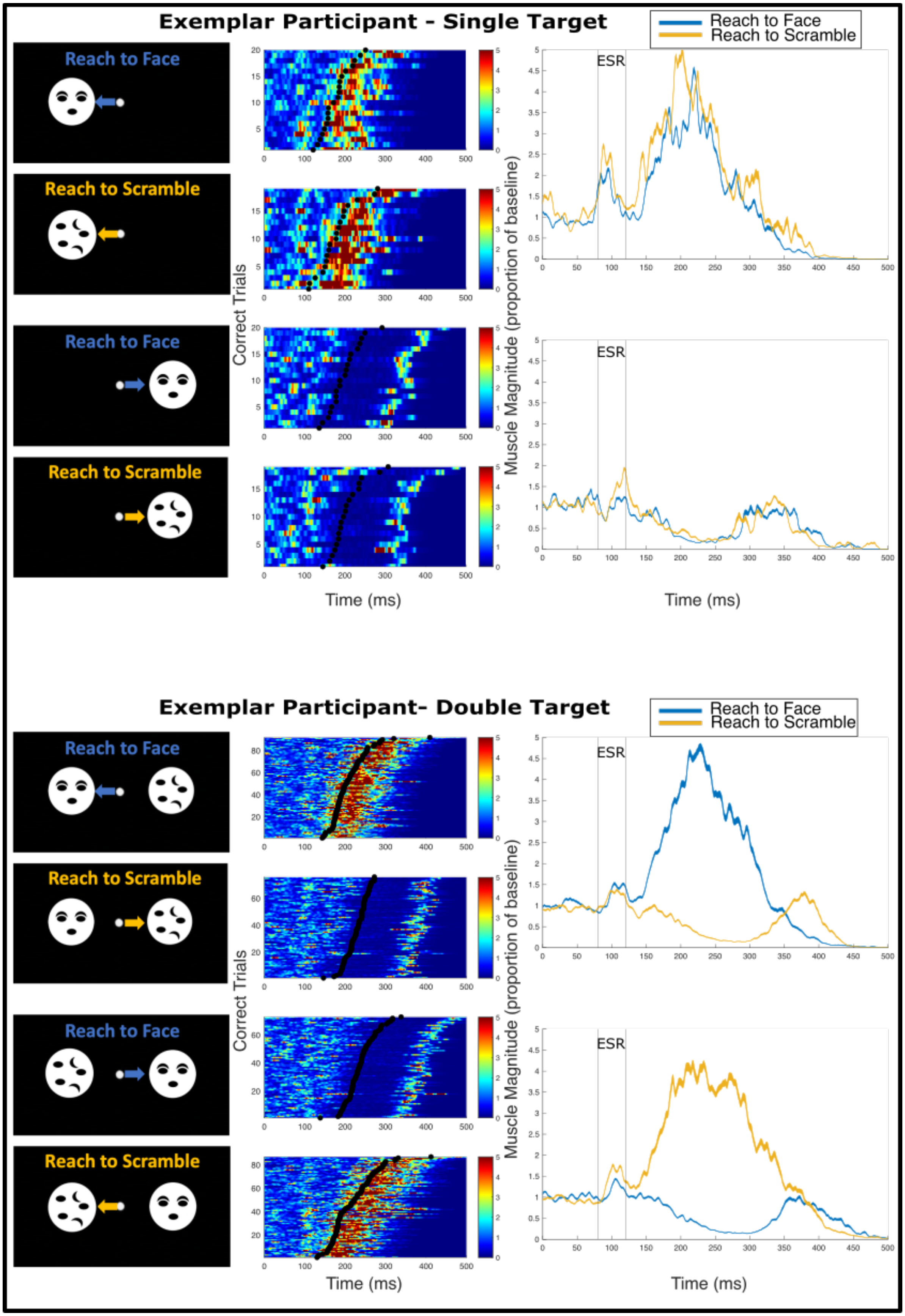
3.2.1 Experiment 2: Error Rate

As previously mentioned, trials were categorized as either correct, wrong-way, or rejected. Like the first experiment, we found no significant difference between the rate of correct and wrong way as measured by a one-way repeated measures ANOVA (F (3,72) =.901, p=.445). These results imply that image categories and direction of the stimulus had no impact on the participant's ability successfully reach towards the targets.

3.2.2 Experiment 2: EMG

As previously mentioned, when interpreting the EMG results, one must consider the muscle being recorded. Since the electrodes are placed on the right pectoralis major muscle an increase in muscle activity from baseline precedes movement to the left and the decrease from baseline precedes movement to the right.

In figure 10, we show a representative participant. The first 4 rows show the data for a single-target condition. The ESR is visible as an increase in muscle activity around 80ms in the first two rows when the target is towards the left. Similarly, the ESR is expressed as a decrease in muscle activity around 80ms in rows 3 and 4 when the targets are on the right. Compared to experiment 1 (see figure 4), the ESR in the single-target conditions appears to be more robust in our exemplar participant in experiment 2 (figure 11). The second section shows data from the double-target conditions. Since there is a target to the left and right to the arm the ESR is lower in magnitude compared to the single-target condition.



Exemplar Participant - Single Target

Exemplar Participant- Double Target

Figure 10. *Experiment 2: EMG data for exemplar participant. EMG data is normalized to baseline on a trial-by-trial basis. Trials in heat plots are organized by reaction time which is denoted by black dots. Line plot shows the mean EMG activity and standard error of the mean for the first 500ms following stimulus onset for correct trials in each condition.*

As with experiment 1, the main prediction of this experiment is that the ESR will display a preference for faces. To test this prediction, the same three statistical comparisons employed in experiment 1 were repeated in experiment 2.

The first comparison was aimed at identifying any effect of target type on the ESR when a single target was presented (face or scrambled face) to the participant (figure 11). This comparison is modeled on the findings that saccades occur faster in response to faces than other categories of visual stimuli (Bannerman et al., 2009). Like experiment 1, we did not find any time points during the ESR epoch where the EMG magnitude was significantly different in experiment 2. Therefore, the stimulus type did not impact ESR expression in a single-stimulus condition.

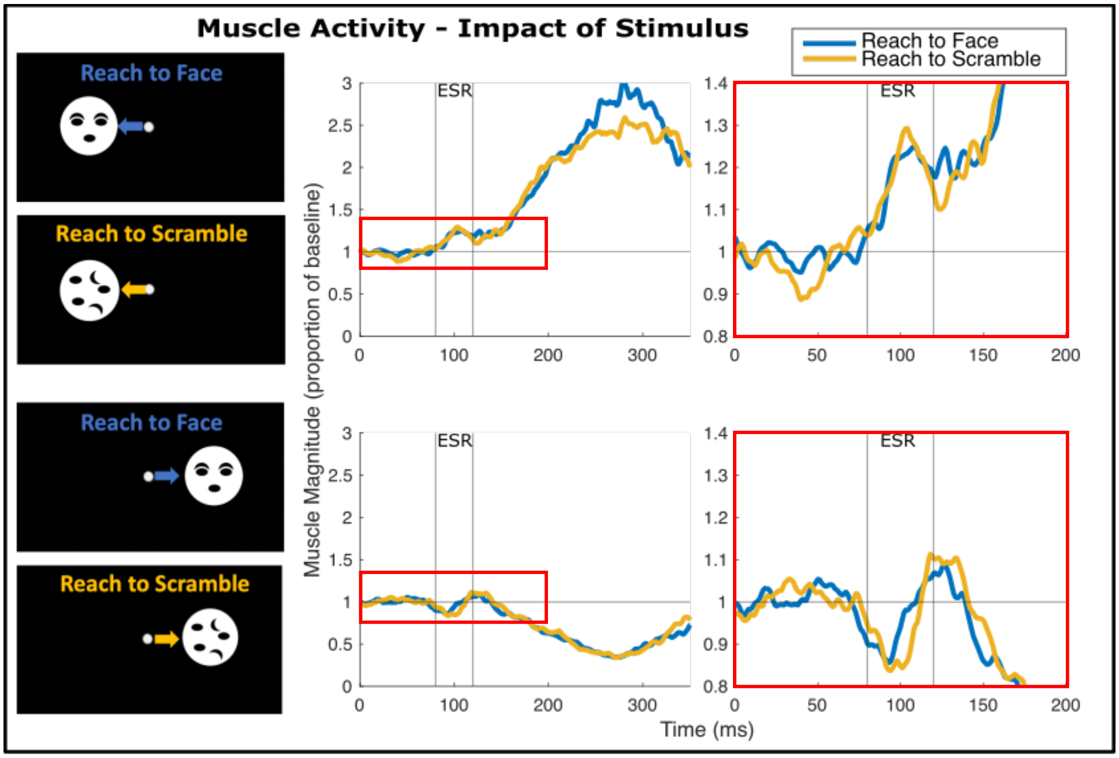


Figure 11. *Experiment 2: Impact of Stimulus on ESR. The first column shows mean muscle activity for correct trials across participants for the first 350ms following stimulus onset (0ms), including both the ESR (80-120ms) and voluntary activity (150ms +) (n=19). The second column focuses in on the ESR. At no point was a statistical difference in muscle activity identified within the ESR epoch, denoted by the vertical black lines.*

The second comparison was aimed at identifying any effect of *instruction* on the ESR during trials where the participants were presented with two targets and have a *choice* between the face and car in a two-target condition (figure 12). This comparison is modelled after the saccadic choice task completed by Crouzet and Thorpe where they found that participants made fewer errors in the face task and more express saccades towards faces. In the context of the ESR, since the same exact images are projected on the retina, any variation in the ESR can be attributed to the task set as determined by the instruction given to the participant for that given block (look towards the face or look towards the scrambled face). In this analysis, we found that when the instructed target was on the left, the magnitude of muscle activity during the ESR epoch was larger than when the target was on the right. This would indicate that the ESR is functioning to direct the arm more to the left when the target is on the left and more to the right when the target is on the right. Surprisingly, this effect was observed whether or not the instructed target was a face or a scrambled face. This suggests that the ESR can be impacted by task set, to identify specific targets and direct orienting movements towards them.

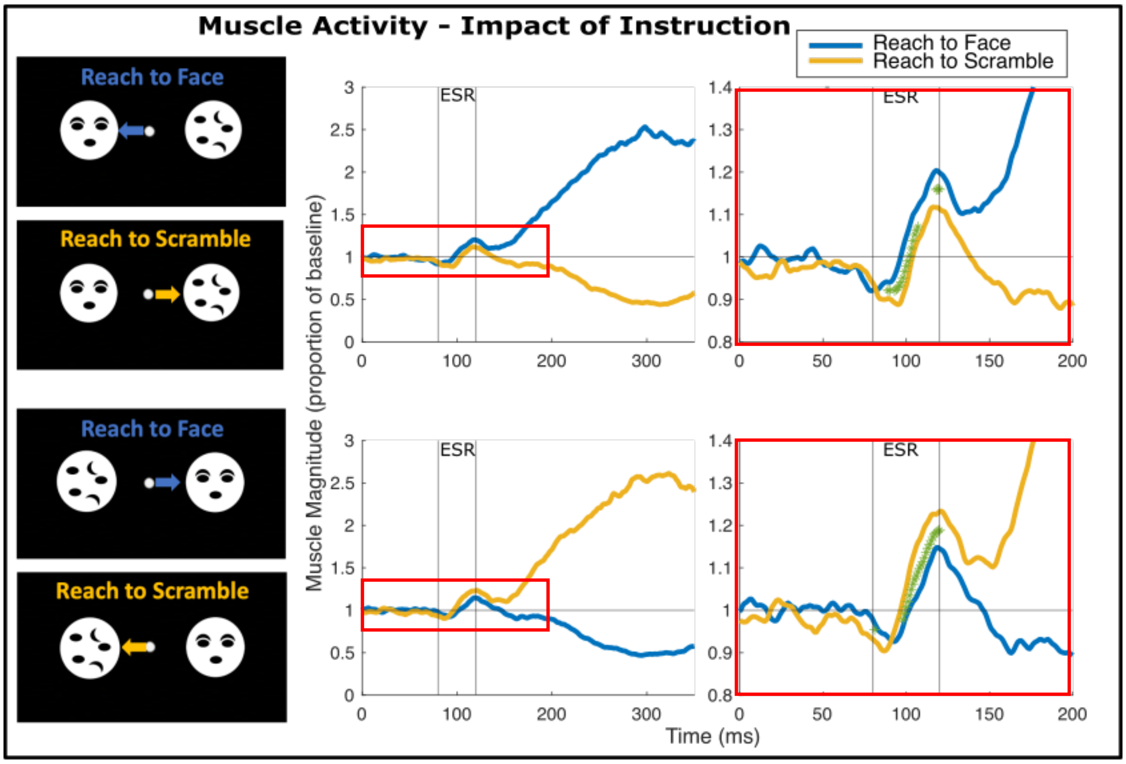


__Figure 12.__ Experiment 2: Impact of Instruction on ESR. Mean muscle activity for correct way trials across participants (n=19). Green asterisks denote time points where a significant difference was identified using a paired timewise rolling T-test followed by a false discovery rate correction.

The third analysis is a comparison between the single-target and double-target trials (figure 13). Since the ESR in the two-target condition can be interpreted as a competition between two different ESRs, one driving the right arm to the left and the other to the right, this analysis allowed us to investigate the effect of the distractor on the ESR. If these stimuli were optimal at eliciting the ESR, the magnitude of muscle activity across the ESR epoch should be significantly different between the single- and double-target conditions. In this analysis, we found that ESR activity was significantly different in the direction of the target when no distractor was present. Muscle activity was higher when the target was to the left and lower when it was to the right. Given that this effect was not observed in experiment 1, the findings in experiment 2 suggest that the ESR in this experiment was tuned to the specified target such that it is this target that optimally elicits the ESR, independent of whether it was a face or a scrambled face.

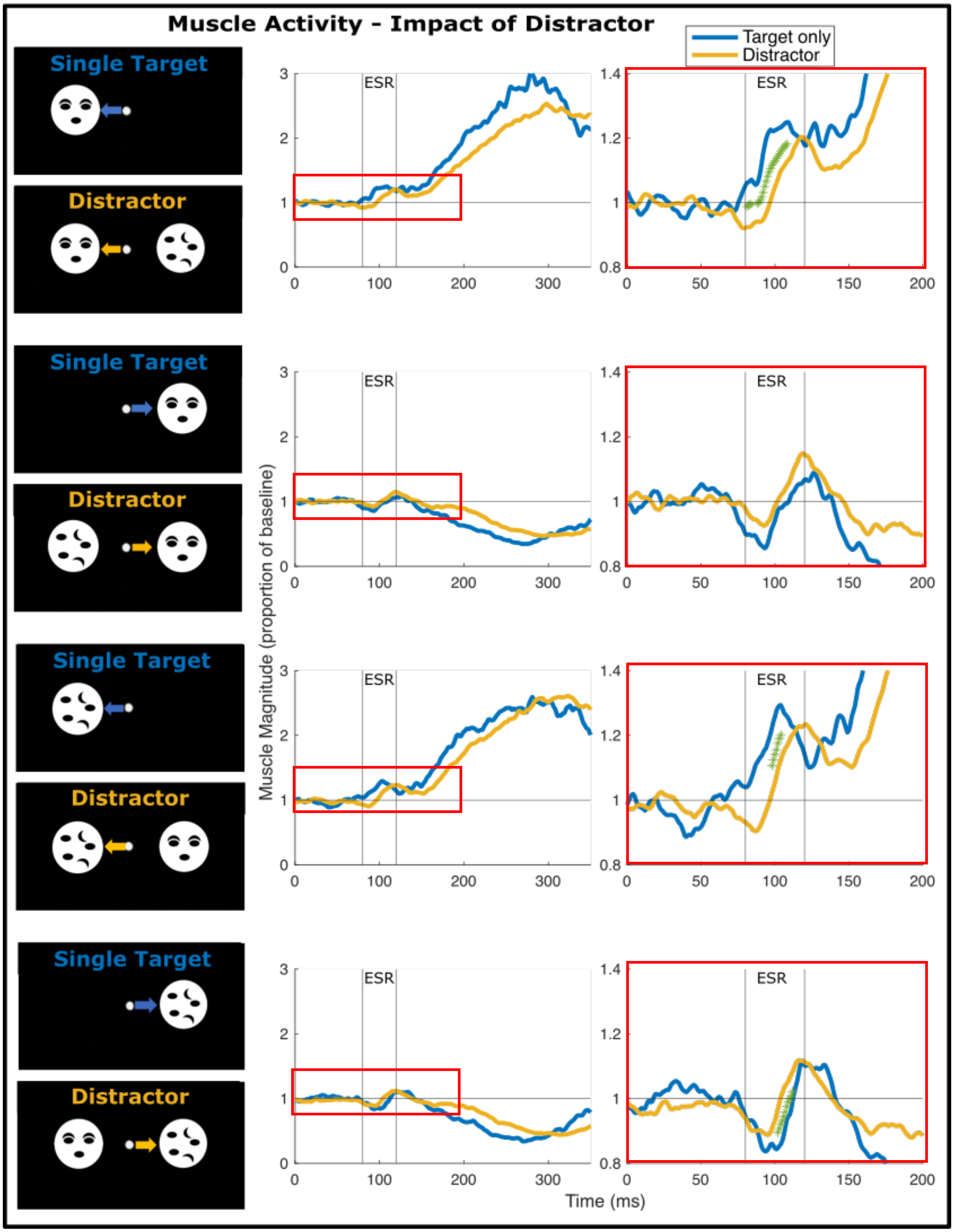

Muscle Activity - Impact of Distractor
Target only
Distractor
Single Target
Distractor
ESR
Muscle Magnitude (proportion of baseline)
Time (ms)
0
100
200
300
50
150
0.8
1
1.2
1.4
2
3

Figure 13. *Experiment 2: Impact of Distractor on ESR. Mean muscle activity for correct way trials across participants (n=19). Green asterisks denote time points where a significant difference was identified using paired timewise rolling T-tests followed by a false discovery rate correction.*

3.2.3 Experiment 2: Kinematic Reaction Time

Since a hypothesized purpose of the ESR is that it facilitates more rapid limb movement, an analysis of reach reaction time was conducted. We predicted that limb movements towards faces would be initiated more rapidly than towards the scrambled image. Since participants completed the task with their right arm holding a manipulandum that was loaded with a force towards the right, movements in each direction were compared between the two target types. A paired T-test followed by a false discovery rate correction was used. We found no significant difference in the reach reaction time (figure 14). We found that the mean reach reaction time in experiment 1 across all conditions (~280ms) was significantly shorter than the reaction time in experiment 2 (~310ms), using a paired T-test [t (18) =4.71, p<0.001].

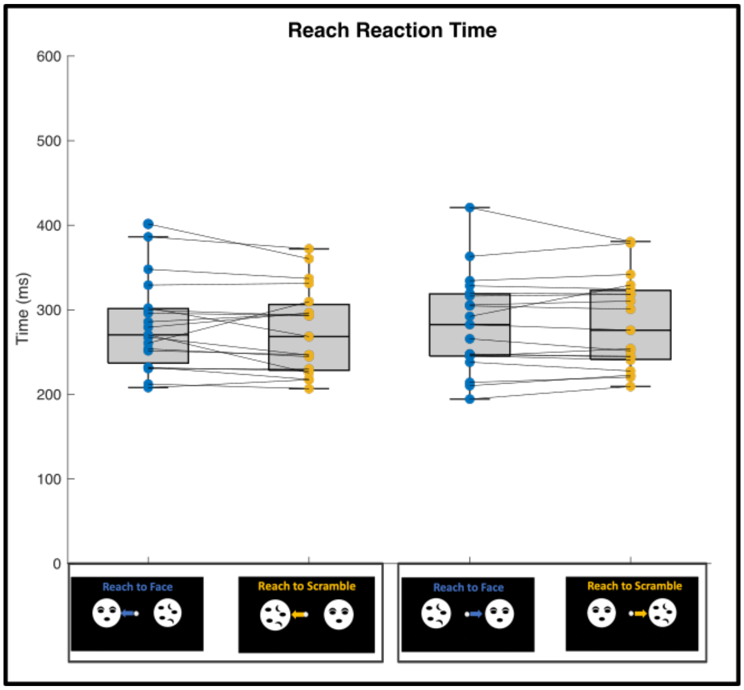


Figure 14. *Experiment 2: Mean Reach Reaction Time. (n=19). No differences were identified.*

3.2.4 Experiment 2: Saccadic Reaction Time

The final analyses were aimed at identifying if the findings relating to the preference of express saccades for faces were replicated within our experimental paradigm. An analysis of the mean saccadic reaction time across participants found no impact of condition. Figure 15 shows the mean frequency distributions of the saccades across time (10ms bins) for 22 participants. A rolling paired T-test comparing the percent likelihood that a saccade will occur within a given time bin found no difference between the distributions of saccades towards faces or cars. Additionally, as seen in experiment 1, this setup was not optimal for eliciting express saccades, since the number of express saccades was very small as a percentage of all saccades performed.

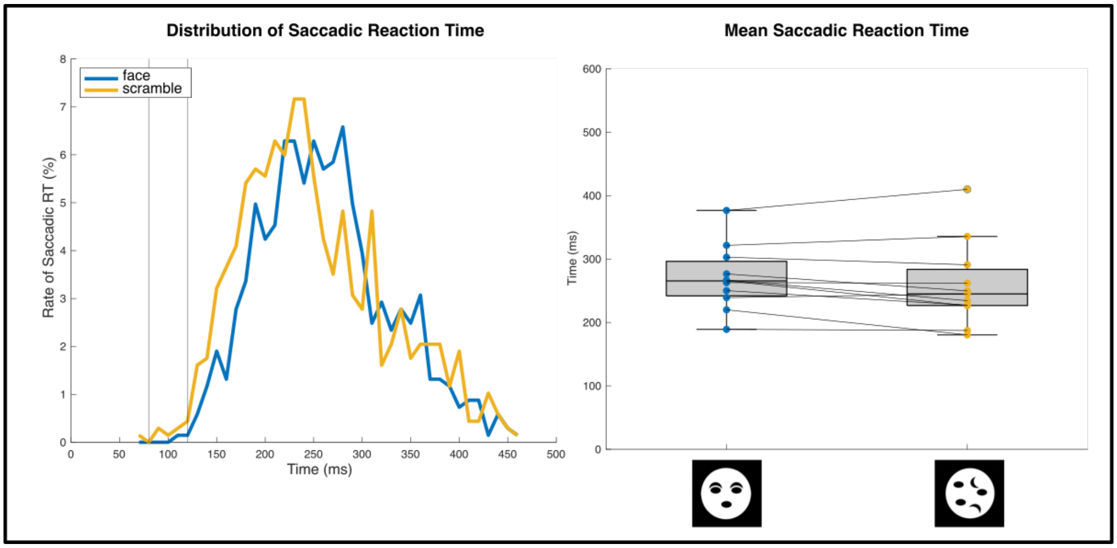


Figure 15. *Experiment 2: Saccadic Reaction Time. (n=11) Vertical black lines demark express saccade epoque (80-120ms). Paired T-tests were conducted to identify any effects of instruction within 10ms time bins. This was followed by a false discovery rate analysis. No significant differences were identified. A paired T-test of the mean reaction time also found no significant difference.*

4 Chapter 4: Discussion

4.1 ESR Feature Detection Not Limited to Faces

Based on our hypothesis, we predicted that the ESR would exhibit a preference for faces compared to less evolutionarily relevant images like cars and scrambled faces. In both experiments, there was no observed effect of target type. However, an effect of instruction on the ESR was observed, but only in experiment 2. In this experiment, right pectoralis recruitment was greater during the ESR epoch when the instructed stimulus was presented to the left. This muscle recruitment would aid in directing the right arm towards the instructed target. Surprisingly, this pattern of results was unaffected by the type of instructed target (face or scrambled face). One potential reason that this phenomenon is occurring may be that the face is present in both block types. As a consequence, the pro-scrambled face condition can be re-interpreted as an anti-face condition. Therefore, if the feature detector is unmodifiable and solely sensitive to faces, the ESR could reflect the same exact observed behaviour if the task is performed as either a pro-face or an anti-face condition.

Another consideration is that this effect was seen because of the influence of voluntary movement, whereby a higher ESR is induced when the voluntary movement involved a contraction of the muscle and a lower ESR when it involved a relaxation. Given that this is a choice task, however, the voluntary muscle recruitment was delayed in the double-target condition, starting at ~150ms following stimulus onset, compared to the single-target condition, where the voluntary muscle recruitment begins earlier (~130ms; figure 13). The delay in the voluntary activity in the double target condition ensures that muscle recruitment during the ESR interval is not affected by the recruitment related to the subsequent arm movement.

4.2 Neural Origins of ESR Modification Based on Instruction

There are several possible neural origins through which these computations underlying target selection by the ESR may be occurring. In our study, we identified ESR activity as early as ~70ms. Since a temporal uncertainty of 100ms is introduced into the task, this indicates that this is unlikely to be predictive activity. Furthermore, if the activity at this early latency is predictive, it should be uniform across all conditions. However, in the single-target conditions (see figure 11), the activity at 70ms diverts from baseline in the direction of the voluntary movement. This latency is a very short time for the signal from the eye to travel to the brain, down the spinal cord, and to the pectoralis muscle. Therefore, the computations relating to the ESR must be completed outside of the cerebral cortex where visual areas in the ventral stream first identify specific images, like faces, at a latency of ~ 130ms (Bentin et al., 1996; Collins & Olson, 2014). It is therefore highly likely that the ESR's selection of the instructed target is mediated through subcortical structures, more specifically the SC. As previously discussed, the SC has a large breadth of connections from the cerebral cortex, basal ganglia (BG), and thalamus, and it has the necessary connectivity with downstream premotor structures in the reticular formation. Recent theories regarding the roles of the BG and thalamus in the computations underlying motor planning may explain the findings of this study (Arber & Costa, 2022; Worden et al., 2021).

Arber and Costa (2022) argue that a BG-brainstem circuitry is responsible for the execution of adaptive behaviour, such as would be required in our choice task (figure 16). Specifically, modulation of the activity in the SC for the execution of saccades is controlled through reciprocal excitatory and inhibitory connections between the SC and the BG.

Additionally, within their model, each node in the network between SC and BG is not simply to relay information, but also to integrate additional inputs from sensory systems and other brain regions like the thalamus or the cerebral cortex. These chains are often found to create loops, both short (e.g. within the brainstem) and long (e.g. SC to motor cortex via the BG) in distance, allowing for the selection and refinement of orienting behaviours. Further, Worden and colleagues (2021) have theorized that the thalamus functions like a blackboard where various potential motor plans can be pre-computed, before being selected and executed.

Another potential contributor to this phenomenon is the prefrontal cortex (PFC). A host of studies have established that the PFC is crucial for the updating, implementation, and selection of task set (Sakai, 2008). Specifically, in the context of an object-matching task, electrophysiological studies have found that the PFC contains match and non-match neurons, which respond selectively in response to instructed targets with a latency of ~150ms. In the context of this current study, the latency of the response is too late to be directly responsible for the initiation of the ESR (~70-130ms) or even the voluntary EMG activity which begins at ~150ms (Wallis et al., 2001). However, given that the PFC is involved in task-based computation, it may be involved in the process of pre-setting the feature detectors and pre-computing motor plans in the subcortex to initiate the ESR. Indeed, there is evidence that the dorsolateral PFC sends task-selective signals to the SC, which pre-set the SC to perform pro or anti-saccades based on instruction (Johnston & Everling, 2006).

The theorized function of the aforementioned circuitry may be the source of the ESR behaviour identified in this study, whereby a task set may be used and implemented to pre-compute two potential behaviours (reach to the right or reach to the left), while modifiable feature detector in the brainstem could function as a go/no-go signal for this pre-constructed motor plan, allowing for the selection of the target without the necessity of visual information being processed in the cerebral cortex.

4.3 Failure to Replicate Express Saccade Findings

The primary inspiration for the design of this task was the study conducted by Crouzet and Thorpe (2011). In this study, participants were presented with two simultaneous images of a face and a vehicle and were asked to make a saccade towards the face in one block and the vehicle in another block. They found that participants could more reliably make a saccade towards pictures of faces (~100ms) earlier than they could towards pictures of vehicles (~140ms). Additionally, participants made more errors during the vehicle block than during the face block.

In the oculomotor version of both experiments conducted in our study, there were very few express saccades, implying that the task was not optimal at eliciting express saccades. Since the ESR is hypothesised to be initiated by the same subcortical circuitry, these experiments may not be an optimal test of the ESR's sensitivity to faces. The results of this study should be viewed in the context of this observation.

Several efforts were made in designing the experiment to maximize the possibility of replicating the Crouzet and Thorpe (2011) finding. Images from the same stimulus bank as the one used in their study were used in experiment 1. These images were normalized to control for spatial frequency and luminance. The images were presented to be within 10 degrees of the central fixation point, as in the previous study. In consideration of the potential influence of task set on saccadic performance, all participants conducted the saccadic task before they were introduced to or practiced the reaching task.

One potential reason for the failure to induce express saccades is the variation in stimulus time up to 100ms which was introduced to reduce temporal predictability and ensure that participants made fewer false early movements in the task. Previous studies have shown that temporal unpredictability reduces the likelihood of express saccade occurrence (Rohrer & Sparks, 1993). Additionally, since the experiment was conducted in the Kinarm Endpoint Robot, the stimuli were presented in the lower visual field, instead of the upper visual field as was the case in the Crouzet and Thorpe (2011) study. Further, since the Kinarm setup makes stabilization of the head difficult participants were asked to rest their heads on the Kinarm device. However, variations in the height and size of the participants certainly resulted in variations of viewing angle and location of the eyes, potentially putting the images outside of the 20-degree window prescribed in the methods of the previous study.

4.4 Differences in ESR Between Single and Double Target Conditions

The choice task offers an opportunity to explore how the different types of stimuli affect the ESR. In addition to allowing a direct contrast of different stimuli, this paradigm delays voluntary movement (see figures 5-7 & 11-13), allowing for the investigation of the ESR independently. This is because muscle recruitment during the ESR epoch is less likely to be contaminated by the subsequent voluntary muscle recruitment. Since two stimuli are being presented in this task, the ESR takes on a unique appearance compared to tasks where only one stimulus is employed. Notably, ESR expression was muted and deviated less from baseline in the double-target conditions compared to the single-target conditions. Further, in lieu of presenting either as a sustained suppression or increase in activation the muscle appears to experience an initial suppression followed by an increase in activation. This can be interpreted as a combination of two different ESRs which occur in quick succession, each towards one of the two simultaneous targets.

The surprising finding that the ESR varies between conditions only in the two target conditions and not in the single target conditions in experiment 2, may indicate that when a single target is presented that the ESR experiences a ceiling effect (at least in the context of this particular experiment), whereby maximum activation is reached independent of the target. This finding is notable, as it establishes a way of testing the ESR's preference for different targets, by setting up a competition between them. Additionally, the choice task could be expanded to include more targets in order to test the ESR in a more real world like environment.

4.5 Differences in ESR Expression Between Experiments

The findings relating to the effect of instruction were different between experiment 1 and experiment 2. There are two reasons why this likely occurred. First, in experiment 1 participants were presented with images selected from a stimulus bank of 20 images composed of 10 face and 10 car pictures. In experiment 2, participants needed to identify only one potential target, which remained consistent, either the face-like symbol or its scrambled counterpart. This factor impacted the ability of the participant to predict what target they needed to select. Second, the images in experiment 1 were normalized to control for spatial frequency and luminance. This reduced the images' contrast and sharpness. In experiment 2, scrambling the elements of the face-like symbol controlled for luminance and spatial frequency without impacting the clarity of the image. Both of these factors likely contributed to the participants' ability to detect and initiate movements towards the targets, making experiment 2 easier than experiment 1. This is reflected in the statistical difference in mean reach reaction time between both tasks (Experiment 1: ~310ms, Experiment 2: ~280ms). Further, the high-contrast stimuli employed in experiment 2 elicited stronger ESRs than the low contrast stimuli in experiment 1 (see figures 5 and 11). A stronger ESR in response to the stimuli in experiment 2, is in line with our predictions. This finding correlates with electrophysiological recordings showing that similar high-contrast stimuli result in higher activation in the SC (Nguyen et al., 2014).

4.6 Limitations and Future Directions

As previously discussed, the result of this experiment should be viewed in the context of the saccadic reaction time findings. Since this study does not replicate the findings of express saccades, another study using stimuli that replicate the Crouzet findings should be conducted to establish that the ESR truly does not have a preference for faces compared to other stimulus types. Furthermore, additional analysis of the current data (supplemented perhaps by additional experiments) could be carried out to identify any temporal links between express saccades and the ESR.

The inconsistency of the kinematic findings may point to a deficiency in the methodology that has yet to be identified. It might be useful, for example, to test the actual timing of the presentation of the different targets in the different conditions (perhaps with the use of light-sensitive diodes) to ensure that stimulus presentation is consistent across the stimulus types.

Given that the choice task has proven to be a way through which the parameters of the ESR could be tested, a wide variety of questions could be answered using this simple task. Primarily, regarding the current finding, several questions remain unanswered. Namely, what caused the discrepancy between the findings in experiments 1 and 2? This could include an exploration of the difference of the impact of image quality, to test the sensitivity of the feature detectors responsible for our observed finding. Further, the impact of the number of potential images may be explored as a possibility for the difference. For example, could the effect of instruction of the ESR be observed in experiment 1 if it was repeated with a stimulus bank of 10 images rather than 20?

The surprising finding that the ESR is sensitive to instruction not only in the choose face block in experiment 2 but also in the choose scramble face block, requires follow up. Firstly, as previously mentioned the pro-scrambled face condition can be re-interpreted as an anti-face condition. Therefore, this study should be replicated with two abstract patterns, which do not resemble any evolutionarily relevant objects to ensure that the observation is not dependent on the inclusion of a face or other relevant real-world objects. The quality of the visual stimuli should also be investigated. For example, what may be the impact of the location of the stimulus as relating to the fovea? What may occur to the ESR if more than one of the instructed targets are presented (Ex. Two faces)? How might this behavior vary if the targets did not appear in predictable locations? Since the stimuli used in this study were black and white, another question is whether this feature detector is sensitive to color? These and many more questions remain regarding the ESR’s ability to respond to specific instruction and visual targets.

Another limitation of the study is that only recordings from one muscle, the pectoralis major, raising the question of what might be occurring in the antagonist muscle, the deltoid. An important question is what form the ESR takes in the double target condition. Specifically, does the ESR in the deltoid mirror that of the pectoralis major, rising above baseline when the other is below baseline and vice versa, or does the deltoid ESR also display an initial suppression in activation before an increase in activation. If the former is true, it would imply that each phase of the ESR observed in this study (suppression then activation) is in itself an independent ESR. If the latter is true, then the initial suppression may be interpreted as a global suppression of muscle activation, before both ESRs occur in the latter half of the ESR epoch, with the peak above baseline being the outcome of the competition.

4.7 Conclusions

The results of this study offer a novel way of evaluating the function and neural origins of the ESR. Firstly, the choice task offers a simple method to test the ESR’s affinity for stimulus types. This method may also be expanded to include more stimuli, to better model the impact of the ESR in a real-world context where one may encounter many possible targets to select from. Secondly, the statistical method used to analyze the ESR in this study is a novel way of identifying changes in the ESR through the identification of small but consistent changes in EMG activity across participants. Finally, the findings indicate that the ESR is more sensitive to instruction than previously thought, opening the door to further exploration of the limits of this capability.

Our findings do not support our initial hypothesis that the face is a uniquely important target which elicits a preferential response from subcortical regions mediating the ESR.

Surprisingly, however, we found that there are feature detectors involved in mediating the ESR and that these feature detectors are malleable and responsive to instruction, likely through top-down control from the cerebral cortex. This deepens our understanding of how top-down control affects the ESR, showing not only that task set impacts motor planning, as has been previously identified, but also that sophisticated feature priming underlies the ESR. This lends support to the understanding of the ESR as an unconscious fast-response system, helping mediate the selection and execution of movements before conscious visual perception or motor commands in the cerebral cortex occur.

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Appendices

Appendix A: Letter of Information, Consent Form, and Screening Form

Western
The Brain and
Mind Institute

Salience responses on human arm muscles during reaching

LETTER OF INFORMATION

Salience responses on human arm muscles during reaching

Principal Investigator: Dr. Brian D Corneil
Robarts Research Institute, [redacted]
Western University
[redacted]

Co-Investigators: Dr. Timothy Doherty MD, PhD, Dr. Melvyn Goodale, PhD, Dr. Paul Gribble, PhD

Invitation to Participate:

You are being invited to participate in a research study designed to investigate the role of your shoulder and chest muscles during reaching movements.

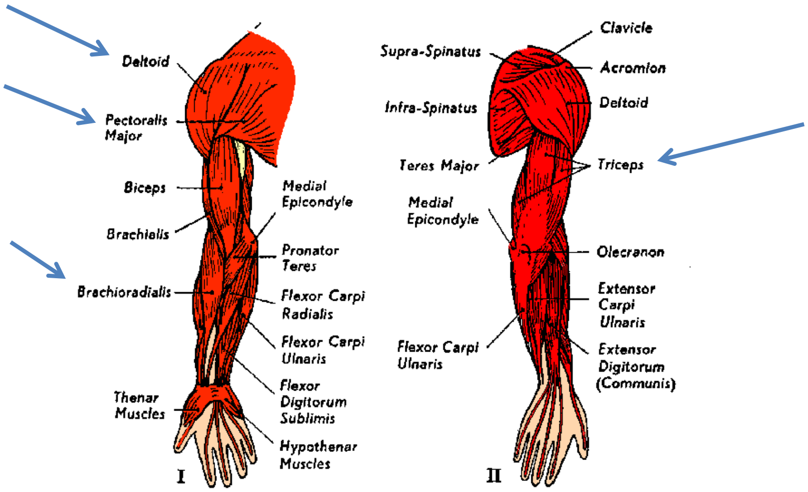
Brief description and Purpose of the Study:

The study of reaching movements provides a window into how the brain works. Previous research has demonstrated that arm muscle activity shows fast responses to visual stimuli.

The aim of this study is to further investigate the activity of human arm muscles, to see if they can provide information about how reach movements are controlled by the central nervous system. This information could be helpful in further diagnosing and caring for individuals with neurodegenerative and neurovascular diseases, or soft-tissue injuries. 100 participants are being enrolled in this study.

Protocol:
You are being invited to participate in a study designed to investigate the role of arm muscles during various reaching tasks requiring you to make arm movements in response to visual and/or auditory stimuli. You will be asked to spend between 2 to 4 hours in the Western Interdisciplinary Research Building of Western University, London, ON. Because the study may involve intramuscular recordings, a small, disposable needle electrode may be used to insert fine recording wires into various muscles in the arm and shoulder (4 maximum). The needle insertion will be performed by either Dr. Doherty or other trained individuals under his supervision, and will be guided via ultrasound images taken prior to insertion. These ultrasound images will help us localize the appropriate targets for the fine-wire electrodes. Ultrasonography is painless, and only requires placing a small amount of conductive jelly and slight pressure from the ultrasound probe. Adhesive surface electrodes will also be placed on the skin over the shoulder or arm muscle. Following electrode placement, you will then be asked to perform various movement tasks that will require changes in arm position. Sufficient instructions as to the details of these tasks will be provided, and short practice sessions may also be run prior to electrode placement.

The following muscles will be tested (See Fig. 1 below for locations): 1) *Deltoid posterior (back of right shoulder muscle)*; 2) *Pectoralis major (right chest muscle)*; 3) *Brachioradialis (outer forearm muscle)*; 4) *Triceps lateral (outer side, back of upper arm muscle).*



Muscles of the Right Upper Limb.
I, anterior aspect. II, posterior aspect.

FIGURE 1. Muscles of the arm.

During data collection for the muscle activity, eye movements as well as two dimensional arm movements will be measured. Eye movements will be measured non-invasively via a head mounted video-oculography (eye movement) system (EyeLinkII). Eye Link II is a video based eye movement tracking system. You will be asked to wear a padded headband on which miniature cameras are mounted. The Eye link II tracks the movement of your cornea (the front part of your eye) to give us a measure of your eye movements. Arm movements will be measured non-invasively via the tracking of the position of a robotic arm apparatus that you will grasp. This robotic arm may be programmed to exert mild forces upon your reaching movements, essentially making them slightly slower. Arm movements will be made in response to visual stimuli presented on a screen in front of you, and/or to auditory stimuli presented via small headphones placed in your external auditory, or via headphones placed over your ears. Sounds will consist of brief (up to 500 ms or less) tones that may be loud (up to 120 dB peak SPL), but are not damaging.

Potential Risks and Side Effects:

1. The procedures used are standard procedures used in routine EMG testing. There is mild to moderate discomfort associated with insertion of the needle for the fine-wire electrodes. This discomfort is generally less than that associated with having blood drawn, and only persists for the time of needle insertion. Dr.

Tim Doherty (who will supervise the needle electrode insertions) is a practicing physician and clinical electromyographer at London Health Sciences Centre with over 15 years of experience in performing intramuscular EMG.

2. Insertion of the needle electrode is associated with a low risk of muscle bruising and mild discomfort for 24 to 48 hours.
3. There is an extremely low risk of skin infection (less than 1 in 10,000) associated with the needle electrode insertion. Again, this would be similar to that associated with a standard vaccination or blood test.
4. There is no risk or discomfort associated with handling the robotic arm apparatus. This apparatus is simply a handle attached to a 2-joint robotic arm that is capable of passively receiving and actively generating forces.
5. There is no risk or discomfort associated with ultrasound, eyetracking, or surface recordings.
6. There are no known risks or discomfort associated with delivering sounds to the ear.

Direct Benefits of Participation in the Study:

There are no direct benefits to you as a participant in the study. Participation in the study will contribute to the advancement of knowledge about how the brain works.

Voluntary Participation

Participation in this study is voluntary. You may refuse to participate, refuse to answer any questions, or withdraw from the study at any time with no effect on your academic or employment status. You do not waive any legal rights by signing the consent form.

Compensation:

You will receive $20.00/hour in appreciation for your participation and to cover any expenses such as parking. This will be paid, even if you do not complete the study.

Confidentiality:

The participant consent form will be maintained in the locked file cabinet of Dr. Brian Corneil and will not be used to identify your data by the other experimenters. If the results of the study are published or presented, your name will not be used. If you do withdraw your consent for us to use your data please inform Dr. Corneil and your data will be immediately destroyed. Your data will be kept on secure password protected networks, and those outside from the study will not have access to the information. Unique identifiers based on your initials will be used to index your data. Paper records of your participation will be destroyed after 7 years. Non-identifiable electrode data will be stored permanently on the experimental computer and an external backup drive.

Questions or Concerns Related to the Study:

If you have any questions or concerns about the conduct of the study, please contact:

Dr. Brian D. Corneil
Robarts Research Institute, [redacted]
Western University
[redacted]

OR

Dr. Timothy Doherty
Dept. of Physical Medicine and Rehabilitation
Western University
[redacted]

Your Questions:

If you have a question about your rights as a research participant or about the conduct of the study, you may contact: Patient Relations Office, LHSC, [redacted] [redacted]

CONSENT FORM

Salience responses on human arm muscles during reaching

I have read the Letter of Information, I have had the nature of the study explained to me, and I agree to participate. All questions have been answered to my satisfaction.

Participant Name (please print): ____

Signature: ____

Date: ____

Name of person obtaining consent: ____

Signature: ____

Date: ____

Western
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Salience responses on human arm muscles during reaching

Participant Screening Form

Name: ______________________________

Phone: ______________________________

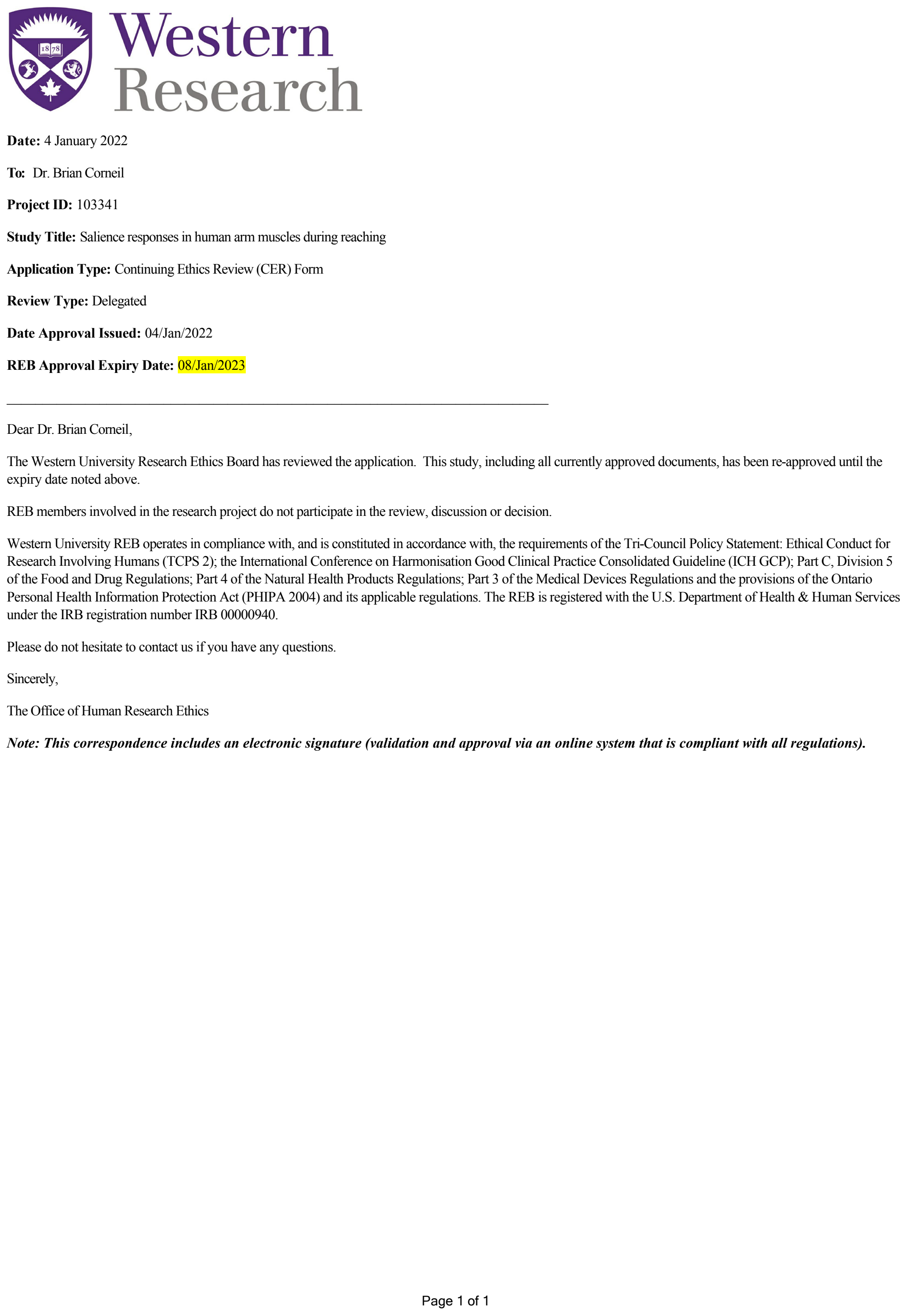
Age: ______

DETERMINATION OF ELIGIBILITY FOR VISUOMOTOR STUDIES USING INTRAMUSCULAR ELECTROMYOGRAPHIC RECORDINGS

	YES	NO
* Do you have any history of easy bleeding or bruising?	____	____
* Do you have any history of fainting?	____	____
* Have you ever had an epileptic seizure?	____	____
* Have you ever had a head injury?	____	____
* Have you had any uncorrected visual disorders?	____	____
* Have you had any movement disorders?	____	____
* Have you sustained significant trauma to your arm and/or shoulder?	____	____
* Are you left-handed?	____	____
* Do you have any musculo-skeletal disorders?	____	____
* Are you taking any medications that could make you drowsy?	____	____
* Do you have a diagnosis of an Axis I disorder, family history of psychotic disorder, suicide, or psychiatric hospitalization?	____	____

Additional comments:
____
____
____

Appendix B: Ethics Approval



Western
Research

Date: 4 January 2022

To: Dr. Brian Corneil

Project ID: 103341

Study Title: Salience responses in human arm muscles during reaching

Application Type: Continuing Ethics Review (CER) Form

Review Type: Delegated

Date Approval Issued: 04/Jan/2022

REB Approval Expiry Date: 08/Jan/2023

Dear Dr. Brian Corneil,

The Western University Research Ethics Board has reviewed the application. This study, including all currently approved documents, has been re-approved until the expiry date noted above.

REB members involved in the research project do not participate in the review, discussion or decision.

Western University REB operates in compliance with, and is constituted in accordance with, the requirements of the Tri-Council Policy Statement: Ethical Conduct for Research Involving Humans (TCPS 2); the International Conference on Harmonisation Good Clinical Practice Consolidated Guideline (ICH GCP); Part C, Division 5 of the Food and Drug Regulations; Part 4 of the Natural Health Products Regulations; Part 3 of the Medical Devices Regulations and the provisions of the Ontario Personal Health Information Protection Act (PHIPA 2004) and its applicable regulations. The REB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000940.

Please do not hesitate to contact us if you have any questions.

Sincerely,

The Office of Human Research Ethics

Note: This correspondence includes an electronic signature (validation and approval via an online system that is compliant with all regulations).

Appendix C: Edinburgh Handedness Inventory

Edinburgh Handedness Questionnaire

For each of the ten activities below, please tell us which hand you prefer to use and whether you ever use the other hand.

Which hand do you prefer when…

	Left or Right	Do you ever use the other hand? Yes or No
Signing		
Writing		
Drawing		
Throwing		
Using scissors		
Using a Toothbrush		
Using a Knife (without a fork)		
Using a Spoon		
Using a Broom (upper hand)		
Striking a Match		
Opening a Box (lid)		
Foot to Kick With		
Bat (swing)		

1. Do you consider yourself:

   Right-handed　　Left Handed　　Ambidextrous (both hands)

2. Is there anyone in your family who is Left-handed? Yes or No
   If yes, who____

3. Did you ever change handedness? Yes or No
   If yes, please explain____________________________________
   ____
   ____

4. Is there any activity not on this list that you do consistently with your left hand? If so, please explain ____
   ____
   ____

This handedness questionnaire was adapted from:

Oldfield, R.C. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia. 9(1):97-113. 1971.

Curriculum Vitae

Name:	David Youhanna Mekhaiel
Post-secondary Education and Degrees:	M.Sc. Neuroscience The University of Western Ontario London, Ontario, Canada 2020-2022 B.Sc. Major in Physiology The University of Western Ontario London, Ontario, Canada 2016-2020
Honours and Awards:	Undergraduate Summer Research Internship Award The University of Western Ontario 2020 Undergraduate Summer Research Award Natural Science and Engineering Research Council 2019
Related Work Experience:	Teaching Assistant The University of Western Ontario 2020-2022 Research Assistant Goodale Lab 2019-2020