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Express Arm Responses Appear Bilaterally on Upper-limb Muscles in Arm Choice Reaching Task

Abbreviated title: Express arm responses appear bilaterally

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Abstract

When required, humans can generate very short latency reaches towards a visual target, like catching a phone falling off a desk. During such rapid reaches, express arm responses are the first wave of upper limb muscle recruitment, occurring within ~80-100 ms of target appearance. There is accumulating evidence that express arm responses arise from signaling along the tecto-reticulo-spinal tract, but the involvement of the reticulo-spinal tract has not been well-studied. Since the reticulospinal tract projects bilaterally, we studied whether express arm responses would be expressed bilaterally. Human participants (n = 14; 7 female) performed visually guided reaches in a modified emerging target paradigm where either arm could be used to intercept a target once it emerged below a barrier. We recorded electromyographic activity bilaterally from the pectoralis major muscle. Our analysis focused on target locations where participants reached with the right arm on some trials, and the left arm on others. In support of the involvement of the reticulospinal tract, the express arm response persisted bilaterally regardless of which arm reached to the target. While the latency of the express arm response was the same on the reaching vs non-reaching arm, the response magnitude was slightly larger on the reaching arm, in part due to anticipatory muscle recruitment related to arm choice. Our results support the involvement of the reticulo-spinal tract in mediating the express arm response, and we surmise that the increased magnitude on the arm chosen to move arises from convergence of cortically derived signals with the largely independent express arm response.

New and Noteworthy: Express arm responses have been proposed to arise from the tecto-reticulo-spinal tract. These responses have been linked to the superior colliculus, but the involvement of the reticulo-spinal tract has not been well studied. Here we show these responses

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appear bilaterally regardless of arm choice when either arm can be used to intercept a newly appearing stimulus, supporting involvement of the reticulo-spinal tract. We propose this response is mediated largely independent of the volitional cortical related activity.

Keywords: express arm response, visually-guided reaches, EMG, reticulo-spinal tract

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Introduction

When time is of the essence, like when catching a phone knocked off a desk, visuomotor transformations can occur at times approaching the minimal afferent and efferent conduction delays. A useful marker for these rapid visuomotor transformations is an express arm response. The express arm response, which has also been termed the stimulus locked response (1) or rapid visual response (2), is a burst of upper-limb muscle recruitment that consistently occurs ~100ms after stimulus appearance, regardless of the reach reaction time (1, 3, 4). The term express arm response was coined to reflect the shared properties of this aspect of upper-limb muscle recruitment with the visual burst of visuomotor neurons in the intermediate and deep layers of the superior colliculus, and with express saccades (5). Express saccades, express arm responses, and the visual burst of visuomotor neurons are all directed toward the location of a visual stimulus, regardless of instructions to move in the opposite direction (4, 6–8). All three responses are also preferentially evoked by stimuli composed of low spatial frequencies and high contrast (9–12). Further, the magnitudes of both express arm responses and the visual burst of the visuomotor neurons are inversely related to the ensuing reaction time (1, 4, 6, 13). These shared properties support the hypothesis that express arm responses are mediated by the superior colliculus (1, 4, 9, 10).

In non-human primates (14) and likely humans, the communication between the superior colliculus and the spinal cord is likely indirect, with an interface in the reticular formation. Consistent with this potential relay, express arm responses in humans are augmented by non-visual stimuli thought to excite the reticular formation (2). A distinctive feature of the reticular formation is its extensive bilateral projections to upper-limb muscles (15–17). To date, express arm responses have been studied only in unimanual reaching tasks. The goal of this study is to

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test whether express arm responses would be expressed bilaterally when either arm can be used to reach to a visual target.

Previous work has shown an emerging target paradigm, wherein a moving target transiently disappears and then emerges from behind a barrier elicits robust express arm responses on the reaching arm in almost every participant (5, 9, 18, 19). Here, we modified this paradigm by increasing the number of potential locations of target emergence and allowing the subject to reach toward the emerging target with either arm. These modifications elicited reaches by either the left or right arm for different target locations, and at certain locations elicited left arm reaches on some trials and right arm reaches on other trials. Muscle recruitment for reaches toward these latter locations is critical for our primary aim, which is to determine whether the expression of express arm responses depended on whether the arm was chosen to reach to the target or not. Further, as our task requires participants to choose which arm to move toward the emerging target, a secondary aim was to determine when limb muscle activity indicated whether the associated arm would reach to the target or not. In doing so, we can assess the presence or absence of any relationship between the commitment to move a particular arm and the express arm response. Overall, we found that express arm responses evolved on both the chosen and non-chosen arm. We also found that the time at which limb muscle recruitment indicated which arm would reach to the target was highly variable and was unrelated to the timing of express arm responses. These findings are consistent with express arm responses being relayed through the reticular formation along a tecto-reticulo-spinal pathway and illustrate a surprising degree of independence between the expression of express arm responses and the decision to commit to moving one arm or the other.

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Methods and Materials

Participants

15 participants (8 males, 7 females; mean age: 21.8 years SD: 1.9) provided informed written consent, were paid for their participation, and were free to withdraw from the experiment at any time. All participants had normal or corrected-to-normal vision, with no current visual, neurological, or musculoskeletal disorders. All participants completed the short form Edinburgh Handedness Inventory (20, 21) which indicated 12 participants were right-handed, 2 mixed-handed, and 1 left-handed. All procedures were approved by the Health Science Research Ethics Board at the University of Western Ontario. One participant (left-handed male) was excluded due to a failure to follow task instruction, as they routinely initiated arm movements before target emergence.

Apparatus

Participants generated reaching movements with their left and right arms in a bimanual KINARM end-point robot (BKIN Technologies, Kingston, ON, Canada). Movements were generated in the horizontal plane via two handles through shoulder and elbow flexion and extension. A custom built-in projector (ProPixx projector, VPixx, Saint-Bruno, QC, Canada) generated visual stimuli onto an upward facing mirror, located at approximately shoulder height. All visual stimuli were white (110 cd/m^2) presented against a black (.6 cd/m^2) background (contrast ratio: 183:1). A shield below the mirror occluded direct vision of the hands, but real-time hand positions were represented via two white dots each with a diameter of 1 cm (which equates to approximately 1 degree of visual angle). Throughout the experiment, constant forces

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of 2 N towards the participant and 5N outward for each hand were applied to increase tonic activity in the pectoralis major (PEC) muscle.

Experimental Design

Participants completed a modified version of the emerging target paradigm (18) (**Figure 1A**). Participants initiated each trial by bringing their left and right hand, represented by a 1.5cm diameter white target, into a round, 2cm diameter white starting position, located 45 cm in front of them, and 23 cm to the left and right of center respectively. These starting positions disappeared once the trial was initiated. Simultaneous with the start of the trial, a white target (1.5 cm) located above an occluder began moving toward the participant at 15 cm/s. The target disappeared behind the occluder for a fixed duration of 1.5 s before emerging in motion at 15 cm/s below the occluder at one of 7 locations, appearing either at the horizontal center of the occluder, or 3, 7, or 17 cm to the left or right of this central position. Target motion was vertical both before and after disappearance behind the occluder, regardless of where the target emerged. Thus, the time between target disappearance and appearance was fixed at 1500 ms for all target locations. The target was only presented in its entirely after it moved beneath the occluder, preventing the presentation of a half-moon stimulus with a lower overall area. At the time of target emergence, a visual stimulus unseen by the subject was also presented to a photodiode, and all electromyographic (EMG) and kinematic data were aligned to this time.

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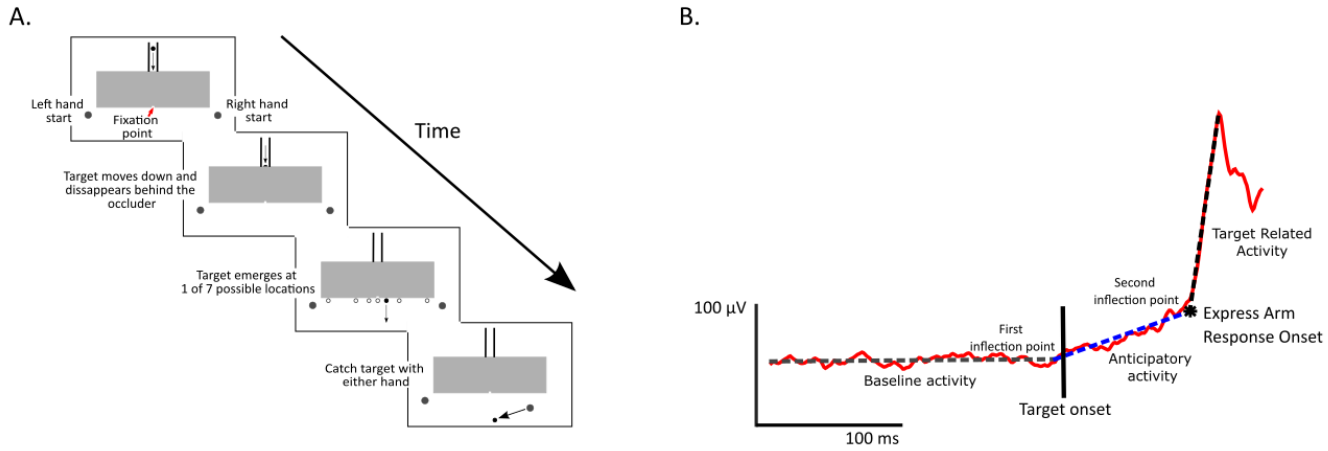

Figure 1. Modified emerging target paradigm and method for classifying express arm responses. A) At the start of each trial, the target appears above an occluder (grey box), and participant brings their right and left hands into the start position. The target then moves down the chute, disappears briefly behind the occluder, before re-emerging below the occluder at one of seven different locations (possible target locations are shown, but these were not presented to the subject). Participants reached to intercept the target with either the right or left arm. B) We fit muscle activity with a three-piece linear regression, differentiating recruitment during a baseline, anticipatory, and target-related interval. The time of the second inflection between anticipatory and target-related activity represents the start of the express arm response onset.

Although eye movements were not measured, participants were instructed to foveate a notch in the center of the occluder, 47 cm in front of them, from the start of each trial until the target re-emerged under the barrier. Upon target emergence, participants were instructed to reach toward the emerging target as quickly as possible and were told that they could use either arm to do so. Participants completed four blocks of 350 trials each, with each block containing 50 pseudorandomly intermixed repetitions of each location, yielding a total of 200 trials for each target location.

Data acquisition and analysis

Surface EMG activity was recorded from the clavicular head of the right and left pectoralis major muscle (PEC) with double-differential surface electrodes (Delsys Inc. Bagnoli-8

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system, Boston, MA USA). Two electrodes were placed on each the right and left PEC, targeting the clavicular and sternal head. Our reasoning for placing two electrodes was to provide a backup in case adhesion was lost during a long experiment. The recording that exhibited the higher signal to noise ratio off-line was chosen for each participant (10). To ensure consistency, the same individual placed electrodes for all participants, using anatomical landmarking and muscle palpation to determine location. EMG signals were amplified by 1000, sampled by the KINARM data system at 1000 Hz, then full wave rectified off-line. Kinematic data was also sampled at 1000 Hz by the KINARM data system.

To allow cross-muscle comparisons, we normalized the EMG activity to baseline, dividing EMG activity on each trial by the average EMG activity between -500 to -100ms before target onset across all trials. Normalized muscle activity was only used when comparing the magnitudes of recruitment across different muscles, otherwise, source EMG voltages was analyzed.

Reaction time (RT) was calculated as the time from target appearance below the occluder, indicated by the photodiode, to the initiation of the reaching movement by the arm that intercepted the target. The reach RT for each trial was determined using a custom MATLAB script that found the time when the hand exceeded 5% of its peak velocity of the hand after target onset, and then moved backwards in time to find the point at which hand acceleration following target onset exceeded the 95% confidence interval of acceleration data taken from a period of 100 ms before to 50 ms after target onset. The offset of hand motion was the time at which hand velocity fell below 5% of its peak velocity. The onset and offset of movements were confirmed offline by an analyst in a graphical user interface and adjusted if necessary. We excluded trials with RTs less than 100 ms due to presumed anticipation, and trials with RTs exceeding 500 ms

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due to presumed inattentiveness. 16% of trials were excluded using these RT constraints, primarily due to anticipatory movements. We also excluded trials consisting of multiple movement segments toward the target, excluding ~2% of trials.

Arm-choice was defined simply as the arm that intercepted the target. A psychometric function was generated using the proportion of right arm reaches as function of target location. For each participant a logistic regression was fit to the data, using the link logit MATLAB function: $f(p) = \log\left(\frac{p}{1-p}\right)$, where p is the proportion of right arm reaches. Using the fitted curve, we estimated the theoretical point where a target would be intercepted with either the left or right arm with equal likelihood. The closest target location to this point, referred to as the target of subjective equality, was then used for further analyses, as this target location permitted the best within-muscle comparison of recruitment when that arm was chosen to reach to the target or not.

Previous work examining the express arm response has used a time-series receiver-operating characteristic analysis, contrasting EMG activity for movements into or away from a muscle's preferred direction (1, 22). Since a given arm only moved in one direction in our study (e.g., all targets lay to the left or right of the right or left arm, respectively), we developed a novel method for detecting and quantifying the express arm response. Our method involves a three-piece linear regression, fitting lines to EMG activity in a baseline, anticipatory, and post-target interval (see (5, 23) for methods based on a two-piece linear fit). Our rationale for using a three-piece linear regression was based on a qualitative observation of mean EMG recruitment, which often started to increase in an anticipatory fashion before and just after target appearance (**Figure 1B**).

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To determine the presence or absence of an express arm response, we took the following steps. First, we ensured that there were at least 25 reaches from a given arm to a particular target (most targets only generated enough reaches from one arm). Whenever there were enough reaches from a given arm, we further analyzed the muscle activity from both the left and right PEC, as this provides us with EMG activity from both the reaching and non-reaching arm. We then fit the mean EMG activity spanning from 100 ms before target onset to the time of the peak EMG activity within 135 ms after target onset with three linear regressions. Doing so involved finding two inflections points that minimized the sum of square errors, delineating the baseline activity (spanning from -100 ms to the first inflection point), anticipatory activity (spanning from the first to second inflection point), and the target-related interval (spanning from the second inflection point to the peak EMG activity; see **Figure 1B**). For an express arm response to be detected, the second inflection point had to occur within 80-105 ms, and the slope of the second and third linear regressions had to be significantly different at $P < 0.05$, as determined by a bootstrapping procedure. When present, the express arm response latency was defined as the time of the second inflection point, and the express arm response magnitude was defined as the difference of the peak EMG activity over the next 15ms to the EMG activity at the onset of the response. Anticipatory activity was defined as the level of normalized muscle activity immediately preceding the express arm response.

In a separate analysis to determine at what point muscle activity reflected arm choice, we used a time-series receiver-operating characteristic (ROC) analysis from EMG activity recorded when participants reach to the target of subjective equality. This target location provided a large sample of EMG activity from a given muscle on trials where the associated arm or the opposite arm reached to the target. We were interested in the time-point when EMG activity from a given

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muscle diverged depending on whether the arm was chosen to reach to the target or not. We separated EMG activity based on which arm reached to the target then analyzed at every time sample (1 ms) from 500ms before target onset to the end of the trial. For each time-point we calculated the area under the ROC curve, which is the probability that an ideal observer could discriminate whether the associated arm would reach to the target or not, based solely on the EMG activity. Values of 1 or 0 indicate perfectly correct or incorrect discrimination respectively, whereas a value of 0.5 indicates chance discrimination. We set the threshold discrimination at 0.6 because this criterion exceeded the 95% confidence intervals determined previously using a bootstrapping procedure (23). The time of discrimination was defined as the first point in time at which the ROC value exceeded 0.6 for at least eight of ten subsequent time-samples.

Statistical Analysis

Statistical analyses were performed in MATLAB (version 2014b, The MathWorks, Inc., Natick, Massachusetts, United States). To compare the proportion of participants expressing an express arm response (termed express arm response prevalence) as a function of muscle, arm choice, and location, a chi-squared test was used, and Bonferroni corrected when necessary. A paired-t test was used to compare the latency and magnitude of the express arm response within a muscle at the target of subjective equality. We relied on non-normalized EMG for our magnitude analysis for within muscle comparisons.

Results

The reticular formation is a likely relay in the pathway mediating express arm responses. Given the bilateral projections from the reticular formation, we wondered whether express arm

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responses would be expressed bilaterally in a task where participants could choose which arm to use to intercept an emerging target. We recorded muscle activity from the right and left PEC muscles as participants completed a modified emerging target paradigm (**Figure 1A**). Targets could emerge at one of seven locations below the barrier, and participants reached to catch the target as fast as possible with either arm. We analysed muscle activity from both the reaching and non-reaching arm to determine the presence of the express arm response. We also examined the time at which muscle activity indicated that the associated arm would reach toward the target or not, relative to the time of the express arm response.

Arm-choice as a function of target location, and defining the target of subjective equality

On every trial, participants chose which arm to move. As shown in **Figure 2**, arm-choice typically reflected the hemifield of target presentation, with the right or left arm reaching for targets emerging in the right or left visual field, respectively. We quantified participant behaviour by fitting a psychometric curve to the proportion of right arm reaches expressed as a function of target location. The point of subjective equality defines the theoretical target location where a participant would reach with one arm on half of all trials, and with the other arm on the other half of trials. From the point of subjective equality, we found the closest actual target location, referred to as the target of subjective equality, for each participant (see **Figure 2A** for a representative subject). This location was associated with a high number of reaches from either arm in all participants. Across our sample, the target of subjective equality was at center (n = 10), 3 cm left (n = 2) or 7 cm left (n = 2) of center (**Figure 2B**). The target of subjective equality permits a within-muscle comparison of recruitment when the associated arm was chosen to reach

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or not. In general, locations other than the target of subjective equality did not generate enough reaches from either arm for within muscle comparisons.

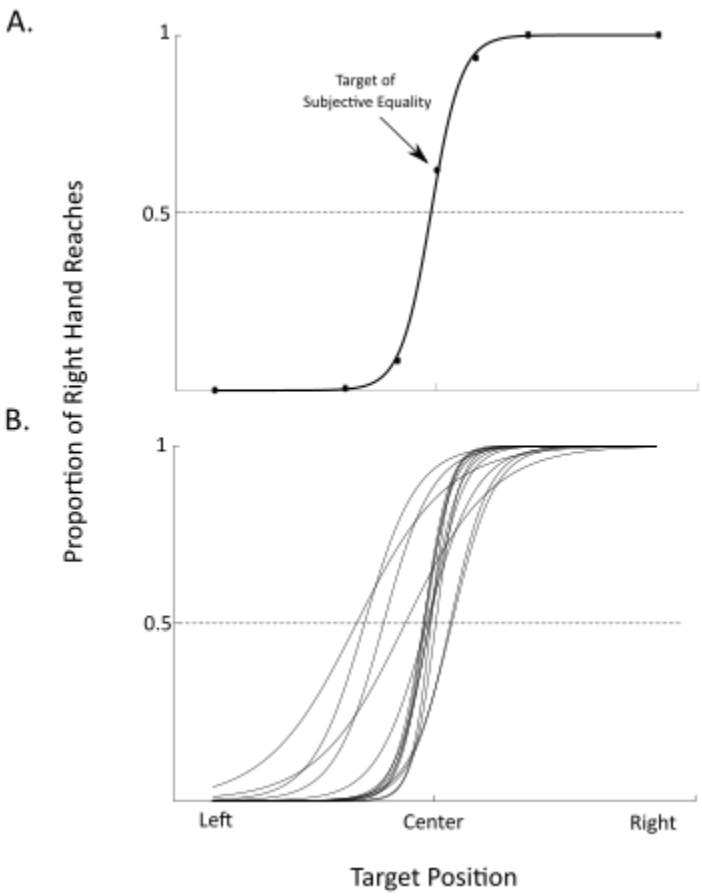

Figure 2. Arm Choice as a Function of Target location. A: A single participant example of right arm choice as a function of target location. Each black dot represents a location where the target emerged on a subset of the trials. A psychometric function was fit to the data and the target of subjective equality was chosen as the target closest to the horizontal dash line. B: Psychometric functions for each participant.

Do express arm responses appear bilaterally?

The main question we wanted to address was whether express arm responses evolve bilaterally when either arm could be used to intercept an emerging target. **Figure 3A** shows the average muscle activity from an exemplar participant (same subject as **Figure 2B**), across all positions where at least 25 reaches were made by the associated arm. This data shows how participants tended to reach with the arm closest to the target (e.g., note how the right or left arm

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tended to reach for targets in the right or left hemifield, respectively). Using a three-piece linear regression to determine whether there was an express arm response (**Figure 1B**, see Methods), we observed express arm responses in both the reaching and non-reaching arm (express arm responses are denoted by the black dots in **Figure 3A**). In some instances where an express arm response was not detected (e.g., left arm reaches to the 0cm target), the slope of the third linear regression was not significantly different from the second linear regression as determined by a bootstrapping procedure, or the time of inflection was below 85 or above 105ms. When detected, express arm responses occurred ~90ms after target appearance in both the reaching and non-reaching arms.

Previous reports have emphasized that the trial-by-trial timing of express arm responses is more aligned to stimulus rather than movement onset (1, 4). We examined trial-by-trial representations of muscle recruitment, and as shown in **Figure 3B**, found indeed that the timing of express arm responses was more tied to stimulus rather than movement onset, regardless of whether the associated arm reached or not. This characteristic feature of express arm responses appears as the vertical banding of EMG activity in **Figure 3B** when muscle activity is aligned to stimulus onset**,** showing a burst of muscle recruitment ~90 ms after target emergence regardless of the ensuing reach RT. Following this bilateral generation of the express arm response, a more prolonged period of increased recruitment was observed only on the reaching arm (the right arm for the data in Figure 3B).

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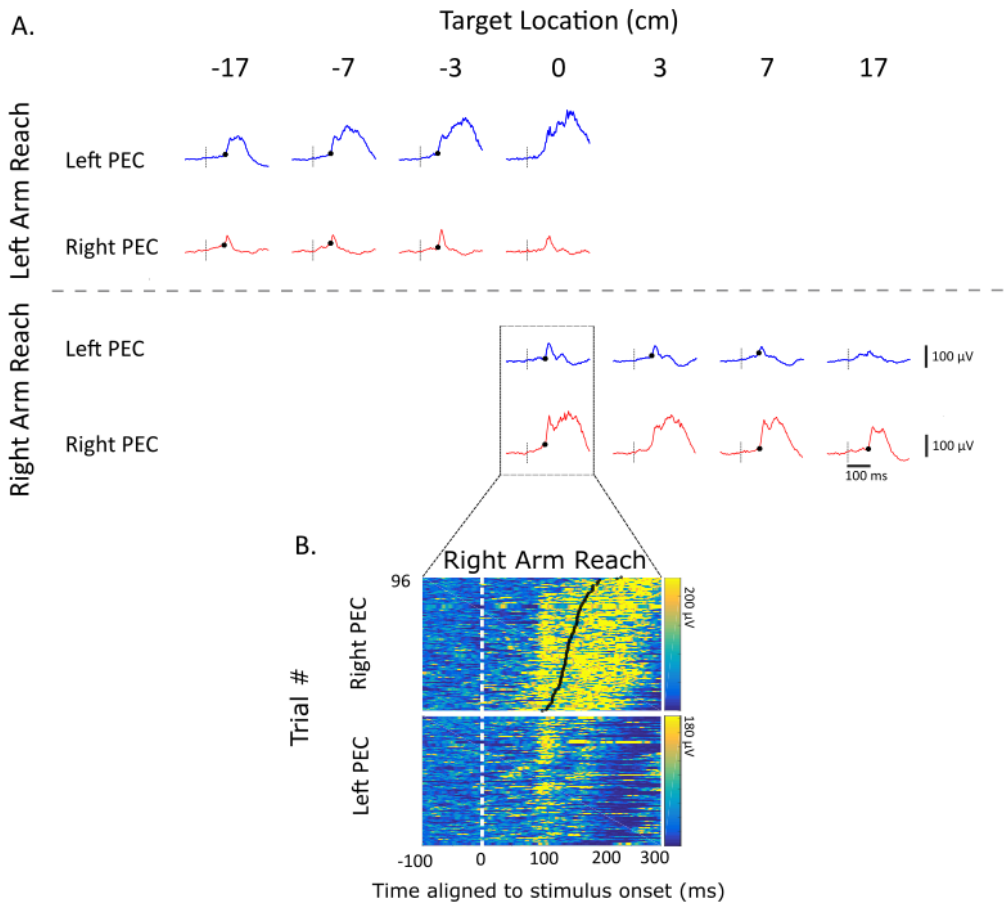

Figure 3. Bilateral muscle recruitment in a representative participant. A) Average muscle activity (+/- SE) for all reaches as a function of target location. Averages are plotted only if there were at least 25 trials where the given arm reached to the target. The 0 cm location is the target of subjective equality, as this featured many trials where either the right or left arm reached to the target. Stimulus onset indicated by the black vertical dotted line. Black dots represent the point at which an express arm response was detected (I.e., the inflection between the second and third linear regressions, providing the slope was significantly different) B) Depiction of trial-by-trial recruitment from right (top) and left (bottom) pectoralis muscle during right arm reaches. Each row is a different trial, with the intensity of color conveying degree of recruitment. Trials are aligned to stimulus onset (white vertical dotted line) and sorted by RT (black dots are only shown on right PEC, since the right arm reached). The express arm response appears as a vertical banding of increased recruitment that is more aligned to stimulus presentation, respectively, rather than movement onset.

The prevalence of express arm responses is known to vary across paradigms and participants (1, 5, 9, 10). We wanted to know whether all participants had express arm responses

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in general, and further whether the responses were equally prevalent in the reaching and non-reaching arms. As shown in **Figure 4**, the modified emerging target paradigm elicited express arm responses from at least three participants at each location. Further, all participants generated express arm responses toward at least one target location. We compared the prevalence of express arm responses in the reaching and non-reaching arm grouped across all locations, and further at each location individually. Using a chi-squared test we found express arm responses occurred at equal prevalence in the reaching and non-reaching arms across all locations ($p= 0.44$, $c2= 0.4385$, $df=1$), and further at each location ($p > 0.05$, $c2 < 3.36$, $df=1$). These analyses reinforce our observations that express responses evolve bilaterally on both upper limbs in this task.

We also examined whether there was a difference in the prevalence of express arm responses as a function of target location. Using a chi-squared test with Bonferroni corrected for multiple comparisons (alpha = 0.0083) and grouping targets based on distance from the center (e.g., combining data for the 17 cm right and 17 cm left targets), we found that express arm responses were significantly less likely for the 17 cm locations ($p < 0.0083$). No other differences were found based on location.

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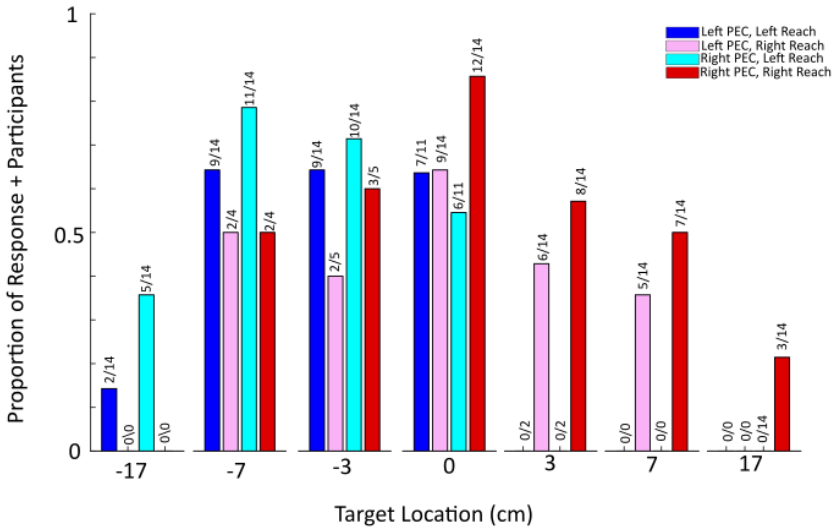

Figure 4. Proportion of subjects exhibiting an express arm response as a function of arm and target location. At each target location prevalence is determined as the proportion of participants exhibiting an express arm response relative to the number of subjects who generated enough reaches with the given arm at that particular location (recall at least 25 reaches had to be made by a given arm for the analysis of the express arm response).

Express arm response properties

Next, we were interested in the latency and magnitude of express arm responses recorded bilaterally, and whether these measures differed depending on whether the associated arm was selected to move or not. If mediated by a common source like the reticular formation, we would expect the magnitude of express arm responses on the reaching and non-reaching arm to be correlated across participants and targets (e.g., a larger express arm response on the reaching arm should be associated with a larger express arm response on the non-reaching arm). For this analysis, we identified target locations where an express arm response was observed on both the reaching and non-reaching arm, and found that express arm response magnitudes were indeed positively correlated between the muscles (**Figure 5A** Pearson correlation, $p < 0.001$, $r = 0.699$; every point represents a unique observation for a participant and target location where express arm responses were objects bilaterally; note magnitudes are normalized here since this is a

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comparison of magnitude across muscles). Thus, larger express arm response magnitudes on the reaching arm tended to be associated with larger express arm response magnitudes on the non-reaching arm. On average, the magnitude of the express arm responses was about twice as large on the reaching versus non-reaching arm.

Previous work has shown that express arm responses may differ in latency (10) and/or magnitude (4) depending on stimulus properties and task context. We examined express arm response latency and magnitude within a given muscle at the target of subjective equality, analyzing these properties depending on whether the associated arm was chosen to reach or not. Note that this is a within-muscle comparison, where we analyze express response latency and magnitude as a function of whether the associated arm was chosen to move or not. Using only paired observations (i.e., when express arm responses were detected in a given muscle regardless of whether the arm was chosen to move or not) we found no difference in express arm response latency with arm choice (**Figure 5B;** $p = 0.5911$, $t = -0.5520$, $df = 12$). Further, using a single factor ANOVA we found no difference in response latency across target locations ($p > 0.05$). These results reinforce the qualitative observation from **Figure 3A** that the express arm response evolves consistently ~90 ms irrespective of arm choice. Although latency was not affected by arm choice, the normalized express arm response magnitude was ~1.5 times larger when the associated arm was chosen to move or not at the point of equal selection (**Figure 5C;** $p = 0.0365$, $t = 2.3534$, $df = 12$), but response magnitude was unchanged across target locations (single factor ANOVA, $p > 0.05$).

While the influence of arm choice on express arm response magnitude was significant at the target of equal selection across our sample, **Figure 5C** shows that this was not the case in all participants, leading us to wonder whether about the influence of other factors. For example, the

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magnitude of the express arm response can be influenced by task instruction (3, 4). In our paradigm, participants knew in advance that targets would appear medial relative to the starting position of both the left and right arm, leading us to wonder if participants anticipated which arm to use prior to target emergence. To analyze the potential influence of such anticipation, we examined anticipatory activity on a given muscle as a function of whether the associated arm was chosen to reach or not and found greater anticipatory activity when the associated arm was chosen to reach to the target (**Figure 5D**; paired t-test, $p = 0.0035$, $t = 3.6278$, $df = 12$). This relationship between anticipatory activity and arm choice can be seen in **Figure 3A** on the right PEC at the 0 cm target; note how anticipatory activity preceding the express arm response was greater when the right rather than left arm reached to the target. This level of anticipatory activity related to the magnitude of the ensuing express arm response (n.b., the latter measure quantifies the EMG magnitude above anticipation), as we found a positive correlation between these measures for both the reaching and non-reaching arms (**Figure 5E;** $r = 0.8394$, $p < 0.001$). Thus, the level of anticipatory activity attained just before the express arm response related to the magnitude of the express arm response.

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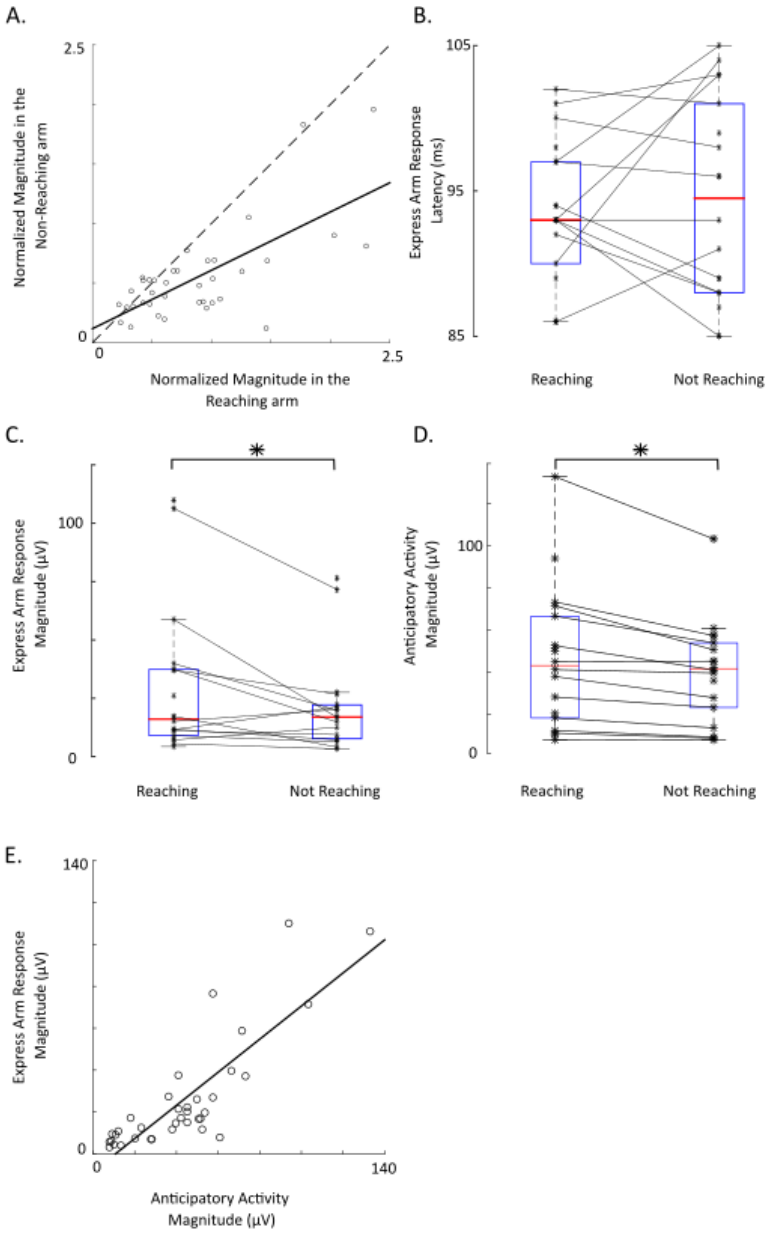

Figure 5. Analyses of the characteristics of express arm response A) The magnitude of the express arm response in the reaching and non-reaching arm are significantly correlated across participants ($r = 0.699$, $p < 0.001$). Each dot represents a unique combination of target and subject where express arm responses were observed on both the reaching and non-reaching arm. The black line indicates the linear regression fit, and the dashed line represents the line of unity. B, C) The latency (B) or magnitude (C) of the express arm response as a function of whether the associated arm reached or not, taken from the target of equal selection. Lines connect within-muscle observations. In C, significantly larger express arm responses are observed on the reaching arm. ($p = 0.03$). D) Anticipatory activity, measured as the level of EMG activity just prior to the express arm response. Same format as B. Anticipatory activity was significantly higher when the arm was selected to reach to the target ($p = 0.0035$). E) Correlation of the level

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of anticipatory activity to the magnitude of the express arm response ($r = 0.8394$, $p < 0.001$). Each dot represents an observation, with the black line indicating the linear regression fit.

When, relative to the express arm response, does muscle activity relate to arm choice?

The preceding analyses showed that greater levels of anticipatory muscle recruitment relate to the choice to use the associated arm to reach to the target. These results lead us to wonder when muscle activity predicts which arm was going to move, and whether this time relates in a systematic way to the latency or expression of an express arm response. To address this, we performed a time-series ROC analysis to compare the muscle activity when the arm was chosen to reach or not and searched for the time at which an ideal observer could correctly discriminate arm choice from such EMG activity (see Methods). The inset of **Figure 6** shows one example of this analysis, showing the average activity of left PEC muscle for the exemplar participant preceding left or right arm reaches to the 0 cm target (top plot, blue or red traces respectively), as well as the associated time-series ROC (bottom plot). For this example, the discrimination time at which EMG activity reliably predicted which arm would reach was 69 ms after target onset, which preceded the express arm response. Across our entire sample, and regardless of whether participants exhibited an express arm response or not, we observed no systematic relationship between the discrimination time indicating which arm would move and the latency of express arm responses, with discrimination times variably preceding, occurring within, or following the express arm response epoch (**Figure 6**). We also observed no obvious relationship between this discrimination time and the generation of express arm responses; subjects exhibited express arm responses regardless of whether the discrimination time occurred earlier or later than the express arm response. This analysis reveals a lack of any relationship between aspects of muscle recruitment reflecting arm choice and the timing and expression of the express arm response.

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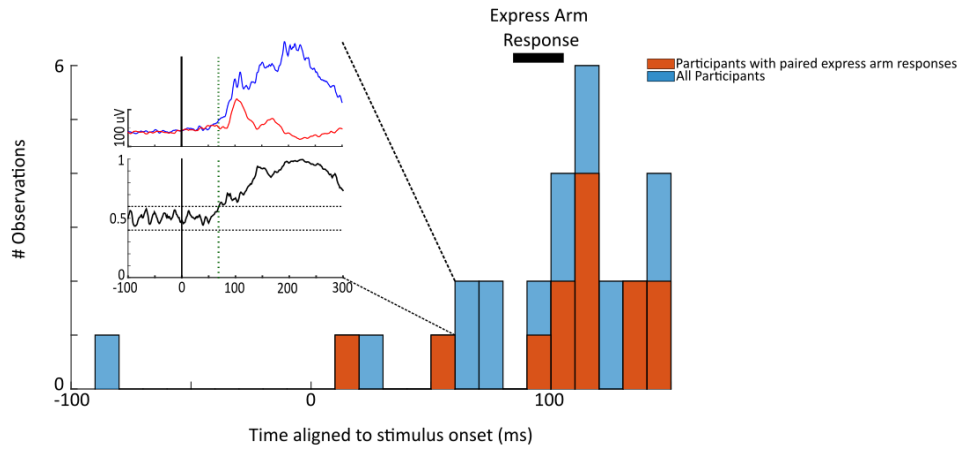

Figure 6. Time of arm choice discrimination based on muscle activity. Histogram of the times of muscle discrimination, organized into bins of 10ms. Orange bins depict observations where the participant exhibited an express arm response on a given muscle when the associated arm was selected to reach or not. Blue bins depict observations where express arm responses were not observed. Inset plot shows data from the exemplar participant, with the top plot depicting mean EMG (+/- SE) from left PEC for reaches using the left (blue) or right (red) arm, and the bottom plot showing the time-series ROC analysis used to determine the time at muscle activity predicts arm choice. Green vertical dotted lines in the inset represents the time of discrimination (69 ms).

Kinematic Consequences of the Express arm response

The express arm response is a brief period of muscle recruitment that increases muscle force. Previous work with unimanual anti-reach, delay, or stop-signal tasks has shown that express arm responses can produce small, task inappropriate, movements toward a target (4, 24, 25). The non-reaching arm provides an opportunity to study the kinematic consequences of express arm responses in isolation from ensuing reach-related activity. First, we looked at the velocity of both the reaching and non-reaching arm at every location and consistently saw a small movement towards the target in the non-reaching arm. This can be seen in **Figure 7A** where we have plotted horizontal velocity from the exemplar participant for both the reaching and non-reaching arms at every location. As expected, the velocity is much higher in the reaching arm than in the non-reaching arm, but there is clearly a small deviation of the non-reaching arm toward the target (the insets in **Figure 7A**). To quantify the non-reaching arm's

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peak velocity and allow cross-participant comparisons, we normalized it by the peak velocity of the reaching arm. We found on average the non-reaching arm had a peak velocity that was 8.11 ± 2.69% of the reaching arm. Compared to a null hypothesis that no movement occurs in the non-reaching arm, the non-reaching arm did indeed move towards the stimulus (Student's t-test, $p < 0.001$, $t = -15.9768$, $df = 27$). Next, we compared the peak velocity in the non-reaching arm based on whether an express arm response was observed but did not find any difference in peak velocity based on whether an express arm response was observed (peak velocity: 8.53 ± 2.15%) or not (peak velocity: 7.35 ± 3.45%) (**Figure 7B;** paired t-test, $p > 0.05$). Thus, although the non-reaching arm did move toward the target, the peak velocity of this movement was unrelated to the detection of an express arm response. This is a somewhat surprising result, but we note that our method for detecting express arm responses may have had a high rate of false negatives where the slope of EMG activity during the express arm response epoch did not differ significantly from the slope of EMG activity during the anticipatory interval (e.g., see EMG data for left and right PEC for left arm reaches in Fig. 3A at the 0 cm target; although there appears to be an express arm response in both muscles, our detection method did not detect an express arm response in either situation).

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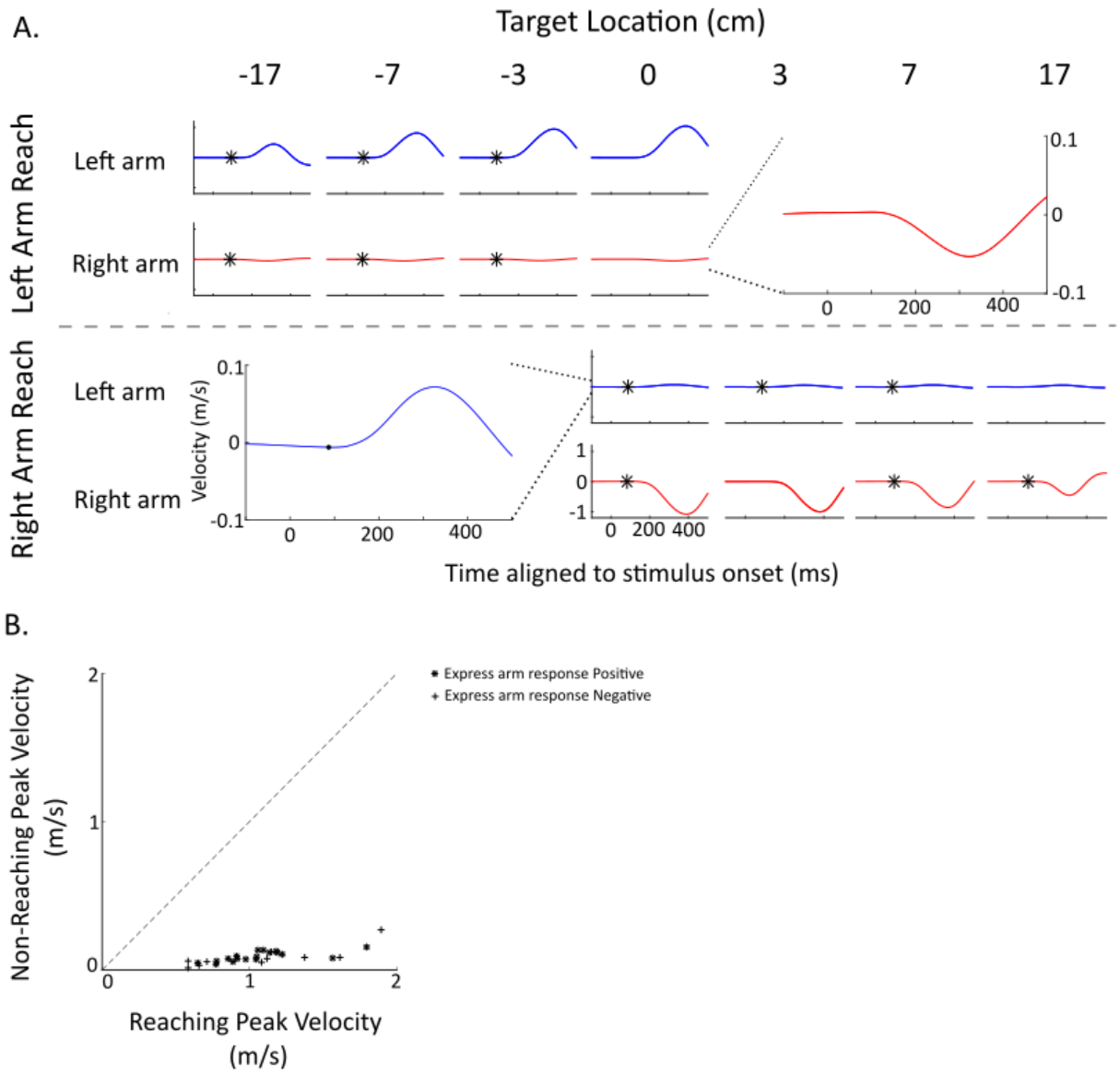

Figure 7. Velocity traces for the exemplar participant. A) Average velocity (+/- SE) for both the reaching and non-reaching arm across locations, with a black star representing the latency of the express arm response when present. Expanded graphs represent the velocity trace from the non-reaching arm at the target of subjective equality, at an enlarged y-axis scale. B) Scatter plot showing the peak velocity of the reaching vs non-reaching arm. Black dashed line shows line of unity and symbols depict whether an express arm response was observed on the non-reaching arm or not.

A key behavioural correlation seen in previous research using unimanual tasks is that larger express arm responses tend to precede shorter-latency reach RTs (1, 4). Given that this study is the first to study express arm responses in a bimanual task, we examined our data for the

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presence of any relationships between express arm responses and RTs. We first confirmed that the express arm response magnitude in the reaching arm is negatively correlated to reach RT (left panel of **Figure 8A** shows trial-by-trial data for the right PEC from the exemplar participant; right panel of **Figure 8A** shows that the r-values across all participants with an express response at the target of equal selection lay significantly below zero; average $r = -0.3436$, $p < 0.001$, $t = 8.35$, $df = 17$). Next, we examined whether the magnitude of the express arm response on the non-reaching arm related to the RT of the reaching arm, as a common drive mechanism predicts that a larger express arm muscle response on the non-reaching arm should precede shorter latency RTs on the reach arm. However, we found no relationship between the magnitude of the express arm response on the non-reaching arm and the RT of the reaching arm either in the exemplar participant (left panel of **Figure 8B**) or across the sample (the distribution of r-values in right panel in **Figure 8B** does not differ from zero, average $r = -0.0045$, $p > 0.05$, $t = 0.15$, $df = 17$). Instead, as we were able to occasionally extract a RT from the movement of the non-reaching arm, we found a weaker albeit significant negative correlation between non-reaching express arm response magnitude and non-reaching movement RT (left panel of **Figure 8C** for exemplar participant; right panel of **Figure 8C** for the sample; average $r = -0.16$, $p = 0.001$, $t = 3.8020$, $df = 17$). This final negative correlation does show a relationship between the express arm response on the non-reaching arm and the reaction time for the small movement of that arm, even when the other arm intercepts the target.

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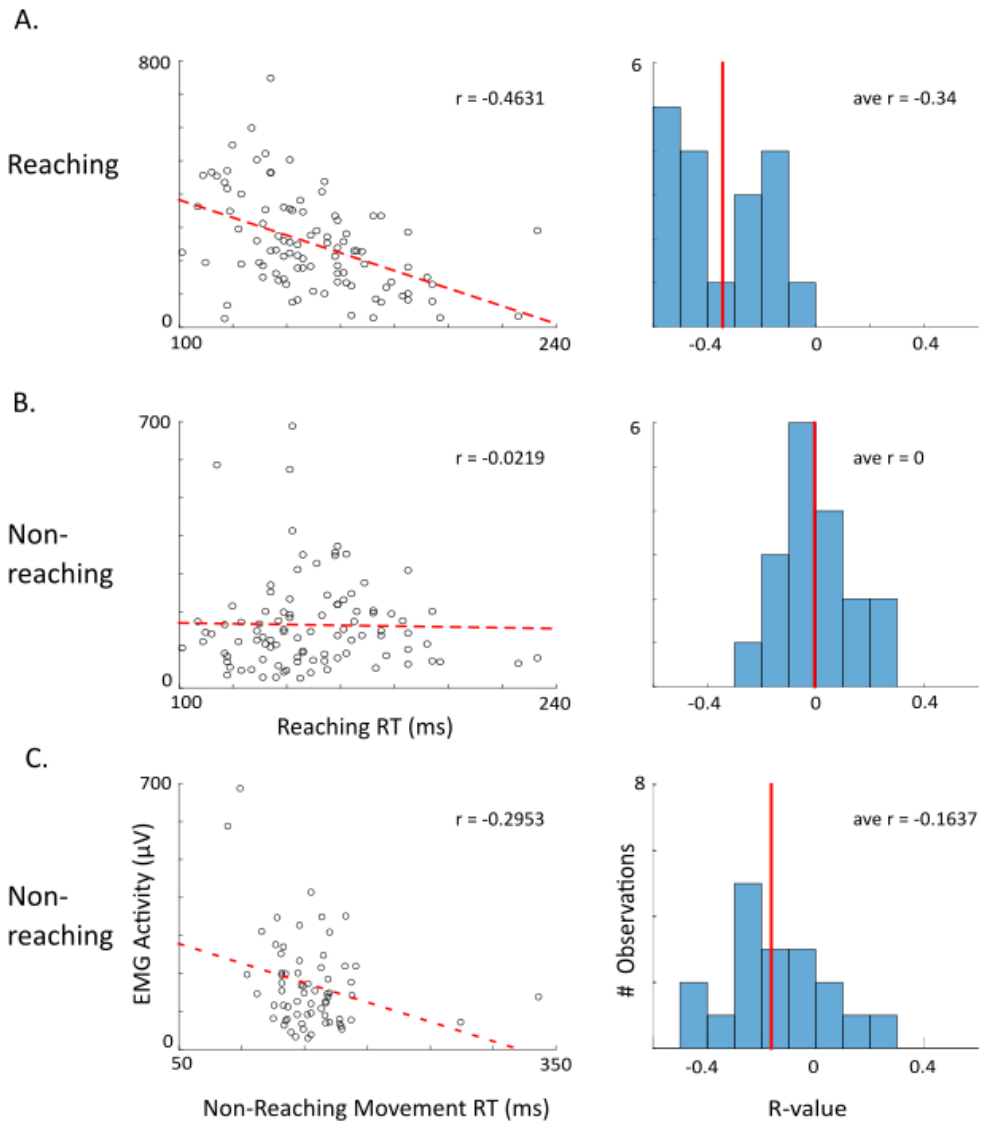

Figure 8. Correlations for express arm response magnitude and associated reaction time. A) In both the exemplar participant (Left; each point represents data from a single trial) and population (Right) there is a negative trial-by-trial correlation between the magnitude of the express arm response in the reaching arm and the reaction time of the movement. B) No such negative relationship was observed between the magnitude of the express arm response on the non-reaching arm and the reaction time of the reaching arm for either the exemplar participant or across the sample. C) A weaker negative correlation was observed between the express arm response on the non-reaching arm and the reaction time of the non-reaching arm (when a movement was present) .

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Discussion

We investigated whether the express arm response occurs bilaterally in a task where either arm can be used to intercept a target. We were particularly interested in the prevalence, timing, and magnitude of any express arm responses in the reaching versus non-reaching arm, as well as how these measures related to anticipatory muscle recruitment attained just before the express arm response and the kinematics of any associated movement. We found that express arm responses occur with equal prevalence on both the reaching and non-reaching arms, and that express arm response magnitude interacted with the preceding level of anticipatory activity. Express arm responses on the non-reaching arm did relate to aspects of small movements of the non-reaching arm, consistent with this phase of muscle recruitment imparting functional consequences. When integrated with reports in the literature on express arm responses in unimanual tasks, our results are consistent with a reticular relay of signals arising soon after target onset in the superior colliculus, and the interaction of such signals with pre-existing activity related to the anticipation of target appearance that presumably have a cortical origin. Interactions between cortical and subcortical descending pathways may occur at spinal or supraspinal levels.

Comparison to past studies and methodological considerations

The emerging target paradigm (18) has emerged as an efficient means to elicit express arm responses, increasing the prevalence and magnitude of the response (5, 9, 19). Past work has investigated how certainty about the time of target emergence (5), cueing (19), or the properties of the emerging target (5, 9) influence the express arm response. All such work using the emerging target task, as well as all past studies of the express arm response (1, 4, 10)

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investigated reaches made with one arm. In contrast, in our modified emerging target paradigm, either arm could be used to intercept the target while muscle activity was recorded bilaterally. Further, we increased the number of potential target locations from two used previously to seven. Despite these changes, express arm responses were reliably observed, as all participants exhibited an express arm response to at least one target. We attribute this to the modified paradigm maintaining implied motion behind the barrier and a high degree of certainty about the time of target emergence, which have been suggested to be the main factors increasing express arm response prevalence and magnitude in this paradigm (5, 9, 18).

In our study, participants were required to choose which arm reached to the emerging target, doing so as quickly as possible. Previous work has shown that arm choice tends to reflect the hemifield of the target, with a slight bias to use the dominant hand at center (26, 27). In the modified emerging target paradigm used in this study, the logarithmic spacing of the targets under the occluder was chosen to try to find a target location which would elicit reaches from the right arm on some trials and from the left arm on others. Previous versions of a hand-choice task did not instruct participants to reach as fast as possible (26, 27) leading to the possibility that the dominant hand would be used for all targets in this version of the modified emerging target paradigm. Instead, we found that even with the added pressure to be fast, hand choice still largely reflected the hemifield of presentation.

Our overall task design was intended to find, for each subject, a target location that elicited reaches with the right arm on some trials, and with the left arm on others; doing so enabled evaluation of muscle activity and express arm responses as a function of whether the associated arm was selected to reach or not, for movements to the exact same visual target. For most participants (n = 10), this target of equal selection was the center, of 0 cm, target. Assuming

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participants followed task instruction, this center target would be almost (~1 degree below) at the fovea. Given that foveal visual stimuli are represented bilaterally in the superior colliculus (28), could this explain our observation of bilateral express arm responses? We think this is unlikely for three reasons. First, equivalent results were obtained for the four participants who had off-centre targets of equal selection (two participants at each of 3 or 7 cm to the left, equating to ~3 or 7 degrees of visual angle); such visual targets are represented unilaterally in the superior colliculus. Second, targets that were not the target of equal selection still provoked bilateral responses; it was simply that reaches to these locations were predominantly done by one arm. Third, past work dissociating initial eye and hand position have shown that the express arm responses encode the location of the visual stimulus relative to the current position of the hand, not the eye (3).

Our paradigm was not designed to control for the retinal velocity of the moving target. As a consequence of our setup, the retinal image of the central target moved more rapidly than the image of more peripheral targets. That being said, we did not find any influence of target location on the magnitude of express arm responses on either the reaching or non-reaching arm. Previous work has reported that faster moving targets evoke larger express arm responses (9), but the range of actual retinal velocities used in our experiment may not have been large enough to reveal this effect. Related work by Cross and colleagues in 2019 requiring on-line corrections following a jump in cursor position has also found that the earliest visuomotor responses are invariant for jumps that are greater than 2 cm in magnitude (29). Given these results, the lack of any relationship between target location and express arm response magnitude is not surprising, although future work that more systematically investigates this question may be needed.

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Another key difference between the current and past studies is the location of potential targets relative to the starting position of the hand. In past work, potential targets were positioned to the left and right of the starting position of the hand, and express arm responses were detected via analysis of increases or decreases in muscle activity following target presentation into or out of the muscle's preferred direction of movement. Here, all targets lay medial to the starting position of the hand, and hence in the preferred direction for pectoralis major. We accordingly developed a new method for detecting express arm responses, which depended on significant differences in the slopes of linear regressions fit to EMG activity during an anticipatory and express arm response interval. This method appears to be conservative, classifying instances of muscle recruitment as not exhibiting an express arm response despite an obvious inflection in muscle recruitment in the express arm response interval (e.g., see the data from left-PEC for the 0cm target in **Figure 3A**). When express arm responses were detected with this method, they invariably displayed the characteristic trial-by-trial changes in muscle recruitment that were more aligned to target rather than movement onset (e.g., **Figure 3B**). The lack of specificity of our detection method, which leads to an increased rate of false negatives (like the data shown in **Figure 3A**) may partly explain the absence of relationship between the presence or absence of express arm responses and peak velocity on the non-reaching arm (**Figure 7B)**

Express arm responses were observed in the reaching and non-reaching arm regardless of whether the dominant or non-dominant arm was chosen to reach. However, all participants included in the analysis were either right hand dominant (n = 12) or ambidextrous (n = 2) as determined by the handedness questionnaire. Previous studies of express arm responses have similarly reported a low number of left-handed participants (1, 5, 9), but there has been no suggestion of any difference in the results of left- and right-handed participants. We speculate

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that the express arm response would remain bilateral in left-hand dominant participants, but further studies using a larger proportion of left-handed participants would be needed to confirm this assertion.

Interactions between anticipatory recruitment, the express arm response, and voluntary reach-related activity

In our task, all targets emerged medial to the starting position of the hand. Combined with certainty about the time of target emergence, it is not surprising that participants anticipated target emergence to a degree that influenced muscle recruitment. Such anticipatory recruitment, which we presume has a cortical origin as participants become quite familiar with task structure over repeated trials, influenced the magnitude but not timing of the express arm response; participants with greater levels of anticipatory recruitment tended to have larger express arm responses (**Figure 5E)**, and both anticipatory recruitment and express arm muscle responses tended to be larger when the associated arm was selected to reach (**Figure 5C,D**). Although our experiment was not designed to systematically vary the muscle recruitment immediately preceding the express arm response, the relationships between anticipatory recruitment and express arm responses resemble gain scaling seen for the spinal stretch reflex following a mechanical perturbation of the arm (30). Gain scaling likely arises from intrinsic properties at the motoneuron pool from the size-recruitment principle; importantly, recruitment from subsequent longer-loop reflexes any not be gain-scaled, if it were to be counterproductive to the task at hand. A future line of research should investigate whether the express arm response indeed exhibits gain scaling; this could be done by systematically varying the loading force on the muscle of

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interest, and investigating the influence on both the express arm responses and on ensuing phases of recruitment.

Regardless of whether the relationship between anticipatory activity and the magnitude of the express arm response arises from gain scaling, anticipatory activity in some participants was significantly greater on the arm that ultimately reached to the target. This is apparent in the time-series ROC analysis in **Figure 7**, where arm choice could frequently be predicted by analyzing muscle activity preceding the express arm response interval. Such anticipatory recruitment suggests that some participants have already committed, to some degree, which arm they were more likely to use to reach to the target. We can only speculate as to why this may be the case; it may be because of trial history or fatigue (e.g., a bias to move one arm if the other arm was used on the previous trials). Development of a bias favoring one arm over the other may explain the lack of a relationship between the magnitude of the express arm response on the non-reaching arm and the reaction time of the reaching arm (**Figure 8B**), as a common bilateral drive to both muscles would predict a negative relationship between the express arm response magnitude of either arm and the reach RT. Instead, since the magnitude of the express arm response is also influenced by anticipatory activity, a bias in anticipatory activity toward the reaching arm and against the non-reaching arm muted the magnitude of the express arm response on the latter.

A common observation in previous work is that larger express arm responses precede shorter RTs (1, 4), and we observed a similar relationship here. Importantly, this was observed on the muscles of both the reaching and non-reaching arm and the reaction time of the associated arm (when a reaction time for the non-reaching arm could be extracted). A comparison of the evolution of muscle activity on the reaching versus non-reaching arm is quite interesting; whereas express arm responses are readily apparent on both, subsequent phases of more

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prolonged recruitment are only observed on the reaching arm. The kinematics of movement of the non-reaching arm provides an opportunity to better understand the kinetic consequences of the relatively brief express arm response, and similar to previous results (4, 24, 25), the express arm response is associated with a small movement of the non-reaching arm toward the target. This reaffirms that, despite the relatively brief nature of the express arm response, it is not without a kinetic consequence even on the non-reaching arm. Further, an express arm response on the reaching arm may also influence the kinetic consequences of the ensuing phases of voluntary reach-related activity through repeated activation of the same muscle fiber (31).

Is the reticular formation involved in the express arm response?

There is considerable circumstantial evidence that express arm responses arise from signalling along a tecto-reticulo-spinal pathway (1, 4, 10, 16, 24). Many of the key response properties of express arm responses resemble those of express saccades, in which the role of the superior colliculus is well understood (32, 33). Further, the related phenomenon of express neck responses has been directly correlated to visual responses in the intermediate superior colliculus of monkeys (34). The interface between the superior colliculus and motor periphery is likely indirect, and our work here adds to a small body of literature that more has considered the potential involvement of other interfaces. For example, Glover and Baker (2019) reported enhanced express arm responses (what they termed rapid visual responses) in a unimanual response task when visual stimuli were combined with other auditory, vestibular, or somatosensory stimuli. Such non-visual stimuli are thought to enhance responses in the reticular formation, hence they attributed the facilitation they observed on express arm responses to the influence of such non-visual stimuli in the reticular formation (2). Further, using an elegant

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combination of transcranial brain stimulation and electrical stimulation of the median nerve, Nakajima, Suzuki and colleagues proposed that rapid limb responses to changing visual inputs attested to the integration within cervical interneurons of corticospinal inputs with visual information rapidly relayed along a subcortical tectoreticulospinal pathways (35, 36). Whether cervical interneurons are involved in the generation of express arm responses, perhaps in conjunction to the reticular formation, remains to be determined but this seems likely given the broad convergence between descending motor pathways (37).

Another area of future research should address how malleable the bilateral distribution of express visuomotor responses would be with changes in body posture, target position, or loading force. Our positioning of targets medial to both hands, with loading forces in the opposite direction, meant that pectoralis major was the only muscle on which the bilateral distribution of express muscle responses could have been assessed. Having established that express arm responses can be distributed bilaterally, future experiments should look at other limb muscles, or configurations where a given target could be reached by contraction of a given muscle in one arm or relaxation of the same muscle on the other arm (e.g., by altering loading forces). Indeed, although there is substantial variability, the most common bilateral recruitment profile evoked by stimulation of the reticular formation is ipsilateral muscle facilitation and contralateral muscle suppression (38). If the pathway mediating the bilateral distribution of express muscle responses is to have any functional benefit, it would seem to be a necessity to be able to flexibly map target locations onto different combinations of bilateral muscle recruitment.

Conclusions

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Our work here contributes to the understanding of the phenomenology of express arm responses, showing for the first time to our knowledge that the underlying pathway distributes the motor signal bilaterally. Our results are largely consistent with the involvement of the reticular formation as an interface between the superior colliculus and motor periphery. Our overall hypothesis is that signalling along the tectoreticulospinal pathway initiates the first wave of limb muscle recruitment in circumstances requiring rapid visually-guided reaching. We are mindful however of the possibility of the convergence of cortical inputs into all nodes of this pathway, including the superior colliculus, the reticular formation, spinal interneuron networks, and the motoneuron. Rather than being directly involved in express arm responses, cortical inputs into these subcortical nodes, for example with anticipatory signals that bias arm choice, can dampen, or augment the vigor of the earliest visually-related responses. Further characterization of the properties of express arm responses, and the integration of such signalling with task-relevant information, can more precisely address the underlying neural mechanisms and the integration of such signalling with cortical inputs that initiate and guide our most rapid visually-guided behaviours.

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