Title: Stopping muscle contractions and relaxations during action inhibition involves global and targeted control dependent on muscle state

Abbreviated title: control of stopping contractions and relaxations

De Havas, Jack[1], Ibañez, Jaime[2,3], Gomi, Hiroaki[4], Bestmann, Sven[1,5,6]

1. Department of Clinical and Movement Neurosciences, UCL Queen Square Institute of Neurology, University College London, WC1N 3BG, UK.
2. Grupo BSICoS, I3A ,Universidad de Zaragoza, IIS Aragón, Zaragoza, 50018, Spain
3. Centro de Investigación Biomédica en Red en Bioingeniería, Biomateriales y, Nanomedicina (CIBER-BBN), Zaragoza, 50009, Spain.
4. NTT Communication Science Labs., NTT Inc., Atsugi, Kanagawa, 243-0124, Japan.
5. Department of Imaging Neuroscience, UCL Queen Square Institute of Neurology, University College London, WC1N 3BG, UK
6. Centre for Clinical Neuroscience, Hospital Los Madroños, Brunete, 28690, Spain

Corresponding author email: j.havas.12@ucl.ac.uk

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Abstract

The mechanisms underpinning the stopping of muscle contractions and relaxations during action inhibition remain unclear. Central stop commands may be targeted and act on task-active muscles only, or instead be global, acting on task-passive muscles as well. We addressed this question in three stop signal task experiments with human participants (n=54; 18 Male, 36 Female). Whilst maintaining baseline force levels (10% MVC) in both index fingers, Go signals required participants to increase or decrease this force in the task-active finger (Task-active Contract vs Task-active Relax) while keeping activity in the task-passive muscle constant. On 30% of trials, delayed stop signals instructed participants to stop the task-active responses. Stop-related activity was detected in task-active muscles at the single trial-level, using electromyography (EMG), and used to determine whether stop-related activity was also present in task-passive muscles. We found that stop commands act on both task-active and task-passive muscles, suggesting global control. This global control was furthermore muscle-state specific, by decreasing muscle activity when stopping contractions, and increasing muscle activity when stopping relaxations. However, stopping muscle contractions involved more sustained suppression of muscle activity in task-active than task-passive muscles, suggesting additional targeted control. This was not the case when stopping muscle relaxations, which only showed evidence of global control. Our results may explain how complex, real-world actions are inhibited. Global stop commands that are sensitive to muscle state may rapidly adjust muscle activity across the body, with additional control targeted to contracting, task-active muscles.

Significance statement

The nature of stop commands sent to the muscles during action inhibition was unclear. We show that action inhibition changes activity in task-passive as well as task-active muscles, suggesting that stop commands are global in nature. Global stop commands were muscle-state specific; they decreased activity when stopping contracting muscles and increased it when stopping relaxing muscles. Evidence for additional targeted commands being sent to task-active muscles (i.e. more sustained suppression than task-passive muscles) was only found when stopping muscle contractions, not when stopping relaxations. Action inhibition may therefore be underpinned by global stop commands that decrease and increase motor output according to whether muscles are contracting or relaxing, with additional targeted commands being sent to suppress contracting, task-active muscles.

Introduction

Action inhibition, such as stopping at a road crossing to avoid an oncoming vehicle, requires rapid state changes in contracting and relaxing muscles. This process involves both global control signals that act on both task-active and task-passive muscles, and targeted control signals that affect only task-active muscles (Diesburg and Wessel, 2021; Hannah and Aron, 2021). However, how these control mechanisms govern the reactive stopping of muscle contractions versus relaxations remains unclear.

Action inhibition models have focused on muscle contractions (Logan & Cowan, 1984; Aron et al., 2014), but muscle relaxations are an equally essential aspect of action—for instance, to release objects, reset posture, or in coordination with contracting agonist muscles (Pope et al., 2007; Kato et al., 2019). State-specific stop

commands can be identified from electromyography (EMG), with decreased EMG activity observed when stopping contractions, and increased activity when stopping relaxations (Raud and Huster, 2017; Atsma et al., 2018; De Havas et al., 2020). This activity occurs in task-active muscles (those involved in the action) 100–200ms after a stop signal, correlates with the behavioural stop signal reaction time (SSRT; De Havas et al., 2020), and is detectable at the single-trial level (Raud et al., 2022). However, to dissociate global and targeted control mechanisms requires identification of the dynamics of task-passive muscles (those uninvolved in the action).

Three proposals explain how global and targeted control may influence muscle contractions and relaxations during stopping (Fig. 1A). First, stopping might act only on task-active muscles, but not task-passive muscles, potentially via the basal ganglia indirect pathway (Aron, 2011). Second, reactive stopping could involve global effects on both task-active and passive muscles, as suggested by global decreases in corticospinal excitability around ~100–150ms post-stop signal (Badry et al., 2009; Cai et al., 2012; Wessel et al., 2013). This suppression has been linked to the basal ganglia hyperdirect pathway (Jana et al., 2020). However, whether such global effects occur only when stopping muscle contractions or also when stopping muscle relaxations remains undetermined.

Finally, stopping may involve both global and targeted control. Global control commands could act on all muscles, while additional targeted control acts only on task-active muscles. Recently proposed ‘Pause-then-Cancel’ models suggest that global, transient suppression via the hyperdirect pathway is followed by targeted suppression specifically of task-active muscles via the indirect pathway (Schmidt and Berke, 2017; Diesburg and Wessel, 2021). However, whether such ‘Pause-then-Cancel’ mechanism also controls the stopping of muscle relaxations is unclear. This is relevant

because halting muscle relaxations is essential for many day-to-day, multi-joint stopping behaviours. We reasoned that if task-active muscles are under global and targeted control, whilst task-passive muscles are only under global control, their activity patterns should vary.

Conceivably, stopping muscle contractions and relaxations may depend on the same control mechanisms (i.e. targeted, global, or global and targeted), differing only in terms of the direction of the stop-related activity (i.e. decreased EMG for stopping contractions, increased EMG for stopping relaxations). Alternatively, divergence of control is possible, since decreases and increases of EMG are likely implemented in different ways: stop-related decreases of muscle activity may only require suppressing central excitatory drive (Wiecki and Frank, 2013), but stop-related increases of muscle activity necessitate excitation within motor pathways and the recruitment of motor units (De Havas et al., 2020). Determining the extent to which the stopping of muscle contractions and relaxations depends on shared control mechanisms may help explain how action inhibition is implemented for complex, multi-limb movements that require changes in the activity of multiple muscles (Ilmane and LaRue, 2011; Kwag et al., 2024).

To test these hypotheses, we conducted three experiments examining the stopping of muscle contractions and relaxations while recording EMG activity from task-active and task-passive muscles. We asked whether global control affects task-passive muscles and whether targeted control operates alongside when stopping contractions and relaxations.

Methods

Participants

Experiment 1 involved 18 participants (6 male; age 24.8±5.7 yrs), with one left-handed. Experiment 2 had 16 participants (5 male; age 24.6±3.8 yrs), as one of the 17 recruited couldn't complete the task; one participant was left-handed. Experiment 3 recruited 21 participants (7 male; age 26.8±6.2 yrs), all right-handed, with one participant not completing the task.

Sample sizes were based on prior research (De Havas et al, 2020), increased by 30-40% to account for lower signal-to-noise ratios in task-passive muscles. Participants free of neurological, psychiatric, or muscular disorders were recruited from the UCL psychology subject pool and reimbursed with £12/h. All experiments followed ethical guidelines (Declaration of Helsinki), with local IRB approval, and with written informed consent obtained from all participants.

Equipment

Participants were seated in an adjustable chair in front of a table with a mounted a custom-built experimental apparatus. This consisted of cushioned arm rests mounted to a wooden board, to which was attached a horizontal metal bar with two vertical struts. Two identical rigid strain gauges (0.78 Kg Micro Load Cell, Phidgets, Canada) were mounted on the outside of each vertical strut (Fig. 1B). Cork disks (diameter = 1cm, thickness 3mm) were stuck to the flat surface of the strain gauges to prevent discomfort. Two adjustable plastic resting plates either side of the two vertical struts allowed for resting the index fingers during the task and included a small vertical flat edge (3cm high) which touched the outside edge of the finger, limiting movement away from the strain gauge.

Electromyography (EMG) was recorded with unipolar surface electrodes (WhiteSensor 40713, Ambu, Ballerup, Denmark) placed over the first dorsal interosseous (FDI) muscle and dorsal tubercule of radius bone of both hands, with the ground attached to the left ear lobe. EMG was recorded using a Digitimer recording system (D360, Digitimer, Welwyn Garden City, UK). Force signals from the strain gauges and surface EMG were amplified (Power 1401, Cambridge Electronic Design, Cambridge, UK) and recorded using Spike2 software (9.09a) at a sampling rate of 1000 Hz, high-pass filtered (0.05 Hz), with an online 50 Hz notch filter.

Task stimuli were presented on a laptop (XPS 15 9520, 1920 x 1200 pixels, 60 Hz, Dell, Round Rock, TX, USA) placed ~60 cm in front of participants. Tasks were programmed in Matlab (R2023a) and Psychtoolbox (3.0.19). To display force level during tasks, force data were streamed to Matlab via a serial line using custom Spike2 scripts. Go and Stop digital event markers were sent from Matlab to Spike2 via a data acquisition box (USB-6009, NI, Reading, UK).

General procedure and pre-task training

Participants sat facing the screen with arms pronated, elbows slightly bent, and wrists supported on cushions to ensure relaxation, especially of the FDI muscles (Fig. 1B). Index fingers were extended, resting on the adjustable plastic resting plate, with the proximal interphalangeal joint in a slightly flexed position. The remaining fingers were in a flexed position. Contact with the strain gauge was via the inside edge of the index finger, halfway between the fingertip and the distal interphalangeal joint. All increases and decreases of force were isometric.

Maximum voluntary contractions (MVC) were measured separately for each finger. Training involved maintaining a 10% MVC baseline and rapidly increasing (to 20% MVC, Exp. 1 & 3) or decreasing (to 0% MVC, Exp. 2 & 3) force, guided by on-screen feedback (Fig. 1). Force changes were trained to be smooth, rapid (<500ms), and held briefly (500–2000ms). EMG was monitored during force decreases to ensure correct muscle relaxation occurred. Training continued (~10–15 minutes) until participants could perform the task (contraction and relaxation) without visual feedback.

The main experimental task in all experiments was a modified version of the classic top signal task (SST, Logan and Cowan, 1984), in which one of two Go stimuli are present on every trial, necessitating action, whilst a single Stop signal is randomly presented on a subset of trials after a varying delay, requiring that participants stopped isometric FDI contractions and relaxations (De Havas et al., 2020), and was designed in accordance with current SST guidelines (Verbruggen et al., 2019).

In all experiments, participants first performed two practice blocks (40 trials) without Stop signals (i.e. a 2- choice reaction time task). This familiarized participants with the task environment and verified that the force increases and/or decreases (i.e. Go task) were performed without visible force changes in task-passive fingers. Secondly, a practice version of the SST was administered (1 block, 60 trials), which differed from the main task in the frequency of Stop signals (50% vs. 30%) and performance feedback being given on Stop trials. Practice tasks took ~15-25 minutes.

Experiment 1: stopping muscle contractions

Experiment 1 was a modified version of the SST. At trial onset, participants maintained a steady force of 10% MVC with both fingers, guided by on-screen feedback (Fig. 1). Next, feedback was removed, and participants maintained the 10% MVC force level during this ready period (variable ISI = 500-1000ms). On appearance of a visual Go signal (triangle pointing left or right, displayed for 2000ms), participants were required to increase the force of the indicated finger to 20% MVC (task-active muscle) as quickly and accurately as possible, while keeping the other finger (task-passive muscle) constant at 10% MVC, in accordance with the pre-task training.

In 30% of trials, a visual Stop signal (a red outline around the Go signal) appeared after the Go signal. Participants were instructed to stop the increase in force in the task-active finger while maintaining the baseline force (10% MVC) in the other finger. Success or failure to stop was determined by comparing the force velocity to a threshold set dynamically based on mean maximum force velocity on Go trials from the previous block. A threshold of 30% of this maximum was used to determine whether a Go response had occurred (De Havas et al., 2020). The stop signal delay (SSD) between the Go and Stop stimuli was set to 250ms at the start of the experiment. Failed stop trials decreased the SSD by 50ms, while successful stop trials increased it by 50ms, thereby maintaining stop success rates at ~50% (Verbruggen and Logan, 2008; Verbruggen et al., 2019). SSD was carried over to the next block (i.e. not reset to 250ms).

The experiment consisted of 8 blocks of 60 trials each (42 Go trials and 18 Stop trials, equal proportion of left and right stimuli). Each block lasted ~7 minutes, with breaks of 2-3 minutes between blocks. Feedback was given to improve performance if participants slowed down their Go responses over time (Verbruggen et al., 2019).

Experiment 2: stopping muscle relaxations

Experiment 2 was a muscle relaxation version of the SST, where participants were instructed to reduce the force in the specified index finger (from 10% to 0% MVC) when the Go signal appeared, and to stop this relaxation when a subsequent Stop signal appeared (Fig. 1C). Procedures were similar to Experiment 1.

Each trial included a baseline phase (10% MVC, visual feedback, 3000ms) and a 'get-ready' period (10% MVC, no feedback, 500-1000ms), followed by the Go stimuli (rightward triangle = relax right finger, leftward triangle = relax left finger). Stop signals (30% of trials) required stopping the relaxation.

Stop-success thresholding and SSD staircasing was the same as in Experiment 1, except that the sign was reversed. Therefore, a minimum force velocity <30% of the mean minimum Go trial force velocity was classified as failed stop trial (SSD decreased by -50ms), and otherwise classified as a successful stop trial (SSD increased by +50ms).

There were 60 trials per block (42 Go, 18 Stop; balanced between fingers), with block durations of ~7 minutes. Eight blocks were completed (~2 hours total), with rest breaks (2-3 minutes) and performance feedback provided after each block. The experiment lasted ~2 hrs.

Experiment 3: stopping muscle contractions and relaxations

Experiment 3 was a contract-and-relax version of the SST (Fig. 1C). On appearance of a Go stimulus, participants had to keep the left index finger at a

constant contraction (10% MVC), while either increasing (to 20%, contraction trial) or decreasing (to 0%, relaxation trial) the right index finger baseline contraction. Stop signals required stopping the right index finger (maintain contraction at 10% MVC), and stopping success was measured separately for contraction and relaxation trials.

The procedure otherwise mirrored Experiments 1 and 2. Upward triangles signaled contraction (10% to 20% MVC), while downward triangles signaled relaxation (10% to 0% MVC). Stop signals appeared randomly in 30% of trials after a variable SSD (250ms ± 50ms).

Each block contained 60 trials (42 Go, 18 Stop, evenly split between contraction and relaxation trials), with 8 blocks in total (~7 minutes each). Rest breaks (2-3 minutes) were provided, and feedback was given if responses showed slowing. The total number of trials per condition was half that of Experiments 1 and 2, with 168 Go trials and 72 Stop trials per muscle state. The experiment lasted ~2 hours.

Data Analyses

Data preprocessing

Force data were smoothed using a low-pass filter (10 Hz zero-phase digital filtering), and force velocity was calculated from the difference between successive time points (two point differentiation). EMG signals were filtered (zero-phase digital filtering; 10–500 Hz), rectified, smoothed (low-pass 5 Hz zero-phase digital filtering). EMG velocity was computed similarly from the smoothed EMG signal.

Trials were removed if they contained movement artifacts (e.g. moving away from force sensor), lacked a response to the Go signal, the force changed in the opposite direction than instructed, or showed excessive force or earlier force in the

passive finger relative to the active finger (>75% of active finger amplitude and/or onset before the task-active finger). These latter criteria were included to remove any trials where participants responded with the wrong hand or with both hands simultaneously. Additionally, trials were excluded if FDI muscle activity fell below 5% MVC at the Go period start, a mistake observed only in Experiment 3.

On average, 5.27% of trials were excluded in Experiment 1 (SD = 3.75%), 3.55% in Experiment 2 (SD = 2.33%), and 10.53% in Experiment 3 (SD = 3.77%).

Response times, SSRT and stop-locking data

Response times (RT) were determined by identifying the onset of force changes in the task-active index finger relative to the Go signal. For contractions (Exp. 1 & 3), this was when force velocity exceeded 30% of peak force velocity; for relaxations (Exp. 2 & 3), the sign was reversed (<30% of minimum). Force and EMG signals were time-locked to this point.

EMG response times (EMG-RT) were calculated similarly, within a window -150 to 50ms around force onset. Stopping success rate was obtained by dividing successful stop trials by total Stop trials. Stop signal reaction time (SSRT) was computed using the integration method (Verbruggen et al., 2019). The Go RT distribution for each participant was sorted into ascending order and non-response trials were replaced with the slowest RT (Verbruggen et al., 2019). The n^{th} RT was found by multiplying the number of trials by the probability of responding on stop trials (i.e. number of failed stop trials divided by total stop trials). Thus, for a given participant, if the probability of responding was 0.49 and the number of Go trials was 336, the n^{th} RT would be the 165^{th} fastest Go trial (after rounding to the nearest

integer). Mean SSD was then subtracted from this Go RT value to give the SSRT. RT, stopping success rates and SSRT were analyzed separately for stopping muscle contractions and relaxations in Exp. 3.

Successful and failed stop trials were time-locked to the Stop signal (stop-locked) and averaged for force, force velocity, and EMG measures. Group-level analysis confirmed stop-related activity in task-active muscles, with contractions showing decreased force and EMG and relaxations showing increased force and EMG (100-300ms post-stop signal), consistent with previous findings (De Havas et al, 2020). This was done to validate the main analysis, which constituted detecting stop-related activity at the single trial level in the task-active muscle, and then time-locking both the task-active and task-passive muscle activity to this point, to address the question of whether state-specific stop-related activity was present in the task-passive muscle.

Trial-level detection of stop-related activity in the task-active muscle

To address whether stopping produced changes in muscle activity in task-passive muscles, we first looked for stop-related activity in task-active muscles. Stop-related activity refers to consistent decreases or increases in EMG that occur after the stop signal. When stopping muscle contractions, this typically manifests as decreases of EMG activity, which is seen both after partial responses on successful stop trials and after a complete response on failed stop trials (Raud and Huster, 2017; Jana et al., 2020; Raud et al., 2022). When stopping muscle relaxations, increases of muscle activity are seen after partial (successful stop trials) and complete (failed stop trials) relaxations (De Havas et al., 2020). This latter effect has also been termed active braking (Goonetilleke et al., 2010; Atsma et al., 2018; De Havas et al., 2020). For

clarity, we refer to both these phenomena as ‘stop-related activity’ and always specify the direction of this effect (i.e. stop-related decrease of activity when stopping contractions, and stop-related increases of activity when stopping relaxations).

Trial-level detection of stop-related activity focused on force velocity and EMG velocity data from the task-active index finger. Only task-active force and EMG data were used, as the main hypothesis was whether stop-related activity could be detected in the task-passive muscle. Velocity data were used for their sensitivity to small signal changes and being agnostic to the absolute levels.

The onset of stop-related activity was identified via troughs (contraction) and peaks (relaxation) in failed and successful stop trials, i.e. state-specific task-active stop-related activity (De Havas et al., 2020). Successful stops were included following previous reports of partial responses and stop-related activity in at least 23% of such trials (Raud et al., 2022). Other studies have reported partial responses and stop-related activity in ~50% of successful stop trials (Jana et al., 2020). During normal isometric force increases (i.e. reaction time tasks without Stop signals) there is braking at the end of the action (Ghez and Gordon, 1987). However, braking at the end of an action is different from stopping (Atsma et al., 2018), and to avoid misclassifying braking at the end of the action as stop-related braking, we excluded any failed stop trials where the force exceeded 90% of the average Go trial amplitude. We also removed failed stop trials where the force velocity did not change for an extended duration (>300ms) before braking activity was detected, as this could indicate that the Go response had naturally ended and a second voluntary response to return the force to baseline might have occurred. This accounted for 30-40% of failed stop trials.

For ease of description, we will explain only how stop-related activity was detected in the case of muscle relaxations. Stop-related activity was identically detected for stopping contractions, but the sign of the data was reversed (i.e. troughs instead of peaks).

To detect stop-related activity during muscle relaxation, stop-related peaks were identified when the signal rose 1 SD above the mean within 100-500ms after the Stop signal (Fig. 2C; upper panel). For failed stop trials, this detection window was sometimes shifted by up to 300ms to capture late responses (<5% of trials). Trials without peaks were discarded, which was ~30% of successful stops and <5% of failed stops (after removal of 30-40% of failed stop trials where end of action braking or voluntary responses were detected). For detected peaks, the onset was when the signal first exceeded 30% of the peak's maximum.

An EMG detection window (-150 to 50ms relative to force velocity onset) accounted for the ~50-100ms delay between EMG and force (Fig. 2C; middle panel). EMG peaks were detected similarly, but trials were discarded if no peak was found or if EMG onset was too late (> -25ms from force onset, De Havas et al., 2020). Only trials with biologically plausible stop-related activity for force and EMG were included. Activity was detected in ~60% of trials, with all participants showing rates above 40%, broadly consistent with other studies (Jana et al., 2020). Details are in Table 1. Some work has found that stop-related activity can be detected in 23% of successful stop trials and 98% of failed stop trials (Raud et al., 2022). However, our task used a different methodology to assess successful and failed stop trials (De Havas et al., 2020), which may have led to differences in how trials were classified. Previous work has shown that the assumptions of the horse race model are met regardless of the amplitude of the threshold that is used to separate successful and failed stop trials

(Hannah et al., 2022). Nevertheless, our detection rates are within the expected range, given it has been reported that across 21 experiments or conditions, stop-related activity can be detected in 23 – 70% of stop trials, with the mean being ~ 50% (Raud et al., 2022).

Identifying stop-related activity in task-passive muscles

To determine stop-related activity in task-passive muscles, force velocity and EMG velocity signals were aligned to onset times detected in task-active muscles (Fig. 2C; lower panel). This was done for both task-active and task-passive muscles at the trial level, using only trials with detected stop-related activity, and applying a 400ms window either side of the onset. The data were averaged separately for successful and failed stop trials.

Two methods were used: a continuous approach with one-sample t-tests against zero at the group level (2-tailed testing used, i.e. significant deviations above and below 0), and a binned analysis. For relaxations, significant positive deviations from zero in task-passive muscles (lasting >10 time-points, $p < 0.05$) indicated stop-related activity, providing they overlapped with those seen in task-active muscles, since we were looking for global stopping (i.e. simultaneous stop-related activity across muscles). For contractions, significant negative deviations from zero were used, again overlapping with those seen in task-active muscles. Both for the stopping of relaxations and contractions, we always used two-tailed testing, to ensure detection of stop-related activity in the opposite direction (i.e. negative deviations for relaxations, positive for contractions), but this was not observed in either case. Late or go-related activity was ignored during plotting.

The binned analysis focused on a 100ms window (-25ms to 75ms from task-active onset), based on prior studies (De Havas et al., 2020) and observations that task-passive muscles sometimes activated earlier. Activity in this bin was compared to zero using group-level t-tests. There was no disagreement between the two methods (i.e. continuous t-test vs. binned analysis). Both methods were applied to force velocity data similarly (see supplementary materials; Suppl. Fig. S4 & S5; Suppl. Table S1).

Comparing task active and passive stop-related activity across muscle states

Next, we analyzed the onset and end of stop-related muscle activity at the participant level. EMG velocity data for task-active and task-passive conditions was normalized using z-transformation to ensure comparability across participants. For stopping relaxations, stopping onset times were identified when normalized EMG velocity first exceeded 30% of the initial local peak within -200 to 200ms (i.e. relative to task-active onsets defined at the single trial level). Only local peaks starting within this window were considered stop-related. For stopping contractions, the procedure was reversed to focus on troughs instead of peaks. Stopping offset times were defined as the next zero crossing of the EMG velocity signal after the onset of stop-related activity. If the signal did not cross zero, the closest point to zero was used (affecting two participants in Exp. 3 only)

We conducted three analyses to compare stopping activity in task-active and task-passive muscles, to address whether task-active muscles showed any evidence of additional targeted stop commands, which we reasoned would show up as: 1) increased stopping duration in task active muscles relative to task-passive muscles, 2) more complete stopping in the task-active muscle, 3) lower correlation between

task-active and task-passive muscles, relative to cases where both muscles received only a shared global stop command.

Firstly, stopping duration was calculated by subtracting stopping onset from stopping offset for each condition. Successful and failed stop durations were averaged, and overall durations for task-active and task-passive muscles were compared using paired t-tests (Exp. 1 & 2) or a 2x2 ANOVA (Exp. 3) with factors Muscle State (stopping contractions vs. stopping relaxations) and Muscle Type (task-active vs. task-passive).

Secondly, we examined the post-stop rebound in muscle activity. For stopping both contractions and relaxations, there were three phases to the EMG velocity time course during Stop trials: 1) partial Go response, 2) stop-related activity, 3) rebound activity. Rebounds in muscle activity were termed ‘Go resumption’ because they were in the same direction as the Go response. We quantified ‘Go resumption’ as the area under or over the curve (AUC/AOC) of EMG velocity in a 100ms window after stopping offset. For stopping relaxations AUC was used; for stopping contractions AOC was used. AUC/AOC was then normalized as a percentage of each participant's peak Go trial AUC/AOC (100ms window). Thus, 0% ‘Go resumption’ indicates no rebound activity, whereas 100% ‘Go resumption’ indicates rebound activity matching the initial Go response. Percentages were compared for task-active and task-passive muscles, as for the stopping duration analysis described above.

Significant ‘Go resumption’ is consistent with transient suppression of the Go process that ‘rebounds’ following this suppression, akin to only the ‘Pause’ command in ‘Pause-then-Cancel’ models (Diesburg and Wessel, 2021). By contrast, absent or small ‘Go resumption’ is consistent with more sustained suppression of the Go

response, consistent with a ‘Pause-then-Cancel’ command being sent. Importantly, since our analysis is based on EMG velocity, it is agnostic to the background level of EMG. The background level of EMG at the point of ‘Go resumption’ depended on a combination of the partial Go response and the subsequent stop-related activity. Thus, high ‘Go resumption’ does not necessarily imply that the Go response has not been successfully stopped, provided that the stop-related activity is of sufficiently high amplitude.

Finally, we assessed the overall degree of similarity of stop-related activity in task-active and task-passive muscles. If a single stop command acted on both muscles concurrently, their activity profile should reveal a high cross-correlation. We used time-shifted cross-correlation analysis (De Havas et al., 2020) to compare task-active and task-passive EMG velocity time courses. A window of -150 to 150ms (relative to task-active stop-related activity onset) was used to capture stop-related activity. Pearson correlations between both muscles were calculated as task-passive data were shifted forward and backward relative to task-active muscle data by 100ms in 1ms steps. We could then plot the correlation values for each subject against the ‘time-shift of task-passive muscle relative to task-active muscle in milliseconds’. We then took each subject’s peak correlation value as an index of the similarity between task-active and task-passive stop-related activity. These Peak cross-correlation values were then compared using t-tests for stopping contractions and relaxations. Between subjects t-tests were used for comparing Exp. 1 and Exp. 2. Within subjects t-tests were used in Exp. 3.

Results

Stop signal task performance

Single trial (Fig. 1D) and group average (Fig. 1E) force and EMG data are shown for contract and relax Go trials in Exp. 1 & 2 (For Exp. 3 data, see Suppl. Fig. S1). Participants successfully increased task-active muscle force/EMG for contract conditions, and decreased task-active muscle force/EMG for relax conditions. Stop signal tasks were performed correctly, with participants responding quickly on Go trials and faster on failed stop trials (Table 2). All participants in all experiments were faster at responding on failed stop trials than go trials (Mean: -88ms, SD: 30ms, range: -28 to -174ms). Stopping success rates were close to 50% in all cases, and behaviorally derived SSRTs were within the normal range (Verbruggen and Logan, 2008). Go trial RT, SSD and SSRT were similar for contractions and relaxations (Suppl. Fig. S2). In all experiments and conditions, Go trial EMG-RT preceded force-RT by 83 to 105ms.

In line with previous work, muscle-state specific stop-related EMG activity was clearly present for *task-active muscles* after time-locking to the Stop signal (Atsma et al., 2018; De Havas et al., 2020). This manifested as decreases of EMG activity when stopping muscle contractions, and increases of EMG when stopping muscle relaxations (~100-300ms post-stop signal), for both successful and failed stop trials (Fig. 2A, B).

Stop-related EMG activity in task-active muscles onsets positively correlated with SSRT (Suppl. Fig. S7), in line with previous work (De Havas et al., 2020).

Muscle-state specific stop-related activity found in task-passive muscles

Stop-related activity could be detected in task-active muscles in ~60% of Stop trials across all experiments (Fig. 2C, Table 1, Suppl. Fig. S3), consistent with previous

reports (Jana et al., 2020). After locking to the onset of stop-related activity in these trials, stop-related activity was also present in the task passive muscle, for both successful and failed stop trials (Fig. 3 & 4). This was the case when the stopping of contractions and relaxations was separate (Exp. 1 & 2, Fig. 3, Suppl. Fig. S4), and when they were combined and intermixed (Exp. 3, Fig. 4, Suppl. Fig. S5).

Task-active and task-passive muscles showed muscle-state specificity. Stop-related decreases in EMG occurred when stopping contractions, whereas stop-related increases in EMG occurred when stopping relaxations (Fig. 3 & 4). Across participants, state-specific stop-related activity was always present for task-passive muscles. When stopping contractions, both on successful and failed stop trials, task-passive muscles showed significant *decreases* of EMG velocity below 0 (Fig. 3C, Table 3). This was replicated in Exp. 3 (Fig. 4C, Table 3). When stopping relaxations, both on successful and failed stop trials, task-passive muscles showed significant *increases* of EMG velocity above 0 (Fig. 3F, Table 3), again replicated in Exp. 3 (Fig. 4F, Table 3). Continuous t-testing was also applied to task-active and task-passive EMG velocity data, which showed significant, overlapping state-specific stop-related activity (Fig. 3 & 4, solid horizonal lines) in all cases.

Thus, muscle state-specific stop-related activity was reliably observed, both when responses were stopped early (successful stop trials) and late (failed stop trials) across all experiments. These results are consistent with global stop control for muscle contractions and relaxations.

Evidence for separable control for stopping muscle contractions and relaxations

Having established that global control governs the stopping of muscle contractions and relaxations, we next sought evidence for additional targeted control in task-active muscles. Specifically, we asked whether 1) additional targeted control is present when stopping muscle contractions, and whether 2) additional targeted control is present when stopping muscle relaxations? To this end, we quantified any EMG differences between task-active and task-passive muscles. We reasoned that differences between muscles could indicate the presence of an additional targeted stop command being used. We first compared the duration of stop-related activity in task-active and task-passive muscles. Longer stop-related activity in task-active vs. task-passive muscles were taken as indication for the presence of additional targeted stop commands. Next, we examined 'Go resumption' after the stop-related activity, with lower 'Go resumption' in task-active muscles than task-passive muscles being taken as evidence for additional targeted stop commands, that further suppress go-related activity in task-active muscles. We also analyzed the cross-correlation between task-active and task-passive muscles, with high cross-correlation being taken as evidence for shared global control.

The concepts of stop-related activity duration and 'Go resumption' are illustrated using single subject data, with group traces shown for comparison (Fig. 5). When stopping muscle contractions (Fig. 5Ai-ii), stop-related activity in this participant was longer in task-active muscles compared to task-passive muscles. Conversely, when stopping relaxations (Fig. 5Aiii-iv), stop-related activity duration was similar across muscles in a representative participant. Group mean onset, offset and duration for successful and failed stop trials for stopping contractions and relaxations in all experiments are given in table 4. In the representative participant (Fig. 5Ai-ii), when stopping contractions, 'Go resumption' was smaller in task-active muscles than task-

passive muscles. However, for a representative single participant (Fig. 5iii-iv), when stopping relaxations 'Go resumption' was equally large across muscles. Group-level results for Exp. 1&2 (Fig. 5B) and Exp. 3 (Fig. 5C) follow the same pattern, namely that stop-related activity differed (i.e. duration and 'Go resumption') across muscles when stopping contractions, and did not differ across muscles when stopping relaxations. Thus, for stopping muscle contractions, task-active muscles showed evidence of more sustained suppression of the Go response relative to task-passive muscles, but this difference between task-active and task-passive muscles was not observed when stopping muscle relaxations.

The duration of stop-related activity dissociates the control of stopping muscle contractions and relaxations

In Exp. 1, mean stop-related activity duration was significantly longer for task active muscles (Mean = 161ms, SD = 84ms) than task-passive muscles (Mean = 89ms, SD = 43ms; $t(17) = 4.16 = , p < 0.001$, Cohen's d = 0.98; Fig. 6D). However, for muscle relaxations, stopping durations were similar for task-active (Mean = 116ms, SD = 32ms) and task-passive muscles (Mean = 123ms, SD = 31ms; $t (15) = -1.028$, p = 0.32, Cohen's d = -0.26). In Exp. 3, contractions and relaxations were compared directly (Fig. 6G). There was no main effect of muscle state (Contract vs Relax; $F (1,19) = 1.092$, P = 0.309 , $\eta p^2 = 0.054$) or muscle type (Task-active vs Task-passive; $F (1,19) = 0.104$, P = 0.751, $\eta p^2 = 0.005$). There was, however, a significant muscle state x muscle type interaction ($F (1,19) = 7.071$, P = 0.015, $\eta p^2 = 0.271$). This was driven by longer durations for task-active muscles (Mean = 121ms, SD = 30ms) than task-passive muscles (Mean = 108ms, SD = 42ms) when stopping muscle contractions ($t(19) = 1.354$, p = 0.191, Cohen's d = 0.3) confirming that it was the same

effect observed in earlier experiments, but also by shorter durations in the task-active muscle (Mean = 104ms, SD = 7ms) than the task-passive muscle (Mean = 112ms, SD = 30ms) when stopping relaxations ($t(19) = -1.155$, $p = 0.262$, Cohen's $d = -0.26$), though neither difference was significant in isolation.

In sum, the duration of stopping activity for stopping muscle contractions was longer for task-active muscles than task-passive muscles, consistent with concurrent global and targeted control (Fig. 6A.iv). By contrast, the duration of stopping activity for stopping muscle relaxations was similar across muscles, consistent with global control (Fig. 6A.ii).

'Go resumption' is attenuated for task-active muscle only when stopping muscle contractions

Across all experiments, 'Go resumption' was almost absent from the task-active muscle when muscle contractions were being stopped (~5% of Go amplitude), consistent with 'cancellation' of the Go response (Fig. 6A.iv). By contrast, we reliably observed evidence for 'Go resumption' (~60% of Go amplitude) in all other conditions, consistent with a transient suppression of the Go response that then rebounds (Fig. 6A. ii). 'Go resumption' activity was significantly different between task-active (Mean = 4% of initial Go response, SD = 4%) and task-passive muscles (Mean = 56%, SD = 43%) when stopping contractions (Exp. 1; $t(17) = -5.21$, $p < 0.001$, Cohen's $d = -1.23$; Fig. 6C). While there was clear evidence for 'Go resumption' activity when stopping muscle relaxations, there was no difference between task-active (Mean = 62%, SD = 41%) and task-passive muscles (Mean = 73%, SD = 39%) (Exp. 2; $t(15) = -1.108$, $p = 0.286$, Cohen's $d = -0.28$). This finding was replicated in Exp. 3 (Fig. 6F), where for stopping muscle contractions, task-active 'Go resumption' (Mean = 5%. SD = 6%) was

lower than task-passive ‘Go resumption’ (Mean = 72%, SD = 46%), but for stopping muscle relaxations task-active (Mean = 62%, SD = 39%) and task-passive (Mean = 73%, SD = 56%) ‘Go resumption’ were similarly high. This translated to a significant main effect of muscle state ($F(1,19) = 7.714$, $P = 0.012$, $\eta p^2 = 0.289$), a significant main effect of muscle type ($F(1,19) = 33.3$, $P < 0.001$, $\eta p^2 = 0.637$) and a significant muscle state x muscle type interaction ($F(1,19) = 11.618$, $P = 0.003$, $\eta p^2 = 0.379$). This interaction was driven by the task-active ‘Go resumption’ being lower than the task-passive ‘Go resumption’ when stopping muscle contractions ($t(19)) = -6.598$, $p < 0.001$, Cohen’s $d = -1.48$; Fig. 6F). Task-active and task-passive ‘Go resumption’ did not differ when stopping relaxations ($t(19 = -0.924$, $p = 0.367$, Cohen’s $d = -0.21$).

These results support the idea of a global ‘Pause’ for stopping of muscle relaxations, whilst stopping contractions may involve a global ‘Pause’, then a targeted ‘Cancel’ command sent to the task-active muscle. A ‘Pause’ command was enough to stop muscle relaxations because it produced a large burst of muscle activity (i.e. stop-related activity was ~2x bigger than go-related activity; see supplementary materials; Suppl. Fig. S6).

Activity in task-active and passive muscles more strongly correlated when stopping muscle relaxations than contractions

Peak correlations between stop-related activity in task-active and task-passive muscles was higher for muscle relaxations compared to muscle contractions (Fig. 6E & H). This was true when comparing across participants in Exp. 1 & 2, where the mean peak Pearson’s r values for stopping relaxations was 0.92 (SD = 0.07) while for stopping contractions it was 0.63 (SD = 0.28; $t(32) = 3.978$, $p < 0.001$, Cohen’s $d = 1.37$). Within participants (Exp. 3), peak Pearson’s r values were higher for relaxation

trials (Mean±SD: 0.78±0.14) compared to contract trials (0.64±0.23; t(19) = 2.3, p = 0.033, Cohen's d = 0.51). The high degree of correlation of stop-related activity between muscles when stopping relaxations is consistent with a shared control signal acting concurrently on both muscles (Fig. 6B).

Stop-related activity continues after behavioral SSRT

Stop-related activity onsets were close in time to the estimated behavioral SSRT in all experiments (Fig. 3 & 4 A,B, D, E; dashed vertical lines). Stop-related activity offsets were all significantly later than behavioral SSRT by ~100ms (see supplementary materials). Allowing for ~20ms conduction delays (Jana et al., 2020), this means that ~80ms of central stop-related processing may take place after traditional SSRT estimates, a finding that may be relevant to debates concerning the timing, relative to SSRT, of neural markers of action inhibition, such as the P3 (Huster et al., 2020; Hervault et al., 2025). Exploratory analyses assessed whether SSRT was more closely associated with putative 'Pause' or 'Pause-then-Cancel' commands, but the results were inconclusive and only showed uniformly stronger correlations with task-active vs. task-passive muscles (see supplementary materials). Future work could address this question by tracking individual motor units during stopping, thereby attaining more precise estimates of different stop-related inputs to the muscle.

Discussion

We asked three questions about how stopping behavior is controlled. Firstly, does stop-related activity occur in both task-active and task-passive muscles when stopping contractions and relaxations? Secondly, is this activity muscle-state specific,

whereby stopping contractions decreases muscle activity while stopping relaxations increases it? Finally, are global and targeted stop commands used together to provide additional control for task-active muscles?

Across three experiments, global stop-related muscle activity was consistently present. This activity was muscle-state specific, reducing activity in both task-active and task-passive muscles for contractions, but increasing it for relaxations. Additionally, we observed sustained suppression of muscle activity when stopping contractions, suggesting additional targeted control to task-active muscles.

Stop commands are global and muscle state-specific

In all three experiments, stop-related activity was detected in task-active and task-passive muscles, demonstrating global stopping. These findings side with previous reports that stopping is associated with global changes in corticospinal excitability across a range of proximal and distal muscles (Badry et al., 2009; Greenhouse et al., 2012; Wessel et al., 2013).

We used the other FDI as the task-passive muscle, and interhemispheric interactions may have contributed to the observed effects (Carson, 2020). Indeed, it remains uncertain whether stopping control is invariant across the body, or shows attenuation with distance from the task-active muscle, as observed during pre-movement inhibition (Labruna et al., 2019). Recent work has shown that successfully stopping foot movements can produce suppression of isometric finger forces (Rangel et al., 2024), indicating that distant muscles can show global effects.

Stop signals must act on muscles differently whether the muscle is contracting or relaxing. Indeed, stop-related decreases of activity occur in contracting muscles,

whereas stop-related increases of muscle activity occur in relaxing muscles (Raud and Huster, 2017; Atsma et al., 2018; De Havas et al., 2020; Jana et al., 2020). It remained unclear whether this muscle state-specificity was targeted to task-active muscles (Fig. 1A; left panel) or is global and occurs in task-active and task-passive muscles (Fig. 1A; middle panel). Here, we found that stop-related decreases of activity occur in both muscles when stopping contractions, whereas stop-related increases of activity occur when stopping relaxations. This global muscle suppression during the stopping of contractions is consistent with the global decreases in corticospinal excitability previously reported (Wessel et al., 2013; Mills et al., 2025). We additionally found global increases of muscle activity when stopping muscle relaxations, which raises the question of how both global decreases and global increases of muscle activity are generated.

Mechanisms of global state-specific stop commands

What pathways underpin global stopping? The basal ganglia hyperdirect pathway, particularly the subthalamic nucleus (STN), is thought to underpin global reductions in motor output (Mink, 1996; Frank, 2006; Coxon et al., 2012; Aron et al., 2016; Chen et al., 2020). However, we also observed global increases of motor output during the stopping of muscle relaxations, which contrasts with the idea of stopping being merely the cutting of motor output. We speculate that the STN may contribute to such increases, as recent studies indicate it can generate bursts of muscle activity (Friedman and Yin, 2023; Callahan et al., 2024).

But how does the brain ‘know’ whether the stop commands should increase or decrease muscle activity? In Experiment 3, we observed muscle-state specificity in stopping without participants having prior knowledge of the required response

683 (contraction vs. relaxation). Stop-related activity is therefore not determined
684 proactively. Other work has shown that the current muscle state can determine the
685 direction of stop-related activity, with both activation and suppression observed
686 according to the stage of a particular movement (De Havas et al., 2020). Where in the
687 motor hierarchy this state-specificity is implemented is unclear. Here, we found stop-
688 related activity bilaterally, as in previous work (Jana et al., 2020; Mills et al., 2025).
689 Rather than being separately generated for each side, state-specificity may be
690 determined before a global stop command is sent to both sides of the body. Such a
691 rapid computation of muscle-state specificity may occur within the basal ganglia
692 (Bingham et al., 2023; Li and Jin, 2023; Rocha et al., 2023), but further research is
693 necessary.

694

695 *Stopping muscle contractions involves both global and targeted stop commands*

696 Stopping could be purely global or involve additional targeted commands for
697 task-active muscles (Fig. 1A). We found evidence for targeted control during the
698 stopping of muscle contractions, with prolonged stop-related activity and enhanced
699 suppression of Go responses. This is consistent with 'Pause-then-Cancel' models
700 (Schmidt & Berke, 2017; Diesburg & Wessel, 2021) in which reactive stopping involves
701 an initial 'Pause' signal via the hyperdirect pathway, followed by cancellation via the
702 indirect pathway (Greenhouse et al., 2012; Schmidt & Berke, 2017; Wessel et al.,
703 2022). Indeed, M1 excitability decreases further when both global *and* targeted stop
704 commands are present, compared to just global stop commands (Tatz et al., 2024).
705 Our results suggest that prolonged EMG suppression without a prominent positive
706 rebound EMG after the stop process may be a marker of global and targeted stop
707 commands acting in a 'Pause-then-Cancel' process. However, while the 'Cancel'

process suppresses task-related activity, it does not necessarily eliminate all muscle output, but fine-tunes it to respond to the task-requirements. This was seen here when stopping muscle contractions, where mean EMG activity in the task-active muscle remained above baseline (10% MVC) rather than stopping altogether.

The 'Pause-then-Cancel' framework encompasses reactive and selective stopping, which differ in reliance on hyperdirect and indirect pathways (Diesburg & Wessel, 2021). Selective stopping typically involves targeted commands, but whether a global command precedes it remains uncertain (Coxon et al., 2007; Majid et al., 2012; Bissett and Logan, 2014; Wadsley et al., 2022). Our experiment required participants to maintain baseline force in a task-passive muscle, which may have introduced an element of selectivity and may explain why both global and targeted control were observed when stopping muscle contractions.

Stopping muscle relaxations involves only global stop commands

We did not find evidence for targeted control during the stopping of muscle relaxations. Stop-related activity (~100ms) and 'Go resumption' (62-73%) were similar between task-active and passive muscles, with a high correlation (~r = 0.8). No evidence of a 'Cancel' process for task-active muscles was observed, suggesting a single global stop command was sufficient.

'Pause-then-Cancel' models argue that a 'Pause' alone may be insufficient to execute a stop (Diesburg & Wessel, 2021). So did participants really stop their muscle relaxations? Our data suggest that participants indeed successfully stopped relaxations, with stop-related activity in both muscles exceeding the Go response amplitude, as in previous work (De Havas et al., 2020). This transient increase in EMG

reversed the go-related decrease in activity, bringing EMG levels back to near baseline levels by the stop process's end. We classified the global stop command as a ‘Pause’ since EMG velocity did not remain elevated but quickly reversed. Whether this ‘Go resumption’ indeed reflects a transient ‘Pause’ (Hervault & Wessel, 2025), or a fast-decaying burst of muscle activity, requires further investigation.

Two sources of control for stopping muscle contractions and relaxations

Models of stopping muscle contractions emphasize a categorical cut in excitatory drive (Jana et al., 2020; Diesburg and Wessel, 2021). While task-passive muscles experience transient suppression (global "Pause"), task-active muscles undergo both transient and sustained suppression (targeted "Cancel"), suggesting multiple pathways are recruited to coordinate successful stopping, based on task relevance.

Stopping muscle relaxations differs from contractions as it requires active contraction and recruiting motor units (De Havas et al., 2020). Unlike contractions, our results suggest that stopping relaxations utilizes a single global stop command rather than both global and targeted control, indicating distinct control systems may exist for contractions and relaxations. Real-world movements (e.g. walking, eating) require simultaneous and concerted control of multiple contracting and relaxing muscles (Ilmane and LaRue, 2011; Koo and Kwon, 2023). The presence of distinct control process acting in parallel on contracting and relaxing muscles to ensure the goal of stopping is accomplished would seem sensible. Our findings expand on the observation of simultaneous alterations of muscle activity in both contracting and relaxing muscles (Kudo and Ohtsuki, 1998; Atsma et al., 2018; De Havas et al., 2020), showing that the simultaneous stopping of contractions and relaxations may be

facilitated by a shared form of global control, with additional targeted control specific to stopping muscle contractions. Moreover, layering discrete suppressive 'Pause-then-Cancel' commands in contracting muscles onto excitatory global signals in relaxing muscle may enhance the reliability, precision, and smoothness of stopping movements.

Conclusion

Stopping affects task-active and task-passive muscles differently depending on whether a contraction or relaxation is halted. Stopping relaxations involved a single global stop command, with similar bursts of stop-related activity in task-active and task-passive muscles. In contrast, stopping contractions combined global suppression with additional targeted suppression in task-active muscles, leading to more sustained inhibition. Overall, we suggest that stopping involves both global control (shared across muscle states) and targeted control (specific to contractions). Shared control may facilitate timing synchronization when both contractions and relaxations need to be stopped. Additional targeted control for stopping muscle contractions may allow greater precision in how action inhibition is coordinated throughout the body.

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Figures and tables

Table 1. The percentage of Stop trials in which stop-related activity was detected for the task-active muscle. Shown are group mean (SD) detection rates of stop-related activity across participants, i.e. the percentage of Stop trials where stop-related activity was present in both force and EMG velocity data for task-active muscles.

Figure 1. Model schematic, task details, and Go trial force and EMG.

A. The hypothesized effects of stop commands acting only on task-active muscles (targeted), both muscles (global), or both muscles differently (targeted and global). "+/-" represents state-specific changes: increased activity for stopping relaxing muscles and decreased activity for stopping contracting muscles.

B. Task set-up.

C. Task structure. Participants held a stable baseline contraction of 10% MVC with both index fingers. In Exp. 1, a triangle Go signal prompted participants to rapidly contract one finger to 20% MVC, keeping the other at 10% MVC (task-passive muscle). In Exp. 2, the same Go signals required relaxing one finger from 10% MVC to 0% MVC, keeping the other constant. In Exp 3, an upward triangle required contracting the right index finger to 20% MVC, whereas a downward triangle required relaxing the right finger to 0% MVC, in both cases keeping the left finger at 10% MVC

(task-passive muscle). In all experiments, Stop signals (30% of trials) required participants to stop the contraction to 20%, or stop the relaxation to 0% in the task-active muscle.

D. Force and EMG responses during example contraction and relaxation trials.

E. Group averages for contraction (Exp. 1) and relaxation (Exp. 2), showing task-active and passive muscle responses, after subtracting baseline activity. Note that plots show averages of right and left hand data.

Table 2. Behavioral measures for all experiments. Mean (SD) are shown.

Figure 2. Group mean stop-locked responses and method for detecting stop-related activity.

A. Group mean EMG velocity for successful (top) and failed (bottom) Stop trials during contractions (left; Exp. 1) and relaxations (right; Exp. 2), aligned to Stop signal onset. Task-active (black) and task-passive (grey) muscle activity is shown. Green areas indicate partial Go responses, and red areas highlight stop-related activity timing. Dashed vertical lines show group mean behavioral SSRT. When stopping relaxions (right) there was clear stop-related activity in both muscle types, while for the stopping of contractions (left) there was flatter task-passive EMG after averaging. Plots show average of right and left hand responses. Error bars show SEM.

B. Data from Exp. 3 show similar patterns as Exp.1 and 2, for successful (top) and failed (bottom) Stop trials on contraction (left) and relaxation (right) trials. Note that in

Exp. 3, task-active muscle is always the right FDI and task-passive muscle is always the left FDI.

C. Detection of stop-related EMG activity, using a successful stop trial from Exp. 2 for illustration. Force velocity onset (top row) was defined as 30% of peak signal (100-500ms post-stop signal, shaded area) if it exceeded the mean baseline velocity + 1SD (dashed line). Detected onset times set the window for identifying EMG velocity peaks (middle row; -150 to 50ms). Task-active and task-passive EMG velocities were time-locked to task-active EMG onset (bottom row).

Figure 3. State-specific stop-related activity in task-passive muscles.

Task-passive muscles showed decreased EMG when stopping contractions (Exp. 1) and increased EMG when stopping relaxations (Exp. 2).

A. Group mean stop-related activity for successful stop trials during contractions, with task-active (black) and task-passive (grey) data aligned to task-active onset. Significant activity ($p < 0.05$) is shown by horizontal lines. Green shading indicates partial Go response timing; red shading marks the analysis window for stop-related activity (-25 to 75ms). Inset highlights a significant EMG decrease in task-passive muscles. Dashed vertical lines show group mean behavioral SSRT.

B. Failed stop trials when stopping contractions (Exp. 1).

C. Group mean stop-related EMG activity (-25 to 75ms) for successful and failed stop trials during stopping of contractions (Exp.1), showing significant decreases in all conditions (t-tests; ***$p < 0.01$, **$p < 0.01$, *$p < 0.05$).

D. Group mean task-active and task-passive stop-related activity for successful stop trials when stopping relaxations (Exp. 2).

E. Failed stop trials when stopping relaxations (Exp. 2).

F. Significant stop-related increase of EMG (-25 to 75ms) observed during stopping of relaxations for all conditions (Exp. 2). All error bars are SEM.

Figure 4. Task-passive muscle state-specific stop-related activity for Exp. 3.

Evidence for state-specific stop-related activity in task passive muscles, i.e. decreased EMG for stopping contractions and increased EMG for stopping relaxations.

A. Task-active (black) and task-passive (grey) group mean traces for successful stops in when stopping muscle contractions, showing timing of significant stop-related decreases in EMG (horizontal lines; $p < 0.5$), with insert focusing on task-passive muscle. Dashed vertical lines show group mean behavioral SSRT.

B. Group mean traces for failed stop trials when stopping contractions.

C. Significant mean stop-related activity (-25 to 75ms; decreased EMG) found for task-active and task-passive muscles for successful and failed stop trials when stopping contractions (one sample t-test against 0; ***$p < 0.01$, ** $p < 0.01$, *$p<0.05$).

D. Group mean traces for successful stop trials when stopping muscle relaxations, showing stop-related EMG increase in task-passive muscles.

E. Group mean traces for failed stop trials when stopping relaxions.

F. Significant stop-related increases in EMG found in all muscles when stopping relaxations (25 to 75ms). All error bars show SEM.

Table 3. State-specific stop-related activity in all muscles for all experiments.

Mean stop-related activity (%MVC/ms) and results of t-tests against 0 performed on the group-level EMG velocity data after averaging within the stop-related activity window (-25 to 75ms, relative to onset of task-active muscle; see Fig. 3 & 4). All state-specific activity (i.e. decreased EMG for stopping contractions, increased EMG for stopping relaxations) was significant in all muscles (task-active and task-passive) for all stop conditions (successful and failed), when stopping both contractions and relaxations in all experiments.

Figure 5. Muscle state differences in stopping duration and 'Go resumption'.

Task-active muscles had longer stopping durations than task-passive muscles during contractions, while stopping durations were matched during relaxations. 'Go resumption' (positive AUC) was larger for task-passive muscles during contractions but similar across muscles during relaxations (negative AUC). Panels A.i–A.iv display mean, normalized EMG velocity data from a single participant in Exp. 1 and Exp. 2, showing successful and failed stop trials for stopping both muscle contractions (i, ii) and relaxations (iii, iv). Duration differences (horizontal arrows) and 'Go resumption' differences (AUC 100ms post offset) are marked. Panels B (Exp. 1&2) and C (Exp. 3)

present group-level data, highlighting the consistency of these patterns across experiments. Error bars show SEM.

Table 4. Onset, offset and duration of stop-related EMG activity. Table shows the group mean (SD) onset, offset and duration in milliseconds of stop-related activity for the task-active and task-passive muscles, separately for successful and failed stop trials across all muscle states/experiments. Onset and offset time is relative to the Stop signal. These values were derived from individual participant averages. Duration values, shown here separately for successful and failed stop trials, were combined for figures and statistical analysis.

Figure 6. Differences in stopping control between muscle contractions and relaxations.

A. Effects of hypothesized 'Pause' and 'Cancel' processes on Go responses (*i.*). A 'Pause' process induced by a Stop signal transiently suppresses the Go process (*ii.*), leading to some 'Go resumption'. A subsequent (but overlapping) 'Cancel' process suppresses the Go process (*iii.*). Combined 'Pause' and 'Cancel' (*iv.*) predicts minimal 'Go resumption' and a longer mean stopping duration.

B. Stop-related activity is expected to be more similar across muscles when only the global 'Pause' process is present.

C. Low 'Go resumption' in task-active muscles when stopping contractions (Exp. 1) but high 'Go resumption' in both muscles when stopping relaxations (Exp. 2). Group mean ±SEM.

D. Stopping duration was longer for task-active than task-passive muscles for stopping contractions (Exp.1), but did not differ for stopping relaxations.

E. Time-shifted cross-correlations between task-passive and task-active EMG velocity (group mean). Stopping relaxations was associated with higher correlations between task-active and passive muscles than stopping contractions, suggesting greater shared control across muscles in the former case (i.e. only global 'Pause' command).

F.-H. Similar patterns observed in Exp. 3.

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, N.S. = not significant. Error bars show SEM.

Muscle state	Successful Stops	Failed Stops	All Stops
Contraction (Exp. 1)	59.54 (10.23)%	58.59 (12.69)%	58.99 (9.4)%
Relaxation (Exp. 2)	69.92 (8.72)%	69.62(10.77)%	69.79 (8.3)%
Contraction (Exp. 3)	63.13 (7.87)%	57.94 (10.52)%	60.63 (7.57)%
Relaxation (Exp. 3)	64.29 (8.27)%	52.05 (14.75)%	58.33 (9.72)%

Muscle State	Go RT (ms)	Fail RT (ms)	SSD (ms)	Stop Succ. (%)	SSRT (ms)
Contract (Exp 1)	484 (93)	404 (73)	289 (102)	50.2 (2.4)	173 (43)
Relax (Exp 2)	504 (81)	419 (67)	294 (101)	51.7 (4.3)	193 (41)
Contract (Exp 3)	545 (64)	448 (57)	334 (54)	51.3 (2.8)	186 (26)
Relax (Exp 3)	532 (79)	443 (72)	317 (81)	51.7 (2.9)	188 (42)

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Muscle state	Successful stop trials				Failed stop trials			
	Mean (SD)	**T**	**P**	**Cohen's d**	**Mean (SD)**	**T**	**P**	**Cohen's d**
Con. (Exp 1)								
Task-active	-5.13 (1.92)	-11.315	<0.001	2.67	-13.87 (5.49)	-10.709	<0.001	2.52
Task-passive	-0.43 (0.56)	-3.260	0.005	0.77	-0.36 (0.55)	-2.756	0.014	0.65
Rel. (Exp 2)								
Task-active	4.48 (2.14)	8.372	<0.001	2.09	8.73 (5.79)	6.032	<0.001	1.51
Task-passive	1.13 (1.05)	4.318	0.001	1.08	1.68 (1.33)	5.073	<0.001	1.27
Con. (Exp 3)								
Task-active	-3.67 (2.23)	-7.361	<0.001	1.65	-11.09 (7.65)	-6.482	<0.001	1.45
Task-passive	-0.62 (0.72)	-3.824	0.001	0.86	-0.39 (0.61)	-2.862	0.010	0.64
Rel. (Exp 3)								
Task-active	3.66 (1.82)	8.967	<0.001	2.01	8.71 (5.05)	7.716	<0.001	1.73
Task-passive	0.62 (1.23)	6.071	<0.001	1.32	1.66 (1.23)	6.071	<0.001	1.36

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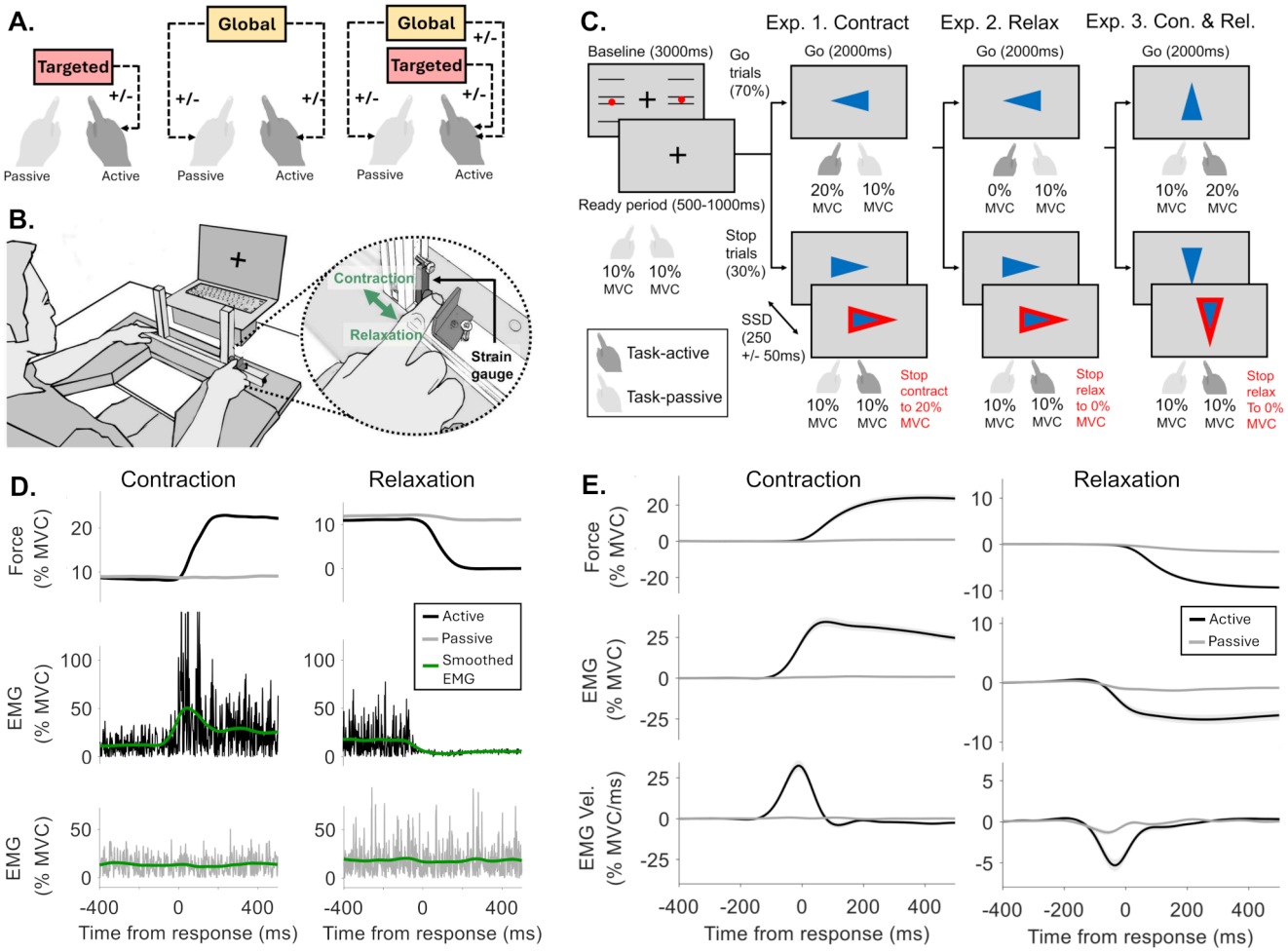
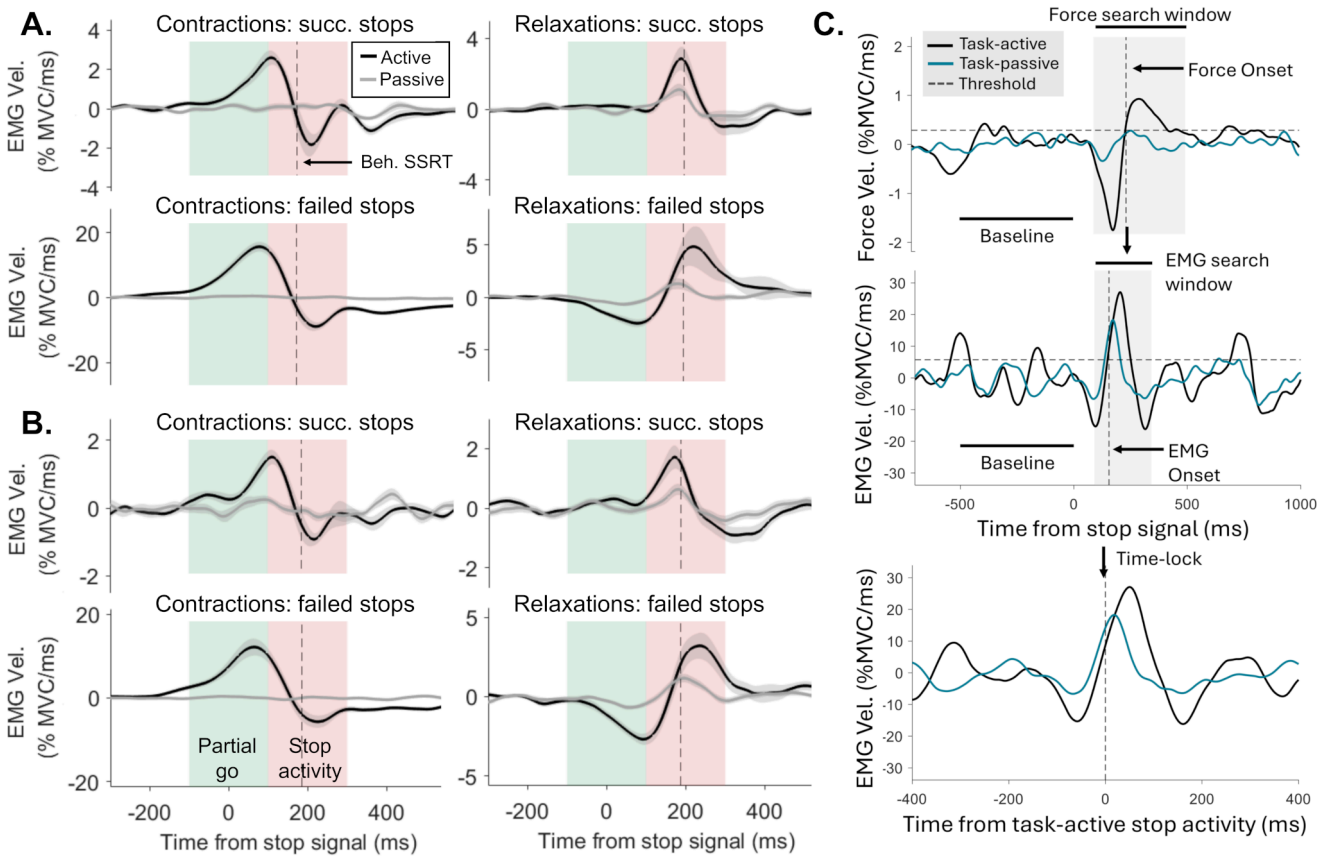
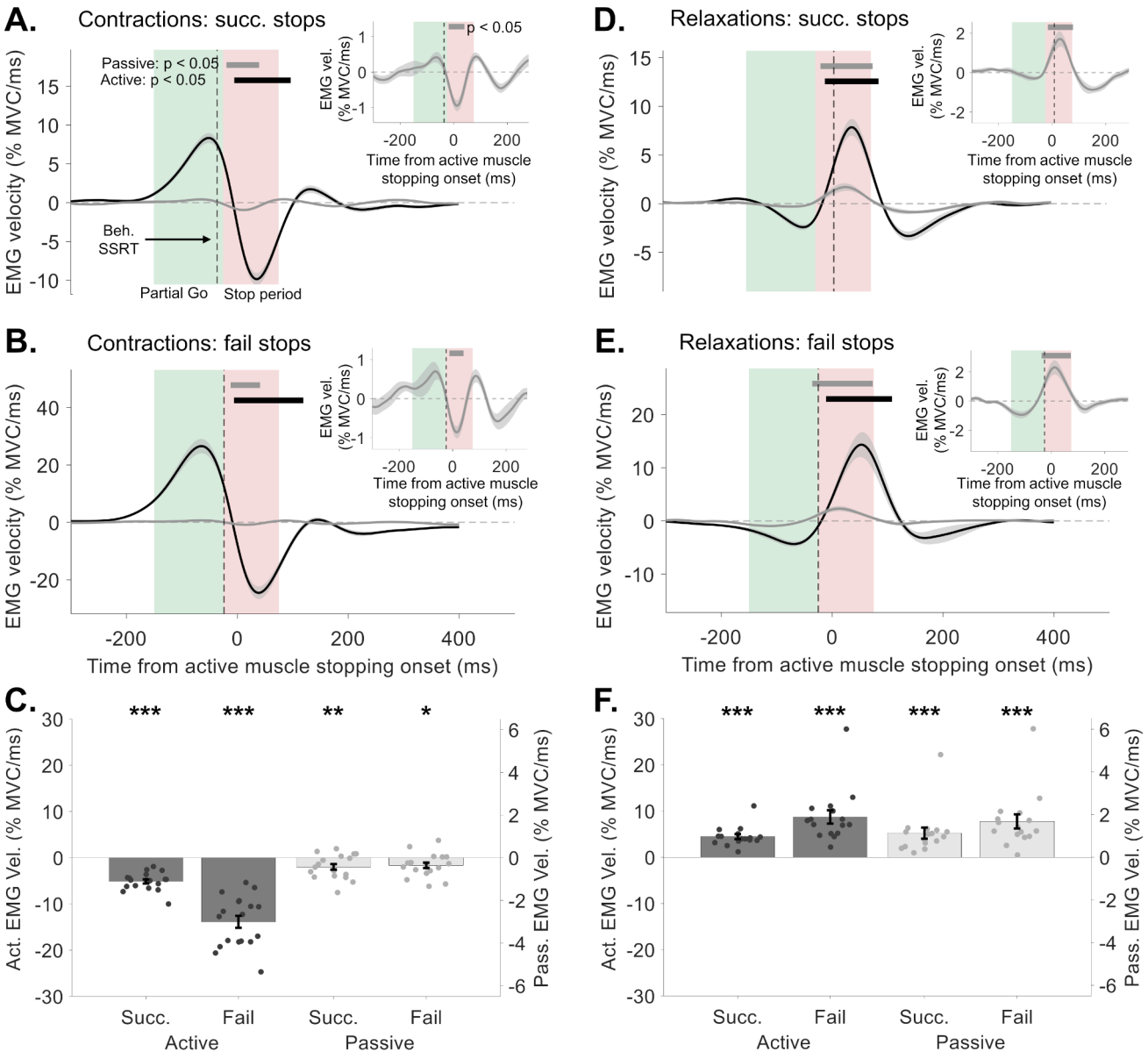
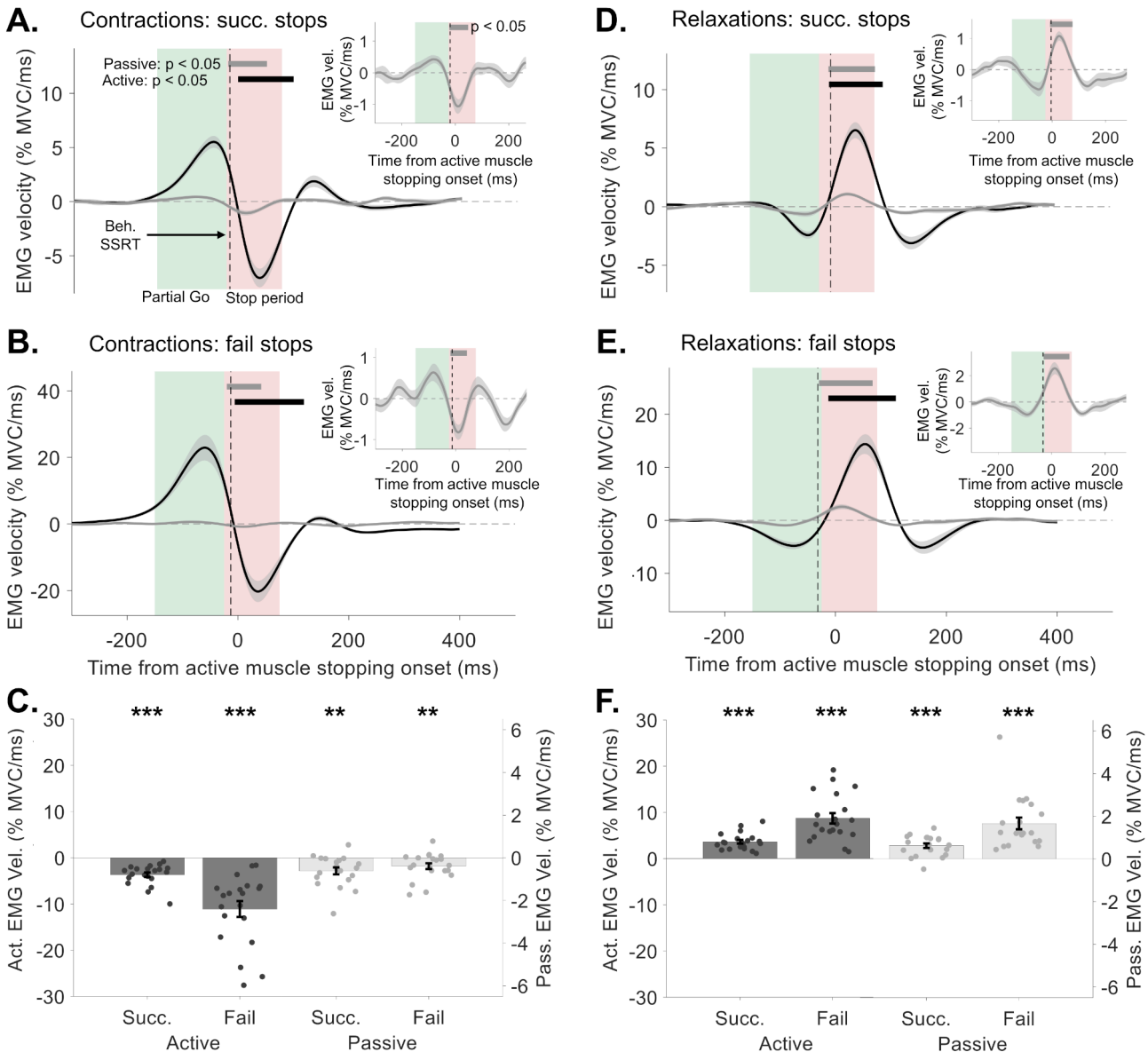
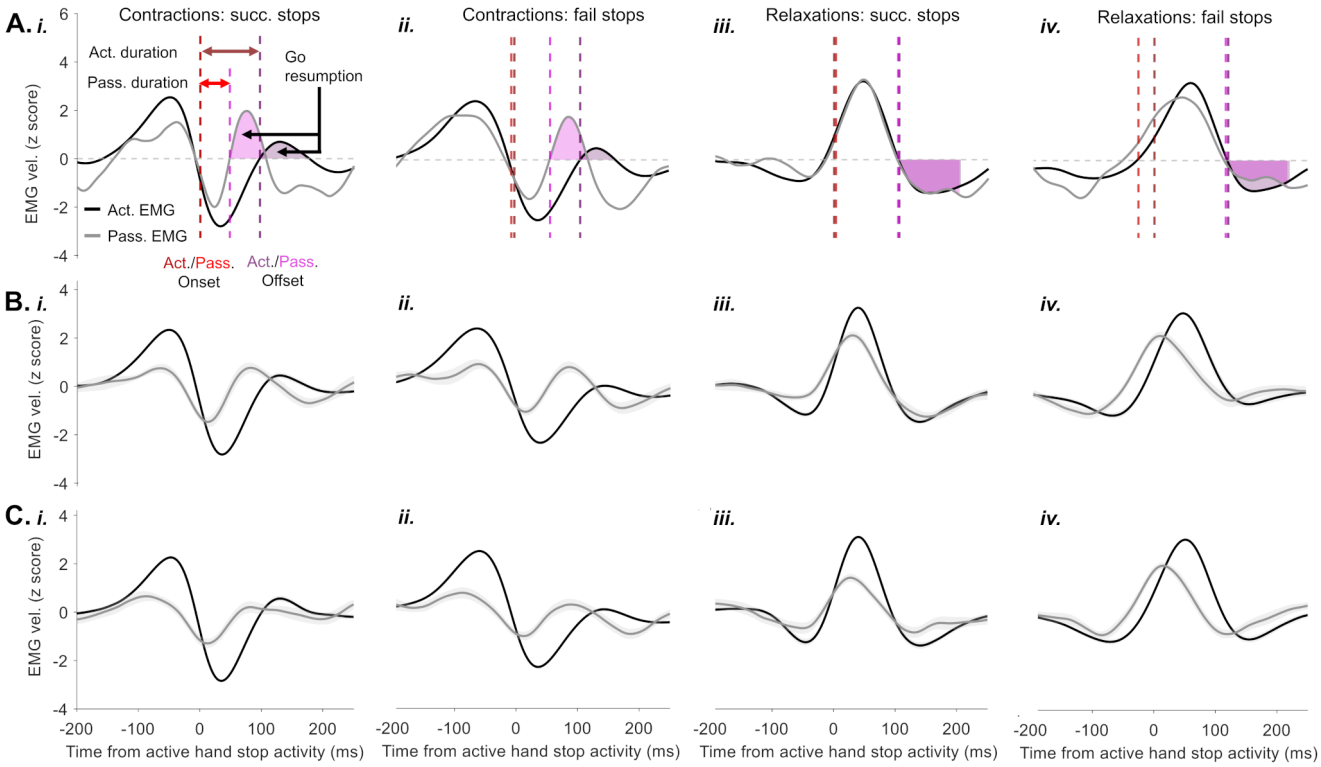
Muscle state	Successful stop trials			Failed stop trials		
	Onset (ms)	Offset (ms)	Duration (ms)	Onset (ms)	Offset (ms)	Duration (ms)
Contract (Exp 1)						
Task-active	209 (36)	336 (95)	127 (77)	197 (43)	393 (131)	196 (114)
Task-passive	179 (50)	276 (86)	98 (57)	179 (60)	261 (74)	81 (35)
Relax (Exp 2)						
Task-active	185 (38)	280 (45)	96 (13)	218 (48)	354 (94)	136 (55)
Task-passive	172 (41)	280 (55)	108 (29)	182 (62)	320 (89)	138 (48)
Contract (Exp 3)						
Task-active	205 (22)	309 (32)	104 (19)	199 (35)	338 (74)	139 (57)
Task-passive	180 (28)	290 (65)	110 (65)	168 (59)	275 (86)	107 (57)
Relax (Exp 3)						
Task-active	192 (35)	286 (37)	95 (10)	220 (46)	333 (47)	113 (9)
Task-passive	177 (41)	286 (51)	110 (54)	188 (41)	302 (51)	114 (32)

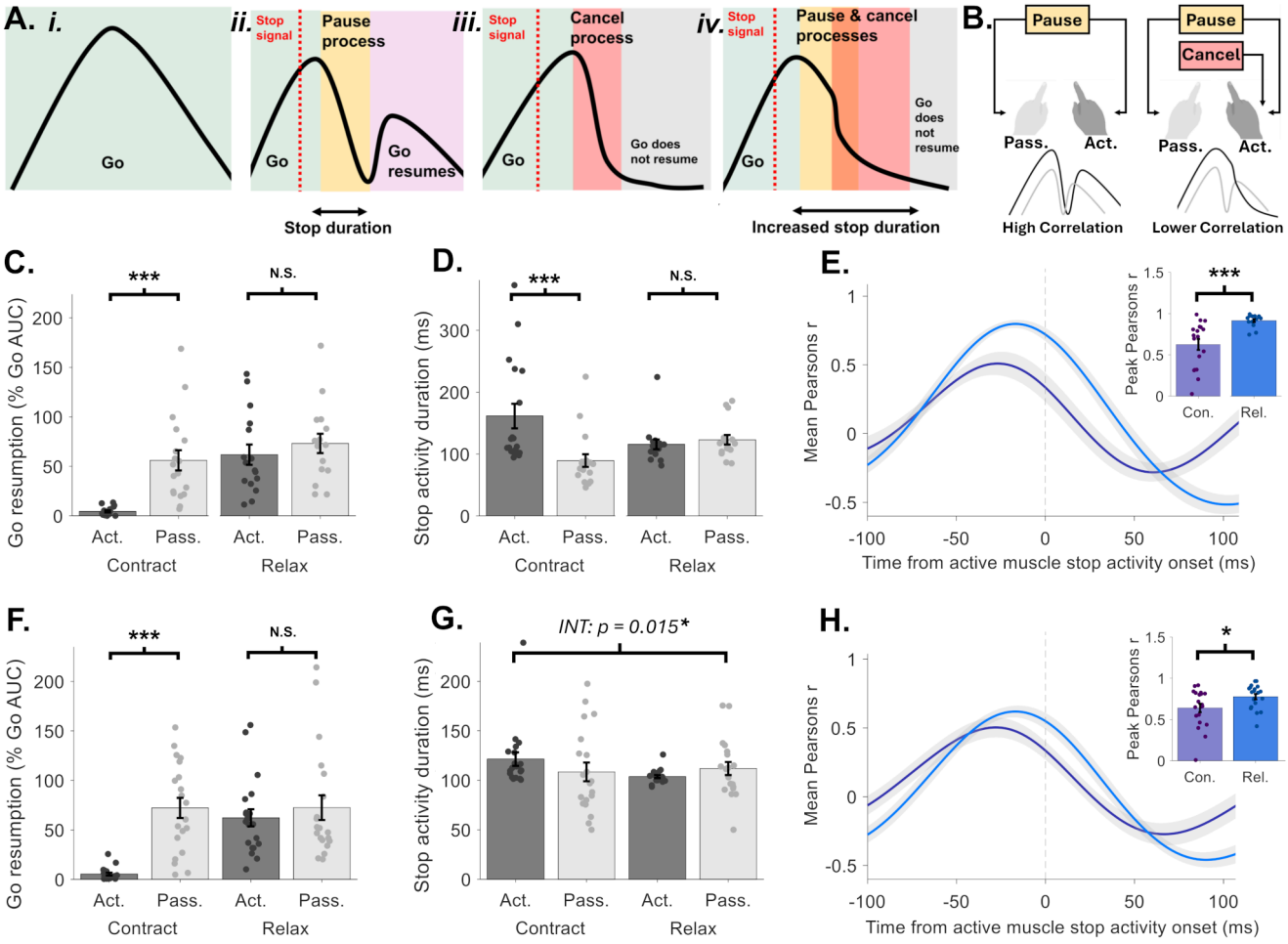

A.
Targeted
Global
Global
Targeted
+/-
Passive
Active
B.
Contraction
Relaxation
Strain gauge
C.
Exp. 1. Contract
Exp. 2. Relax
Exp. 3. Con. & Rel.
Baseline (3000ms)
Ready period (500-1000ms)
Go trials (70%)
Stop trials (30%)
SSD (250 +/- 50ms)
Go (2000ms)
20% MVC
10% MVC
0% MVC
Task-active
Task-passive
Stop contract to 20% MVC
Stop relax to 0% MVC
Stop relax To 0% MVC
D.
Contraction
Relaxation
Force (% MVC)
EMG (% MVC)
Active
Passive
Smoothed EMG
Time from response (ms)
E.
EMG Vel. (% MVC/ms)


A.
Contractions: succ. stops
Relaxations: succ. stops
Active
Passive
Beh. SSRT
Contractions: failed stops
Relaxations: failed stops
EMG Vel. (% MVC/ms)
B.
Partial go
Stop activity
Time from stop signal (ms)
C.
Force search window
Task-active
Task-passive
Threshold
Force Onset
Force Vel. (%MVC/ms)
Baseline
EMG search window
EMG Onset
Time from stop signal (ms)
Time-lock
Time from task-active stop activity (ms)


A.
Contractions: succ. stops
Passive: p < 0.05
Active: p < 0.05
p < 0.05
EMG velocity (% MVC/ms)
EMG vel. (% MVC/ms)
Time from active muscle stopping onset (ms)
Beh. SSRT
Partial Go
Stop period
D.
Relaxations: succ. stops
B.
Contractions: fail stops
E.
Relaxations: fail stops
C.
F.
***
**
*
Act. EMG Vel. (% MVC/ms)
Pass. EMG Vel. (% MVC/ms)
Succ.
Fail
Active
Passive


A.
Contractions: succ. stops
Passive: p < 0.05
Active: p < 0.05
p < 0.05
EMG velocity (% MVC/ms)
EMG vel. (% MVC/ms)
Beh. SSRT
Partial Go
Stop period
Time from active muscle stopping onset (ms)
D.
Relaxations: succ. stops
B.
Contractions: fail stops
E.
Relaxations: fail stops
C.
F.
Act. EMG Vel. (% MVC/ms)
Pass. EMG Vel. (% MVC/ms)
Succ.
Fail
Active
Passive


A. i.
Contractions: succ. stops
ii.
Contractions: fail stops
iii.
Relaxations: succ. stops
iv.
Relaxations: fail stops
Act. duration
Pass. duration
Go resumption
Act. EMG
Pass. EMG
Act./Pass. Onset
Act./Pass. Offset
B.
C.
EMG vel. (z score)
Time from active hand stop activity (ms)


A.
i.
Go
ii.
Stop signal
Pause process
Go
Go resumes
Stop duration
iii.
Stop signal
Cancel process
Go
Go does not resume
iv.
Stop signal
Pause & cancel processes
Go
Go does not resume
Increased stop duration
B.
Pause
Pass.
Act.
High Correlation
Pause
Cancel
Pass.
Act.
Lower Correlation
C.
***
N.S.
Go resumption (% Go AUC)
Act.
Pass.
Act.
Pass.
Contract
Relax
D.
***
N.S.
Stop activity duration (ms)
Act.
Pass.
Act.
Pass.
Contract
Relax
E.
Mean Pearsons r
Time from active muscle stop activity onset (ms)
Peak Pearsons r
***
Con.
Rel.
F.
***
N.S.
Go resumption (% Go AUC)
Act.
Pass.
Act.
Pass.
Contract
Relax
G.
INT: p = 0.015*
Stop activity duration (ms)
Act.
Pass.
Act.
Pass.
Contract
Relax
H.
Mean Pearsons r
Time from active muscle stop activity onset (ms)
Peak Pearsons r
*
Con.
Rel.