Posture interacts with arm weight support to modulate corticomotor excitability to the upper limb

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Keywords

arm weight support; posture; motor cortical excitability; transcranial magnetic stimulation; integrated control

Abstract

The use of arm weight support (WS) to optimize movement quality may be an avenue for improved upper limb stroke rehabilitation, however the underlying neurophysiological effects of WS are not well understood. Rehabilitation exercises may be performed when sitting or standing but the interaction of posture with WS has not been examined until now. We explored the effect of posture with WS on corticomotor excitability (CME) in healthy adults. Thirteen participants performed static shoulder abduction in two postures (sitting and standing) at three levels of WS (0, 45, and 90% of full support). Transcranial magnetic stimulation of primary motor cortex was used to elicit motor-evoked potentials (MEPs) in eight upper limb muscles. Stimulus-response (SR) curves were fitted to the MEP data using nonlinear regression. Whole body posture interacted with WS to influence tonic activity and CME in all muscles examined. SR curve parameters revealed greater CME when standing compared to sitting for upper arm muscles but lower CME to the shoulder, forearm, and hand. Distal to the shoulder, tonic activity and CME were modulated independent of any explicit differences in task requirements. Overall, these results support a model of integrated upper limb control influenced by whole body posture and WS. These findings have implications for the application of WS in settings such as upper limb rehabilitation after stroke.

Introduction

Stroke is a leading cause of adult disability with two-thirds of stroke survivors experiencing lingering upper limb impairment (Feigin et al. 2010; Mendis 2013). Regaining independence in daily living activities depends on the recovery of motor function (Patel et al. 2000; Veerbeek et al. 2011). Weight support (WS) can be used to augment arm movements made during stroke rehabilitation therapy (Prange et al. 2006; Brewer et al. 2007; Kwakkel et al. 2008; Mehrholz et al. 2015). WS may be applied manually, or through devices ranging from passive supports to sophisticated robotic systems (Loureiro et al. 2011). The benefits of WS for upper limb rehabilitation have been ascribed to increasing the intensity or volume of therapeutic exercises (Kwakkel and Meskers 2014). Recovery processes that rely on use-dependent plasticity and adaptive cortical reorganization could be facilitated with a greater dosage of exercise enabled by WS (Nudo et al. 1996; Woldag and Hummelsheim 2002; Kleim and Jones 2008). An alternative avenue for research into the potential benefits of WS for upper limb rehabilitation is based on improvements in movement quality rather than quantity.

Beyond its role in facilitating increased training dosage, WS can also improve movement quality. For example, in reaching tasks the application of WS results in a reduction in antagonist muscle activity in both healthy older adults and chronic stroke patients (Prange et al. 2009b; Prange et al. 2009a). WS can lessen abnormal coupling of joint torques between the shoulder and elbow through a reduction in antigravity torques required for shoulder abduction (Dewald and Beer 2001; Beer et al. 2004). As a functional consequence individuals who express the stereotyped flexor synergy can achieve greater elbow extension under gravity-compensated conditions thereby increasing access to the

reaching workspace (Sukal et al. 2007). To date, the neural mechanisms underlying transient changes in motor behavior with WS have received less attention and are not well understood.

Modulation of neuromuscular activity with WS may be mediated indirectly through proximal-distal neural linkages or synergies. Centrally mediated changes in the accessibility of muscles for activation may be assessed using transcranial magnetic stimulation (TMS). For example, in healthy adults, voluntary *anterior deltoid* activation was positively associated with corticomotor excitability (CME) evident in motor evoked potentials (MEPs) of a forearm extensor (Devanne et al. 2002). The effects of parametric WS on tonic muscle activity and CME to proximal and distal upper limb muscles have been examined during static and rhythmic isometric tasks. During static shoulder abduction, involuntary tonic muscle activity modulated with the amount of WS provided to the upper limb (Runnalls et al. 2014). Additionally, CME responses were muscle-dependent and nonlinear with respect to the amount of WS provided. Application of any WS, led to a decrease in CME to the forearm muscle *extensor carpi radialis*. In contrast, CME to the *first dorsal interosseous* of the hand increased but only at a high level of WS. In rhythmic movement tasks requiring selective elbow flexion or forearm pronation, CME to *biceps brachii* was differentially modulated by WS depending on its role as an agonist or antagonist (Runnalls et al. 2015). Preceding agonist elbow flexion, CME decreased with incrementally greater WS whereas for antagonist forearm pronation, CME was lower only at the highest level of WS. Taken together, WS appears to interact with proximal-distal neural linkages in a not generalized way across the limb and may involve both excitatory and inhibitory mechanisms.

Change in whole body posture can also affect motor control of the upper limb but its interaction with WS has not been investigated. Standing postures introduce balance requirements that alter the way arm movements are coordinated and increase the complexity of reaching and pointing tasks (Pozzo et al. 2001; Pozzo et al. 2002; Berrigan et al. 2006). Compared to sitting, standing results in greater CME to the *anterior deltoid* but no change in CME to the *first dorsal interosseous* (Kantak et al. 2013). Posture-related modulation of shoulder, but not hand, CME likely reflects a greater mechanical role played by proximal muscles in shifting the center of mass; e.g., to maintain stability in response to a perturbation. Whether neural mechanisms underpinning posture-related changes in upper limb control interact with the neural linkages modulated by WS is unknown.

In the present study, we sought to examine the interaction of whole body posture and WS on CME to upper limb muscles. TMS was used to elicit motor evoked potentials (MEPs) from muscles in the shoulder, arm, forearm, and hand of healthy adults. We expected that tonic muscle activity would modulate with both WS and posture manipulations. It was hypothesized that tonic activity would be reduced with greater WS, and greater during standing compared to sitting. CME was examined by analyzing MEP area and comparing stimulus-response (SR) curves fitted to group means. It was hypothesized that SR curves would reflect greater CME with a standing posture, evident by steeper slope, and associated parameters. Furthermore, we expected the magnitude of posture-related differences would be greater with WS.

Methods

Participants

Thirteen neurologically healthy right handed adults without history of upper limb impairment participated in this study (mean age: 28 y, range: 20–50 y, 3 female). All participants gave written informed consent and were screened for contraindications to TMS by a neurologist. Study procedures were approved by the University of Auckland Human Participants Research Ethics Committee in accordance with the Declaration of Helsinki.

Design

All procedures were completed in a single-session using a repeated measures design. Single-pulse TMS was used to elicit MEPs from muscles of the arm during 2 postures (sitting and standing) at 3 levels of WS (low, medium, high). The order of the 6 experimental conditions was randomized between participants. Within each experimental condition, a range of TMS intensities was randomized on a trial-by-trial basis. Each session lasted approximately three hours.

Posture and arm support

Figure 1 illustrates the sitting and standing experimental conditions. The right arm was supported by a SaeboMAS arm support system (Saebo Inc., Charlotte, NC). Force was provided and adjusted via spring tension. A custom brace provided a rigid and cushioned surface for the forearm and hand. Elasticized fabric wrap was used to secure the forearm to the brace in a palm-down position. For both sitting and standing conditions, TMS was performed in a standardized arm position with the shoulder flexed forward approximately

80° and abducted 45˚ in the horizontal plane, and the elbow flexed at 90°. Joint angles were initially set using a goniometer and subsequently maintained by aligning a laser pointer to a reference point on the wall. The brace prevented rotation in the vertical plane ensuring the forearm was parallel to the floor. In the sitting condition, participants sat in a chair with their feet on the floor and left arm resting on their lap. In the standing condition, participants stood with their feet shoulder width apart and left arm resting at their side.

Three discrete levels of WS were defined relative to the force required to fully compensate for the weight of the arm. At low support (0 %), the device carried its own weight but provided no additional support to the arm. The force required for full support (100 %) was determined using a force titration procedure. While maintaining the standardized arm position, supportive force was incrementally decreased from a high setting until root mean square EMG amplitude (rmsEMG) in the *anterior deltoid* was observed to deflect away from baseline (Runnalls et al. 2014; Runnalls et al. 2015). Medium and high support levels were then defined as 45 and 90 % of full support.

Electromyography

Surface electromyography was used to record activity from eight muscles of the right arm and hand: *anterior deltoid* (AD), *biceps brachii* (BB), *triceps brachii* (TB), *brachioradialis* (BRD), *extensor carpi radialis* (ECR), *flexor carpi radialis* (FCR), *first dorsal interosseous* (FDI), and *abductor pollicis brevis* (APB). Following standard skin preparation, self-adhesive Ag-AgCl electrodes (Blue Sensor N; Ambu, Denmark) were placed approximately 2 cm apart in a bipolar montage over the belly of each muscle. The

common ground electrode was placed over the acromion process (Red Dot; 3M Health Care, Canada). Signals were amplified (AMT-8; Bortec Biomedical, Calgary, Canada) with 1000× gain, band-pass filtered (10–1000 Hz), sampled at 2 kHz (CED Power 1401 mkII; Cambridge Electronic Design, Cambridge, UK), and saved for subsequent offline analysis using CED Signal software (v6.03c).

Transcranial magnetic stimulation

Single-pulse TMS was applied over the left motor cortex using a MagPro X100 magnetic stimulator and MC-B70 butterfly coil (MagVenture, Denmark). The coil was held tangentially to the scalp and angled approximately 45˚ away from midline. A monophasic pulse was used to induce a posterior to anterior current flow in M1. The coil was positioned at the optimal site for eliciting MEPs in the right ECR muscle. Task motor threshold (MT) for the right ECR was defined as the minimum stimulus intensity that elicited a 50 μV MEP in four out of eight trials while seated with the arm in the standardized position at the high support level.

For each of the six experimental conditions, stimulus–response (SR) curves were collected using a single stimulation site to concurrently elicit MEPs in all muscles. Eleven stimulus intensities were set relative to task motor threshold of ECR: -10, -5, 0, +5, +10, +15, +20, +25, +30, +35, +40 % of maximum stimulator output (% MSO). For each curve, 88 stimuli (8 at each intensity) were delivered in a randomized order. To mitigate fatigue, participants rested their arm on a table for approximately 15 seconds after every six stimuli.

Data analysis

Individual EMG traces were inspected for the presence of an appropriate stimulus artifact and absence of phasic muscle activity. Trials that did not meet these criteria were discarded from further analysis. The main dependent measure, MEP area, was calculated over a 20 ms window determined manually for each muscle for each participant. To account for systematic differences in MEP size between participants, raw MEP area values were normalized between 0 and 1 across conditions within each muscle. As a covariate, background muscle activity was measured as the rmsEMG amplitude over a 50 ms window preceding the stimulus.

Statistical analysis

Analyses of background muscle activity and MEP area were conducted using R 3.1.2 (R Core Team 2014) with the nlme: Linear and Nonlinear Mixed Effects Models (Pinheiro et al. 2015) and predict means: Calculate Predicted Means for Linear Models packages (Luo et al. 2014). Outlying data points were identified by analyzing background muscle activity on a within subject basis. Observations of rmsEMG more than 1.5× the interquartile range either above the third quartile or below the first quartile, along with their associated MEP values, were excluded from further analysis. Data were log transformed to better satisfy the assumption of normally distributed residuals.

To assess the interaction of weight support and posture on background muscle activity across the upper limb, separate linear mixed effects analyses were carried out for each muscle. In each case, BACKGROUND MUSCLE ACTIVITY was modeled as a function of SUPPORT LEVEL and POSTURE as factors, with random intercepts for SUBJECT. The sequential sum of squares was used for Wald tests of model terms (Pinheiro and Bates

2000). As a measure of effect size, log response ratios were calculated for differences between marginal means (Hedges et al. 1999). For support level, the response ratio was expressed as the natural logarithm of high support relative to low with negative values indicating less muscle activity with high support. For posture, the response ratio was expressed as the natural logarithm of standing relative to sitting; negative values indicate less muscle activity when standing.

For MEP area, separate linear mixed effects models were constructed for each muscle. In each case, MEP AREA was modeled as a function of STIMULUS INTENSITY, SUPPORT LEVEL, and POSTURE as factors. BACKGROUND MUSCLE ACTIVITY was included as a continuous covariate term. The error term included random slopes for BACKGROUND MUSCLE ACTIVITY and random intercepts for SUBJECT. Each model was subsequently used to infer predicted means and standard errors for MEP AREA at the median value of the BACKGROUND MUSCLE ACTIVITY distribution (Welham et al. 2004). This procedure permitted comparisons of MEP area between experimental conditions by accounting for underlying differences in background muscle activity.

Stimulus-response curves were fitted to group level data for each muscle using nonlinear regression in Prism 7 (GraphPad, San Diego, CA). For each experimental condition, a three parameter Boltzmann function was fitted to both observed and predicted mean MEP areas (Devanne et al. 1997). The upper plateau was constrained to be between 0 and 1. The half-maximal stimulus intensity (S50) was constrained to be between 0 and 40. The slope was unconstrained. Omnibus extra sum-of-squares F tests were used to assess whether individual regression curves for each condition fit the data significantly better than a single curve for the muscle across conditions. To examine whether the posture

manipulation shifted the SR curve within each support level, log response ratios were calculated as the natural logarithm of the standing value divided by the sitting value for the S50 and slope parameters that defined each curve. For each muscle, the best-fit parameters were tested separately using one-way ANOVA. Post-hoc tests were conducted on the difference between postures within each support level. Multiple comparisons were corrected by controlling the false discovery rate ($Q = 0.05$) with a two stage step-up method (Benjamini et al. 2006).

Results

Data from all 13 participants were included in the analysis. Of the 88 stimuli delivered to each participant per condition, an average of 79 traces (range: 64–86) were retained in the final analysis. Trials containing outlying values of background muscle activity were discarded. Example EMG traces are presented in Figure 2.

Effects of weight support and posture on background muscle activity

Group means for background muscle activity are presented in Figure 3. There were significant main effects of both the support level and posture factors, as well as a concomitant interaction between support level and posture in all muscles (Table 1). As expected, the magnitude of the support level effect was greatest for proximal muscles AD, BB, and TB. The direction of the effect was uniform across muscles, with less background muscle activity at high support. For the effect of posture on background muscle activity, the magnitude and direction of the response were not consistent across all muscles.

Effects of weight support and posture on stimulus-response curves

The left column of Figure 4 presents SR curves fitted to group means of observed MEP area. Significant effects of the experimental manipulations on background muscle activity warranted further analysis of MEP data using values derived from the statistical models. Mean MEP area and standard error were predicted for each combination of support level, posture, and stimulus intensity. The procedure accounted for co-varying background muscle activity. SR curves fitted to the predicted means are presented in the right column

of Figure 4. For all muscles, extra sum-of-squares F tests indicated that SR curves for each condition fit the data significantly better than a single regression curve (AD: $F_{(15,46)} = 30.72$, $p < 0.0001$; BB: $F_{(15,46)} = 207.6$, $p < 0.0001$; TB: $F_{(15,43)} = 108.0$, $p < 0.0001$; BRD: $F_{(15,48)} = 18.04$, $p < 0.0001$; ECR: $F_{(15,48)} = 14.46$, $p < 0.0001$; FCR: $F_{(15,45)} = 4.64$, $p < 0.0001$; FDI: $F_{(15,47)} = 9.02$, $p < 0.0001$; APB: $F_{(15,42)} = 2.95$, $p = 0.0029$).

Shifts in SR curves were examined by testing for differences in the in the S50 and slope parameters that defined each curve. Results of the one-way ANOVAs for curve parameters are presented in Table 2. Log response ratios for posture-related change in the S50 and slope parameters are presented in Figures 5 and 6 respectively. For S50, the average magnitude of change across muscles was greatest at high support (5.8% MSO) followed by low (3.9% MSO) and medium support (2.0% MSO). Similarly for slope, the average magnitude of change was also greatest at high support (0.022% MSO^{-1}) followed by low (0.014% MSO^{-1}) and medium support (0.006% MSO^{-1}).

Discussion

In this study we examined the interaction of change in whole body posture and systematic variation of arm weight support (WS) on corticomotor excitability (CME) to upper limb muscles. In support of our hypothesis, there was an interaction of whole body posture and WS on CME for all muscles examined. In line with previous findings, tonic activity of muscles across the upper limb was less when WS was high, compared to when WS was medium or absent (low). Tonic muscle activity was also affected by posture. However, the hypothesis that activity would be greater when standing was found for only a subset of muscles (AD, BB, APB). As expected, CME modulated with WS and posture manipulation. Consistent with our hypothesis, analyses of CME measures indicated a trend for smaller half-maximal stimulus intensity (S50) and larger slope parameters to accompany standing for BB and TB. In contrast, muscles in the shoulder, forearm, and hand exhibited the opposite pattern reflecting lower CME when standing. We also expected that the magnitude of posture-related differences would be largest with greatest levels of WS, but support for this hypothesis was equivocal. While the S50 and slope parameters both exhibited the largest average difference at high support, the smallest magnitude difference occurred with medium rather than low support. Apart from the direct effect of WS on AD activity, the observed modulation of tonic activity and CME across upper limb muscles occurred independent of any differences in explicit task requirements.

Interactions of weight support and posture on tonic muscle activity and CME

The change in tonic muscle activity in response to changes in WS provides evidence for a common neural drive to muscles of the upper limb. Tonic muscle activity diminished with greater WS as indicated by values of background EMG (Table 1, Figure 3).. The largest magnitude of EMG activity and the greatest difference between high and low WS were exhibited by AD. This finding reflects the role of AD as the principal muscle generating antigravity torque and confirms the efficacy of the WS manipulation. The finding is consistent with results reported by previous studies employing multiple levels of WS (Coscia et al. 2014; Runnalls et al. 2014; Runnalls et al. 2015). Changes is WS did not alter the task requirements for forearm and hand muscles because the forearm was fully supported and secured to the brace. Task requirements did not vary for BB and TB because they were not oriented to act against gravity. Observed differences in tonic activity were involuntary and remote to the primary action of WS at the shoulder. This tendency for WS to influence tonic muscle activity is indicative of a common neural drive across the upper limb.

Dissociation between muscles for the response to sitting versus standing suggests the influence of whole body posture on tonic activity of upper limb muscles is mediated by distinct mechanisms in addition to common neural drive. As evidenced by response ratios (Table 1), AD was the most sensitive muscle to WS but the least sensitive to posture. The relatively small response of tonic muscle activity to change in posture may reflect a strong independent voluntary descending drive to maintain shoulder abduction. In more distal muscles that receive mostly involuntary input, larger relative responses may indicate that the signals conveying postural information interact with neural linking mechanisms responsible for distributing common drive. The factors determining whether

a muscle will express greater tonic activity in sitting or standing are not clear from the present results. A reciprocal relation between agonist and antagonist is supported for BB and TB. It is possible that mechanical restriction from the WS brace contributed to the absence of similar reciprocity in the forearm. A non-global influence on tonic activity across the upper limb refutes the hypothesis that standing would result in a general increase of muscle activity and suggests postural information can modulate neural drive on a muscle-specific basis.

Posture exerted an influence on upper limb CME over and above those changes evident in tonic muscle activity alone. This was borne out in statistical analyses of MEP area which accounted for differences in background EMG. A similar postural manipulation without WS was previously reported to elicit increased CME to the proximal AD but not the distal FDI (Kantak et al. 2013). The present findings indicate that whole body posture can affect CME to the arm, forearm, and hand, as evidenced by SR curve parameters (Table 2, Figures 5 & 6) . The discrepancy between the earlier reports and present findings could be attributed to the arm postures examined. Kantak *et al* tested the arm in a resting state hanging at the side whereas the present study examined a task-relevant arm posture that elicited involuntary tonic activity. The additional neural elements engaged by the reaching-related arm posture could provide a substrate for interaction with whole body postural information. Consistent with previous findings, an up-regulation of CME with less WS (Figure 4) appears to subserve both voluntary activity in AD and involuntary activity in more distal upper limb muscles. Whole body posture also influences CME, however the factors determining whether changing posture has a facilitatory or inhibitory effect for a specific muscle are not clear.

Postural demands and mechanisms for integrated upper limb control

Integrated control of neuromuscular activity may facilitate the coordination of voluntary actions like forward reaching and involuntary actions for postural stabilization. In the present study, changes in tonic activity and CME provide evidence for integrated control along the proximal-distal axis. Unlike previous reports of distal responses to shoulder activation (Devanne et al. 2002; Runnalls et al. 2014; Runnalls et al. 2015) and shoulder position (Dominici et al. 2005; Ginanneschi et al. 2005; Ginanneschi et al. 2006) the present findings do not exhibit a clear anatomical or task-related pattern. Differential modulation of CME to upper limb muscles could reflect non-universal membership within specific neural linkages or synergies, or it may be an expression of multiple synergies with complex or competing interactions. Further studies are warranted to distinguish between these possibilities.

Modulation of CME with whole-body posture could reflect the priming of a response that satisfies potential mechanical demands imposed by the specific task. Standing postures have greater stability requirements than sitting and require larger displacements of the arm for compensatory reactions to perturbations (Allum et al. 2002; Roos et al. 2008). Standing also increases the complexity of arm dynamics for goal-directed movements like reaching (Berrigan et al. 2006). One or more posture-sensitive upper limb synergies may act to prepare the arm for its altered biomechanical role. For example, standing may necessitate a general increase of CME to muscles that have a significant influence on the center of mass. Putative posture-sensitive neural linkages may interact with those that respond to descending drive to the shoulder and are thus sensitive to WS.

It is worth considering the neural mechanisms that may mediate the proximal-distal neural linkages. In primary motor cortex, anatomical co-location of muscle representations may facilitate functional interaction. Multiple non-contiguous representations overlap with those of other muscles in animals (Donoghue et al. 1992; Schneider et al. 2001; Rathelot and Strick 2006), and humans (Sanes et al. 1995; Devanne et al. 2006). Furthermore, representations of distal forelimb muscles are systematically surrounded by those of proximal muscles (Park et al. 2001). Functionally, intracortical disinhibition has been implicated as a mechanism contributing to modulation of CME with shoulder activation and whole body posture (Devanne et al. 2002; Kantak et al. 2013). Passive shoulder position influences distal CME through intracortical facilitation (Ginanneschi et al. 2005; Ginanneschi et al. 2006). Subcortical and spinal mechanisms may also play a role. Anatomically, divergence of descending corticomotor pathways can provide correlated input to multiple motor neuron pools (McKiernan et al. 1998). Propriospinal neurons link multiple spinal segments and can modulate descending drive to the forearm (Pauvert et al. 1998; Pierrot-Deseilligny 2002). Additionally, spinal interneuron circuits are a substrate for stable muscle synergies (Bizzi and Cheung 2013). Functionally, differences in limb position can impact motor neuron excitability through multiple proprioceptive inputs (Mogk et al. 2014; Nuzzo et al. 2016). In summary, there are many neural elements and mechanisms that may act to link neuromuscular activity to control movement and posture of the upper limb. It is likely that multiple mechanisms are sensitive to posture and WS, thus contributing to the complex pattern of CME modulation observed in this study.

Potential limitations

A limitation of the present study is the absence of a dynamic movement task. Although participants were required to accurately maintain their static posture, there was no dynamic component to challenge stability or introduce a goal-directed movement intention. It is unclear whether additional dynamic constraints would have biased CME in a more consistent pattern. The present study was conducted with healthy adults who may easily adapt reaching behavior across levels of WS (Coscia et al. 2014). Future studies may be warranted to investigate the interaction of posture and WS in the elderly, and in those with motor impairment such as after stroke. It is possible a sensorimotor system with reduced capacity would be less adaptable at a neural level to posture and WS manipulation.

Conclusions

A novel combination of WS and posture manipulations led to changes in tonic muscle activity across the upper limb and some modulation of CME to muscles in the arm, forearm, and hand. Tonic activity and CME are not uniformly greater in standing compared to sitting. Whole body posture may increase or decrease CME depending on the muscle and level of WS. The results support a model of integrated upper limb control and suggest posture-sensitive neural linkages may be distinct from those responsible for modulation with WS. These findings may have relevance for upper limb rehabilitation e.g., after stroke. With further characterization, the combination of WS and posture manipulation may create avenues to uniquely balance CME for optimal engagement in rehabilitation exercises.

394 Table 1. Omnibus analyses for linear mixed models of background muscle activity.

395 Negative response ratios represent smaller values at high support relative to low, and

396 when standing relative to sitting.

Muscle	Model Term	numDF	denDF	F-value	p-value	log response ratio
AD	support level	2	6343	5438.59	< .0001	-1.489
	posture	1	6343	163.86	< .0001	0.004
	support level × posture	2	6343	229.70	< .0001	
BB	support level	2	6150	3526.31	< .0001	-0.962
	posture	1	6150	256.03	< .0001	0.137
	support level × posture	2	6150	64.33	< .0001	
TB	support level	2	6249	3087.72	< .0001	-0.872
	posture	1	6249	692.82	< .0001	-0.277
	support level × posture	2	6249	21.12	< .0001	
BRD	support level	2	6211	2516.46	< .0001	-0.341
	posture	1	6211	124.38	< .0001	-0.041
	support level × posture	2	6211	16.62	< .0001	
ECR	support level	2	6192	3568.81	< .0001	-0.781
	posture	1	6192	66.70	< .0001	-0.047
	support level × posture	2	6192	35.01	< .0001	
FCR	support level	2	6110	914.94	< .0001	-0.163
	posture	1	6110	18.79	< .0001	-0.008
	support level × posture	2	6110	20.94	< .0001	
FDI	support level	2	5847	66.72	< .0001	-0.096
	posture	1	5847	17.07	< .0001	-0.030
	support level × posture	2	5847	3.89	0.0205	
APB	support level	2	6037	81.44	< .0001	-0.318
	posture	1	6037	30.31	< .0001	0.104
	support level × posture	2	6037	5.67	0.0035	

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Table 2. One-way ANOVAs for SR curve parameters.

Muscle	Parameter	numDF	denDF	F-value	p-value
AD	S50	5	46	0.59	0.7052
	slope	5	46	1.89	0.1153
BB	S50	5	46	24.43	< .0001
	slope	5	46	3.85	0.0054
TB	S50	5	43	0.25	0.9387
	slope	5	43	0.07	0.9965
BRD	S50	5	48	15.68	<.0001
	slope	5	48	3.40	0.0105
ECR	S50	5	48	21.10	<.0001
	slope	5	48	3.40	0.0104
FCR	S50	5	45	6.87	<.0001
	slope	5	45	1.42	0.2362
FDI	S50	5	47	6.01	0.0002
	slope	5	47	2.29	0.0606
APB	S50	5	42	0.97	0.4459
	slope	5	42	0.74	0.5958

Figure 1: Demonstration of sitting (A) and standing (B) postures.

Figure 2: A) Single EMG traces recorded from a representative participant. Traces from all muscles were recorded simultaneously during the seated high support condition. Intensity of the stimulus was 35% MSO above task motor threshold. B) Average EMG traces for TB and ECR as representative muscles from the same participant and stimulus intensity. Color shade corresponds to WS level.

Figure 3: Background muscle activity responds to changes in support level and posture. Group averages for background muscle activity are plotted at low (0 %), medium (45 %), and high (90 %) levels of weight support. Solid lines represent data from the seated condition while dashed lines are used for the standing condition. Error bars represent ±1 SEM.

Figure 4: SR curves shift in response to changes in support level and posture. On the left, SR curves are fitted to group means of observed MEP area. On the right, SR curves are fitted to means predicted using the linear mixed effects model for the median level of background muscle activity.

Figure 5. Shift in S50 parameter plotted as log response ratios between postures. Positive response ratios reflect larger S50 values for standing relative to sitting. Bar shading represents support level. Vertical lines indicate the mean across support levels for each muscle. Statistical significance is indicated next to muscle labels for omnibus tests and next to the respective bar for post-hoc comparisons (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

Figure 6. Shift in slope parameter plotted as log response ratios between postures. Negative response ratios reflect smaller (less steep) slopes for standing relative to sitting. Bar shading represents support level. Vertical lines indicate the mean across support levels for each muscle. Statistical significance is indicated next to muscle labels for omnibus tests and next to the respective bar for post-hoc comparisons (*$p < 0.05$, **$p < 0.01$).

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