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CONSTANCY OF PREPARATORY POSTURAL ADJUSTMENTS FOR REACHING TO VIRTUAL TARGETS ACROSS DIFFERENT POSTURAL CONFIGURATIONS

Alexander STAMENKOVIC[1]
Mark A. HOLLANDS[2]
Paul J. STAPLEY[1]

[1] Neural Control of Movement Laboratory
School of Medicine,
Faculty of Science, Medicine & Health
University of Wollongong
Northfields Avenue
Wollongong NSW 2522
AUSTRALIA

[2] Research Institute for Sports and Exercise Sciences (RISES), Tom Reilly Building
School of Sport and Exercise Sciences, Faculty of Science
Liverpool John Moores University
Byrom Street
Liverpool L3 3AF
UNITED KINGDOM

Current address of corresponding author:
Dr. Alexander Stamenkovic
Department of Physical Therapy
College of Health Professions
Virginia Commonwealth University
900 E. Leigh St, Box 980224
Richmond, VA 23298
UNITED STATES OF AMERICA
Email: astamenkovic@vcu.edu

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Abstract

Postural and movement components must be coordinated without significant disturbance to balance when reaching from a standing position. Traditional theories propose that muscle activity prior to movement onset create the mechanics to counteract the internal torques generated by the future limb movement, reducing possible instability via centre of mass (CoM) displacement. However, during goal-directed reach movements executed on a fixed base of support (BoS), preparatory postural activity (or *p*PAs) promote movement of the CoM within the BoS. Considering this dichotomy, the current study investigated if *p*PAs constitute part of a whole-body strategy that is tied to the efficient execution of movement, rather than the constraints of balance. We reasoned that if *p*PAs were tied primarily to balance control, they would modulate as a function of perceived instability. Alternatively, if tied to dynamics necessary for movement initiation, they would remain unchanged, with feedback-based changes being sufficient to retain balance following volitional arm movement. Participants executed beyond-arm reaching movements in four different postural configurations that altered the quality of the BoS. Quantification of these changes to stability did not drastically alter the tuning or timing of preparatory muscle activity despite modifications to arm and CoM trajectories necessary to complete the reaching movement. In contrast to traditional views, preparatory postural muscle activity is not always tuned for balance maintenance or even as a calculation of upcoming instability but may reflect a requirement of voluntary movement towards a pre-defined location.

Highlights:

- We assessed the influences of postural instability on reaching preparation and execution.
- Postural challenges produced adaptive changes to CoM displacement and arm kinematics.
- Surprisingly, CoM displacement was similar across postures during reach acceleration phase.
- Despite kinematic changes, spatial preparatory muscle activity was preserved across postures.
- Preparatory postural adjustments drive a whole-body strategy necessary for movement initiation.

KEYWORDS: postural adjustments; balance; reach; centre of mass; muscle coordination; postural challenge

INTRODUCTION

Reaching has been used extensively to study visuomotor control during goal-directed actions in humans and primates (Batista et al., 1999; Biguer et al., 1982; Goodale et al., 1986; Henriques and Crawford, 2002; Smeets et al., 1996). However, the vast majority of findings have arisen through experimental paradigms devised and implemented with participants being seated. The possible interaction of balance constraints on posture and goal-directed arm movements are less clear. When reaching is executed in the standing position, muscle coordination (through synergy analysis of muscle recruitment) and reaching kinematics remain unaltered despite changes to centre of mass (CoM) and centre of pressure (CoP) displacements that occur when base of support conditions are altered (Berret et al., 2009; Fautrelle et al., 2010). In fact, accurate reconstruction of whole-body kinematics only required greater components when specific constraints were imposed on the task (i.e., through a forced endpoint finger trajectory) rather than on postural constraint (i.e., changes to base of support). This suggests that for free, unrestrained reaching during stance, joint displacements across postural segments are produced to satisfy a preferred hand trajectory to the end goal.

The relationship between equilibrium and the goal-directed aspects of voluntary movement can also be investigated from another perspective. Theoretically, if equilibrium constraints represent high-level task variables that need to be overcome during arm movement planning and execution, it is plausible that the postural conditions under which reaching is executed (i.e., that provide relatively more or less stability) may change how arm movements are executed. Initial investigations by our group have shown that reaching to fixed targets (e.g. single step) and movements that require online corrections (e.g. double-step), do not differ in arm kinematics between seated and standing positions (Hua et al., 2013). Moreover, across a wider range of postures, no distinct changes in gaze trajectory or accuracy are observed despite clear differences in segmental contributions to movement (Stamenkovic et al., 2018). These studies suggest that equilibrium constraints seem to be well accounted for by the CNS during the execution of reaching, with task variables such as CoM displacement, endpoint trajectory and gaze position prioritised during the early programming of coordinated, accurate reach movements.

Such consistency in arm movement execution across various postural conditions may arise as a result of the postural adjustments produced prior to reach initiation. This possibility depends however, upon the theoretical context under which they are interpreted. Traditionally, postural-related muscle activity that precedes voluntary movement is thought to produce the internal dynamics necessary to counteract movement-related torques and minimize excursions of the CoM that may become destabilizing to posture (Bouisset and Zattara, 1981; Hodges et al., 1999). Yet under different contexts, similar preparatory activity can also play an opposing role, for example, when producing a forward step during locomotion (Breniere et al., 1987; Burleigh et al., 1994), shifting the CoM within the base of support to execute lifting (Commissaris et al., 2001) or to execute reaching movements upon a stable base of support (Stapley et al., 1998, 1999; Pozzo et al, 2001). Further evidence suggests that the 'sign' of leg or trunk muscle activity, when recorded or modelled, favours movement over balance during reaching either in the seated (Tyler and Hasan, 1995) or standing position (Leonard et al., 2009; Stamenkovic and Stapley, 2016). Under the traditional interpretation of the role of preparatory (or anticipatory) postural activity, threats to equilibrium arising from the internal torques generated by a voluntary movement may be exacerbated by increasing postural constraints. Therefore, it may be that the preparatory postural activity that precedes standing reaches executed upon a regular, stable base of support differs from that in more unstable conditions as the CNS weights stability above action. Alternatively, if the preparatory postural activity is related to the goal-directed aspects of the movement, their characteristics would remain consistent and tied to the movement-related components of the action necessary for movement initiation (Le Mouel and Brette, 2017), regardless of changes to postural stability.

To examine this, the present study aimed to investigate if preparatory postural adjustments for reaching are modulated with respect to changes in postural constraints. We hypothesised that preparatory postural adjustments would show uniformity across different postures as they are consistently related to movement initiation, rather than accounting for an evaluation of upcoming instability generated by a voluntary movement. To place these postural adjustments within the context of movement outcomes, secondary analyses investigated the influence of postural configuration on kinematic arm and centre of mass movement features. We show that for the standing conditions, preparatory postural adjustments show consistent activity across postures and arm kinematics are also stereotypical during the early phases of reaching but are modified as a function of postural condition during the latter reaching phase (as the arm/hand reaches the target).

EXPERIMENTAL PROCEDURES

Participants

The data analysed in this study was collected during an experiment previously reported investigating the influences of postural control on visuomotor characteristics (Stamenkovic et al., 2018). Here we analyse the muscular activity of selected arm, trunk and leg muscles in relation to chosen kinematic characteristics of the arm and centre of mass (CoM). Eleven healthy participants (8 male, 3 female; age: 24.3+2.2 years), with normal or corrected vision, and without any known neurological or orthopaedic impairments were recruited from the university student population. Institutional ethics approval (UREC: 14/SPS/021) and informed consent was received for all experimental procedures in accordance with the Declaration of Helsinki (1975). Muscles and target locations were defined by their position in relation to the participant midline and reaching arm (i.e. dominant arm) such that muscles located on the same side of the body as the reaching arm, (i.e. targets that did not require the arm to cross the midline) were termed ipsilateral, while those residing on the opposite side were termed contralateral.

Apparatus & configuration

Participants faced a blank screen upon which five circular light targets were projected (diameter: ~3º, target eccentricity: 23° and 38° from central target at participant midline) and aligned horizontally (**Figure 1a**). Whole body three-dimensional kinematics were captured using thirty-nine passive retro-reflective markers attached to participants' bodies as in the Vicon Plug-in Gait full body model, and recorded using an eight camera Bonita motion capture system (Vicon, Oxford, U.K) sampling at 200 Hz. This allowed for the quantification of arm kinematics and future determination of CoM displacement (for which the Plug-in Gait model uses the Dempster (1955) method to estimate CoM position). Muscle activity for representative muscles of the limbs and trunk segments were recorded using a MA-300 12-channel surface electromyography (sEMG) system (Motion Lab Systems, Baton Rouge, LA) and 4-channel Bagnoli (Delsys, Natick, MA) sEMG system sampling at 1,000 Hz. Recordings occurred bilaterally and included: tibialis anterior (*c*TA, *i*TA) and soleus (*c*Sol, *i*Sol) for the lower limb, combined obliquus internus and transversus abdominis (*c*IOTrA, *i*IOTrA) and multifidus (*c*Mult, *i*Mult) for the trunk, sternocleidomastoid (*c*SCM, *i*SCM) for the neck and the anterior head of the deltoid muscle (ADelt) for the focal (reaching) arm.

Surface electrode placement followed SENIAM guidelines for upper and lower limb musculature (Hermens et al., 2000) and previously identified sites for trunk musculature (Stamenkovic and Stapley, 2016). All analog data signals were controlled and recorded using a customized program written in LabVIEW (National Instruments, Austin, TX) at 1,000 Hz. The customized program delivered a pulse to a strobe light situated within the motion capture volume behind the participant to allow for synchronization of kinematic data with recorded analog signals.

Procedures

Experimental procedures have been described in detail previously (Stamenkovic et al.,2018). Briefly, participants undertook two main task conditions; simple gaze fixation (LOOK) or whole body coordinated reaching (REACH) movements under four separate postural configurations (SIT; STAND; NARROW; BEAM, see **Figure 1b**). These four conditions were chosen as they altered the size and quality of the base of support, known to be the primary biomechanical constraint to balance (Bouisset and Le Bozec, 2002; Horak, 2006). Mediolateral stance width remained identical for three of the four configurations (SIT, STAND, and BEAM) and was determined by taking the average distance between medial malleoli of the ankles after three 15-m walking trials at the participant's preferred walking speed. For the NARROW posture, the feet were placed together such that the medial malleoli of the two ankles touched. For SIT trials, a stool with no back support, and unable to rotate was used to allow for neutral vertebral and shoulder position and a constant 90° knee flexion. During the BEAM configuration, participants stood on a wooden beam (dimensions: 800-mm length x 80-mm height x 80-mm width) aligned with the approximate centre of the ankle joint (line between the medial and lateral malleoli). This was to ensure that the feet did not touch the ground for support throughout the entirety of the reaching movement and that the base of support was reduced in the anteroposterior plane.

As measures related to the LOOK condition have previously been reported (Stamenkovic et al., 2018), only methods relating to the REACH trials (for which postural adjustments were evident) are described here. For REACH trials, movements were made to a remembered and virtual target position beyond arm's length (130% of reaching arm length) which was in the same plane as each of the five visual fixation targets (**Figure 1a**). This distance was shown to be able to be achieved during familiarization prior to data collection without a further step to retain balance (regardless of posture) and was adopted to implicitly require the preparation and execution of a whole-body reaching response. The lack of a physical endpoint also removed the potential for future tactile information to influence movement preparation and termination strategies (Clapp and Wing, 1999; Jeka, 1997).

Participants were instructed of the type of the upcoming trial (LOOK; REACH) prior to a pseudo-randomized time delay (500 – 2,000 ms) preceding target light onset. Upon illumination, participants reached with their preferred arm from the starting posture where the index finger was affixed to the xiphoid process, to the final posture with the arm outstretched and held at the remembered target position until the end of data collection. No other instructions were given as to how the movement should be conducted. Trials within each postural configuration were conducted in a blocked fashion, with the order of postural configuration, task condition and desired movement direction presented randomly across participants. Additional trials (n = 10) where no visual fixation target illuminated were provided to reduce generalised anticipation of movement. 5-minute rest periods were given between each postural configuration block to counteract any fatiguing effects of the protocol. In total, 60 trials per postural configuration were conducted (5 trials x 5 directions x 2 tasks conditions + 10 ‘catch’ trials), and a collection period totalling 5,000 ms captured all relevant data within each trial.

Data analysis

All analyses were completed offline using customized scripts created using MATLAB (The Mathworks, Natick, MA). Kinematics were low-pass filtered using a second-order Butterworth algorithm at 20 Hz. Raw analog EMG signals were high-pass filtered at 35 Hz (to remove motion artefact), de-meaned, rectified and low-pass filtered at 100 Hz (second order Butterworth) for visualization (Leonard et al., 2009; 2011).

Reach measures. Onset of the focal arm movement was determined using the bell-shaped tangential velocity profile of the reaching index finger. A relative measure of 5% of the peak finger velocity was used as a threshold, with movement initiation being the first value exceeding and movement termination reducing after the peak (Sainburg and Schaefer, 2004). From this, salient features of finger kinematics, including movement time **(Figure 1c**: Movement Time), time to peak velocity (**Figure 1c**: circle) and the associated measures of acceleration (**Figure 1c**: light grey) and deceleration phases (**Figure 1c**: dark grey) could be calculated to determine symmetry ratio of movements. Initial finger error and endpoint finger error (in degrees) were calculated by comparing the planar (x, y) position of the finger at both peak finger velocity and movement termination with respect to the prescribed target; however, accuracy was not explicitly determined to be a criterion for successful movement. The degree to which finger trajectories deviated from a straight line connecting initial and final finger positions was also calculated (see linearity index – Atkeson and Hollerbach, 1985; Messier and Kalaska, 1999). This was taken as a ratio between the amplitude of greatest deviation of the actual finger path (**Figure 1c**: minor axis) and a linear trajectory (**Figure 1c**: major axis) from movement onset to termination.

Centre of Mass measures. Cumulative (total) and planar (anteroposterior, AP; mediolateral, ML) CoM displacements was calculated across 4 phases of movement preparation and execution; 1) the preparatory postural adjustment period (or pPA period), 250 ms prior to movement onset, 2) during finger acceleration, and 3) finger deceleration phases, and 4) across the entire movement phase.

Muscle activity measures. A period of 250 ms preceding movement onset was assessed to depict the spatial evolution of postural muscle activity prior to movement onset. Initially, this preparatory postural adjustment period (or *p*PA period) was divided into 50 ms time intervals and mean activity within each bin for every trial was calculated for each individual muscle. Values were normalized to their respective maximum amplitude across bin and reach direction for each individual muscle so that all values for each muscle were between 0 and 1. These were then plotted as muscle tuning curves (Leonard et al., 2009, Torres-Oviedo and Ting, 2007). Individual muscle onsets latencies were determined when activation exceeded 2 standard deviations above baseline muscle activity (**Figure 1d**). Muscle amplitude was summarised prior to movement onset and termination through the calculation of the co-contraction index for agonist-antagonist pairing in the lower limb and trunk (Rudolph et al., 2000; Stamenkovic et al., 2020).

Statistical analysis

Finger kinematics, CoM displacements and muscle latencies were assessed using separate two-way repeated measures ANOVA (POSTURE X DIRECTION) using the SPSS statistical package (ver. 21, IBM, OR, USA). Bonferroni-Holm adjustments were applied to main ANOVA results to reduce the family-wise error rate before determining significance across related measures. This was achieved by altering the initial level of significance ($p < 0.05$)

with respect to the total number of tests performed (e.g. 11 muscles x 3 main effects/interaction) to produce a more conservative significance level ($p < 0.0015$). Greenhouse-Geisser adjustments were made in cases where violations of sphericity were observed. When applicable, post-hoc analyses were conducted with Bonferroni adjustment for multiple pairwise comparisons. Muscle tuning curves was assessed using principal component analysis, where the 1st principal component (and respective total percentage of variability accounted for, VAF) acted as a measure of similarity in tuning across participants. To assess whether muscle activation latencies were better aligned to the trigger event (i.e. light onset) or movement event (i.e. finger onset) correlations were calculated using Type II major axis regression (Schepens and Drew, 2003). Following ANOVA testing and in an effort to determine whether a lack of significant differences in CoM displacement during the acceleration phase were driven by similarity in measures, a Bayesian repeated measures ANOVA was calculated across postures with open-source JASP software using default priors (JASP team, 2017). Bayes Factor (BF_{10}) were reported expressing the probability of the data given the alternative relative to the null hypothesis and assessed using the Lee and Wagenmaker's classification scheme, where values smaller than 1 represent increasing favour towards the null hypothesis (Quintana and Williams, 2018).

RESULTS

Reach kinematics

In order to investigate how posture affected the production of the focal component of the movement, a number of reaching kinematics derived from finger velocity were quantified across each postural configuration. Despite familiarising themselves with the reaching distance, participants often undershot the position of the remembered target (see **Table 1** for grand averages, **Figure 2a** for individual finger trajectories and **Figure 2b** for endpoint distributions), with changes occurring to a different extent across postures ($F_{3,30} = 14.849$, $p < 0.001$, $\eta^2_p = 0.598$). As such, reach distances (represented with respect to total reach length) progressively decreased as postures moved through to configurations with a reduced base of support (SIT vs. NARROW, $p = 0.049$; SIT vs. BEAM, $p = 0.004$; STAND vs. BEAM, $p = 0.004$), with the only the exception being between STAND and NARROW ($p = 0.086$). Trajectory profiles (**Figure 2a**) were often curvilinear towards targets and did not change significantly across both posture and direction (**Table 2**).

Participants showed a similarity in the distribution of the speed of their movements within each configuration, such that participants who moved slower during the stable SIT configuration also tended to move slower across all configurations (see **Figure 2a** for distribution of individual velocity profiles for all participants). Regarding finger kinematics, only peak finger velocity was altered by postural configuration ($F_{3,30} = 3.177$, $p = 0.038$, $\eta^2_p = 0.241$) with significantly reduced peak velocities achieved in the BEAM configuration when compared to STAND ($p = 0.048$). Directional biases were also present for the most lateral targets (i.e. contralateral 38° vs. ipsilateral 38°). This included greater peak finger velocities ($F_{1.336,13.362} = 11.427$, $p = 0.003$, $\eta^2_p = 0.533$; ipsi38 vs. contra38, $p = 0.012$), shorter acceleration phases ($F_{1.443,14.427} = 30.252$, $p < 0.001$, $\eta^2_p = 0.752$; ipsi38 vs. contra38, $p = 0.001$) and shorter time to the inflection point ($F_{1.623,16.226} = 19.840$, $p < 0.001$, $\eta^2_p = 0.665$; ipsi38 vs. contra38, $p = 0.002$, see **Figure 1c** for example) for movement to the ipsilateral target.

Standing postures showed a distribution of endpoints (**Figure 2b**, represented as 95% confidence ellipses) that tended to reduce in amplitude for the anteroposterior component with endpoint variability stemming from mediolateral deviations from the target. This was evident in the shift from spherical to elongated distributions as postural instability was altered across configurations (e.g. compare **Figure 2b**, ipsilateral SIT vs. ipsilateral BEAM).

These errors were evident during the initial phases of the reach (i.e. during the acceleration phase) with a main effect of POSTURE observed for initial finger error ($F_{3,30} = 6.726$, $p < 0.001$, $\eta^2_p = 0.402$). In particular, there was a significant difference between SIT and STAND ($p = 0.038$) postures, but these differences did not reach significance when compared to other postures (e.g. vs. BEAM, $p = 0.068$). Negative values of initial finger error for the seated posture (SIT) indicated that trajectories continued closer to the participant midline before curving towards the target of interest. This varied from standing postures, where positive initial finger error values represented trajectories deviating laterally away from the target. Trajectories often continued along this deviated path compounding errors further at finger endpoint ($F_{3,30} = 12.117$, $p < 0.001$, $\eta^2_p = 0.548$). This remained similar across targets, as significant differences were not seen as a function of reach direction (see **Table 2**, Finger trajectory curvature).

Effects of changing posture on body centre of mass displacement

CoM displacements showed characteristics that aligned with expectations based on the alterations made to the base of support in each postural configuration (**Figure 3a-d**). For example, antero-posterior displacements were constrained in the BEAM configuration (**Figure 3d**) while medio-lateral displacements were constrained in the SIT (**Figure 3a**) and NARROW configurations (**Figure 3c**). When divided into different phases of movement results showed a significant main effect of POSTURE on CoM displacement for total displacement (**Figure 4a**) for the *p*PA period ($F_{1.407,14.069} = 5.142$, $p = 0.030$, $\eta^2_p = 0.340$), deceleration phase ($F_{1.596,15.956} = 5.675$, $p = 0.018$, $\eta^2_p = 0.362$), and movement time ($F_{(3,30)} = 3.169$, $p = 0.039$, $\eta^2_p = 0.241$). These were also reflected in AP displacements (**Figure 4b**) for the *p*PA period ($F_{3,30} = 11.027$, $p < 0.001$, $\eta^2_p = 0.524$), deceleration phase ($F_{3,30} = 9.528$, $p = 0.002$, $\eta^2_p = 0.488$), and movement time ($F_{1.703,17.030} = 6.825$, $p = 0.009$, $\eta^2_p = 0.406$), but only in the latter phases for ML displacement (**Figure 4c**) during the deceleration ($F_{1.186,11.862} = 16.598$, $p < 0.001$, $\eta^2_p = 0.624$) and movement time ($F_{2.064,20.64} = 8.161$, $p = 0.002$, $\eta^2_p = 0.449$). Specifically, greater anterior CoM displacement occurred in all standing postures during the *p*PA period (SIT vs. STAND, $p = 0.002$; SIT vs. NARROW, $p = 0.001$; SIT vs. BEAM, $p = 0.024$), while CoM AP displacement was significantly decreased during deceleration phase for the BEAM configuration (SIT vs. BEAM, $p = 0.002$; STAND vs.

BEAM, $p = 0.018$). CoM ML displacements were significantly decreased between STAND and other postural configurations during the deceleration phase of movement (SIT vs. STAND, $p = 0.009$; STAND vs. NARROW, $p = 0.001$; STAND vs. BEAM, $p = 0.004$; STAND vs. BEAM, $p = 0.007$). Interestingly, this was in stark contrast to the lack of significant changes to CoM displacement observed between postures during the acceleration phase of the movement (‘CoM total’: $F_{1.412,14.115} = 0.061$, $p = 0.885$, $\eta^2_p = 0.006$; ‘CoM AP’: $F_{1.628,16.277} = 2.011$, $p = 0.134$, $\eta^2_p = 0.167$; ‘CoM ML’: $F_{1.125,11.252} = 1.645$, $p = 0.229$, $\eta^2_p = 0.141$). Further investigation of the lack of changes in the acceleration phase using Bayesian inference showed a Bayes Factor of 0.031, suggesting that displacements were 32 times more likely to be observed under the null hypothesis, and signifying strong to very-strong evidence towards favouring the null hypothesis (according the Lee and Wagemaker’s classification scheme).

Spatial tuning of predictive postural muscle activity

Mean muscle activation profiles of axial and lower limb muscles during reaching movements made to the ipsilateral and contralateral target (38° eccentricity) for a typical participant (S03) are shown in **Figure 5**. Activation of the focal arm muscle (i.e., anterior deltoid, ADelt) remained consistent prior to reach, and across postural configuration. Aligning with their expected contributions to reaching, lower limb muscles showed little activity during the *p*PA period in the SIT configuration when compared to the standing postural configurations (**Figure 5**, SIT ‘*p*PA’ period). This was in contrast to proximal trunk muscles which showed similar profiles across each of the four postural configurations, and was reflected in the evolution of such preparatory muscle activity over the time course of the *p*PA period (e.g. *c*IOTrA to contralateral target from *p*PA 1-5). Across standing postures, directional biases in activity profiles were present for IOTrA and TA such that participant movements to contralateral targets were preceded by activity from *c*IOTrA and *i*TA, with movements to ipsilateral targets preceded by their oppositely positioned pairs (i.e. *i*IOTrA and *c*TA). This generally manifested during the later stages of movement preparation (i.e. starting ~150 ms preceding finger onset, *p*PA 3-5, see **Figure 6**, cyan, green and magenta traces). Increases in background activity of the soleus also revealed phases of inhibition during the *p*PA period, especially within the standing configurations, such that *i*Sol decreased for ipsilateral movements and *c*Sol for contralateral movements (**Figure 5**, *p*PA4/5 STAND, NARROW, and BEAM). When co-contraction indexes were summarized for the phases prior to movement onset, a clear increase in co-contraction index was seen between seated (**Figure 7**, grey) and standing postures. Across standing postures, the highest co-contraction indexes were seen for the NARROW and BEAM conditions for ipsilateral TA/Sol relationship while for the trunk segment, changes in co-contraction index across direction were seen for the contralateral IOTrA/Mult relationship. These were reduced for movements to contralateral targets.

Mean spatial tuning curves for all participants were constructed for the preparatory period highlighted in **Figure 5** (i.e., *p*PA period) to compare patterns of activation across the entire cohort (**Figure 6**). When the similarity of tuning was assessed across all postural configurations for the final preparatory epoch (i.e., *p*PA5), pooled tuning curves tended to display one of two main characteristics; 1) a directional bias of muscle activity for movements towards the contralateral (**Figure 6**, black, dashed POOLED *p*PA5) or ipsilateral (**Figure 6**, grey, dashed POOLED *p*PA5) target respectively, or 2) a central bias where activity was peaked towards midline (**Figure 6**, light blue, dashed, POOLED *p*PA5). Muscles showed preserved tuning when compared across postures and quantified using the variance accounted for (i.e., VAF) for the first principal component (PC1) extracted from the pooled dataset. When pooled, *c*SCM, *i*IOTrA, *i*Mult, *c*Sol, and bilateral TA activity were tuned to ipsilateral targets (**Figure 6**, grey dashed). In contrast, *i*SCM, *c*IOTrA, *c*Mult, and *i*Sol activity was tuned to contralateral reach directions (**Figure 6**, black dashed).

Temporal patterns of muscle activation

Figure 8 shows the distribution of muscles activation latencies within a 500 ms period before and after finger onset. Postural configuration (**Figure 8a-d**) had no significant effect upon the timing of muscle activation of the muscles studied. After Bonferroni-Holm adjustment, a two-way repeated measures ANOVA revealed only a single main effect of DIRECTION ($F_{1,10} = 52.499$, $p < 0.001$, $\eta^2_p = 0.840$) with activation of the *c*IOTrA occurring earlier for movements to contralateral targets (vs. ipsilateral, $p < 0.001$). In addition, muscle latencies were compared to stimulus (i.e. light onset) and to movement onset (i.e. finger onset). **Figure 9** plots coefficients of determination (r^2) for all muscle activations between finger (x-axis) and light onsets (y-axis). Regardless of postural configuration or direction of reach (see **Figure 9** for legend), the majority of r^2 values were located to the right of the reference line (i.e. below the diagonal line) indicating that they were more strongly associated with movement onset.

DISCUSSION

Based upon traditional interpretations of postural adjustments prior to voluntary movement we expected that as postural configuration was altered to reduce the quality of the base of support, preparatory muscle activity would be modified to limit CoM displacement and the instability that arises from its perturbation. In contrast, the current study shows that spatial and temporal characteristics of muscle activity were preserved regardless of postural configuration. This aligns with previously proposed strategies adopted prior to goal-directed reaching movements (Leonard et al., 2009; Stamenkovic and Stapley, 2016) and provides further evidence to the theoretical perspective of mobility as the purpose of postural control (for review, see Le Mouel and Brette, 2017). When combined with our recent analysis of visuomotor coordination under postural constraint (Stamenkovic et al., 2018), the functional outcomes of this ‘tuned’ muscle activity, and consistency in *p*PA production, further supports a coordinated whole body approach to movement initiation, with postural adjustments being an integral part of voluntary movement.

Preparatory postural adjustments are not programmed based on the perception of upcoming instability

The idea that postural adjustments create the dynamic conditions for movement rather than a perception of upcoming instability is supported by the evolution of CoM displacement during the acceleration and deceleration phases of the movement (see **Figure 3 and 4**). CoM displacement is traditionally considered to be a primary controlled variable in the production of postural adjustments, and in parallel control theories of mechanisms that dictate CNS control of postural and movement goals (Massion, 1992; Yakovenko and Drew, 2009). Therefore, if counter rotatory segmental torques were produced in preparation of stabilizing the upcoming arm movement, it would be assumed that changes to CoM displacement and trajectory would occur that aimed to ‘retain’ its stationary position during these early stages (Stapley et al., 1999). Yet, the presence of muscle spatial tuning despite the limited directional (or mediolateral) component of movement (compared to the greater anteroposterior displacement requirement, see **Figure 6**), and consistency in the progression of CoM displacement leading up to peak velocity of the finger (**Figure 4a-c**, light grey) suggests that the stereotyped muscle activity prior to reaching represents the ensuing requirements necessary to displace the CoM within the base of support for movement generation (Stapley et al., 1999). This is as the acceleration phase of the movement is programmed prior to movement onset and is primarily feed-forward in nature (Gribble et al., 2002).

Further, the constraints afforded by the available base of support of each postural configuration become more evident when examining CoM displacement during the final stages of movement, where significant reduction in CoM displacement (**Figure 4a-c**, dark grey), and undershooting of remembered finger endpoint (**Figure 2a-b, and Table 1**) were observed for the standing postures that challenged stability (e.g., NARROW, BEAM). The undershooting of target position was surprising given that participants were given some familiarization of the task prior to data collection. However, undershooting of target position for beyond-reach targets has been reported previously (Heath and Binsted, 2007), and it is important to note that the target position was not to promote accuracy of movement per se but employed to ensure that a whole body ‘beyond arm’ reaching strategy would be utilized for movement. It was postulated that a beyond-reach target would implicitly ensure that the intention behind the programming of movements would remain similar across reach conditions.

The arm (and by extension the CoM) seem to move less as a function of postural configuration in order to protect stability, occurring once updated feedback of the arm movement became available towards the terminal phases of reaching. This may be part of a conservative strategy (Gribble et al., 2002), whereby the absolute magnitude of preparatory activity is modulated to allow for future online corrections of movement to be made, explaining why significant changes to peak finger velocity were present for both the NARROW and BEAM configuration. A lack of kinematic changes for the finger between the SIT and STAND configurations; however, suggests that the mechanical challenges associated simply with standing may be well accounted for by the CNS. This is also supported by previous work for perturbed and unperturbed reaching (Hua et al., 2013).

One consideration is that the stereotyped nature of postural adjustments is responsible for eventual inaccuracies of the arm as postural challenge was altered. In fact, accuracy to remembered targets is thought to be a central process planned prior to reaching onset (Soechting and Flanders, 1989). Also, intra-limb postural adjustments and their appropriate tuning is key in producing accurate movements (Caronni et al., 2013; Cavallari et al., 2016). While endpoint accuracy clearly changed as a consequence of standing within the current study, when we consider the area bounded by the 95% confidence ellipses (**Figure 2b**), the precision of the movements across postural configurations remained similar. When coupled with stereotyped curvilinear finger trajectories and deviations away from the target in the initial stages of the reach, it would suggest that inaccuracies likely stem from an interaction between the remembered nature of targets, the importance placed on accuracy, and the postural configuration. As the direction and extent of reaching is thought to be planned and reconciled in parallel over time (Messier and Kalaska, 1999), one could argue that under a lack of explicit task constraints (via instruction of movement), a stereotyped preparation of movement is desirable to reduce the complexity of motor planning.

We have shown that significant differences in the total displacement of the CoM and finger remain across postures, despite preserved spatiotemporal muscle tuning. Alternatively, one could argue that the self-selected speed of movement within the current paradigm may not have produced a large enough perturbation to require an anticipatory stabilising strategy. In fact, a number of studies have provided evidence to support the specificity of postural adjustments to changes in movement amplitude (Aruin and Shiratori, 2004; Kaminski and Simpkins, 2001), speed (Horak et al., 1984; Mochizuki et al., 2004) and direction (Aruin and Latash, 1995a). Yet, while the peak velocity of movements within the current study did change as a function of posture, it is important to place our results within the context of similar reaching studies. For example, in the current study movements generally took ~900 ms (average range movement time, i.e. *MT*: 763 – 1049 ms; average range peak velocity, i.e. *PVel*: 2.31 – 2.92). When compared to results within our own laboratory using a similar paradigm (with the notable differences of physical vs. remembered targets and greater range of target directions) movement time and peak velocities were relatively quicker and faster respectively (*MT* = 746 - 881 ms, Leonard et al., 2009; *MT* = 627 – 1190 ms, *PVel* = 1.1 – 2.2 m/s, Hua et al., 2013; *MT* = 740 – 940 ms, *PVel* = 1.4 – 3.8 m/s, Stamenkovic and Stapley, 2016). Further comparison with studies examining reaching during classic seated scenarios and whole body reaching paradigms place our results well within reported movement speeds (***seated***: *PVel* ~ 1.8 – 2.2 m/s, Kaminski et al., 1995; *PVel*: fast = 3 – 4 m/s, semi-fast = 0.8 – 1.2 m/s, Kitazawa et al., 1997; *PVel*: slow = 0.2 – 0.4 m/s, natural = 1.5 – 2 m/s, fast = 2 – 3 m/s, Messier et al., 2003; *PVel*: slow ~1.5 m/s, fast ~3 m/s, Pigeon et al., 2003; ***whole body reaching***: *MT* = 710, *PVel* = 2.02, Berret et al., 2009; *MT* = 830 ms, *PVel* = 1.98 m/s, Chiovetto et al., 2010; *MT*: normal BoS = 800, reduced BoS = 760, *PVel*: normal BoS = 1.54, reduced BoS = 1.48, Fautrelle et al., 2010; *PVel*: without trunk movement ~ 4 m/s, with trunk movement ~ 2 – 3 m/s, Ma and Feldman, 1995). Whilst it is difficult to determine the point of partition between posture and movement, the greater speeds of movement achieved across even the most challenging of postures in the current study would infer that postural adjustments are designated to produce the dynamics of the upcoming movement.

Implications for whole body motor preparation

Considering the functional role of the spatiotemporal characteristics of preparatory muscle activity in the current study, an argument can be put forward for a high-level integration of posture and movement commands. The relative spatial tuning reflects previous findings for reaching during stance in both the lower limb (Leonard et al., 2009) and trunk (Stamenkovic and Stapley, 2016), whereby a global command was hypothesized to drive movement initiation. When coupled with the average timing of initial muscle activation, a disto-proximal sequence of activation is seen (Bonnetblanc et al., 2004) that also aims to promote displacement of the CoM. By comparing muscle onsets to stimulus or movement initiation, a partition between focal and postural components can be examined as a function of stability requirements across postures (Schepens and Drew, 2003, Yakovenko and Drew, 2009). Ultimately, the greater proportion of relationships where muscle activations were linked with movement onset (**Figure 9**) strengthens the notion that posture, and movement commands are integrated.

Within the current study, preparatory muscle activations may have remained unaltered as stability was achieved through co-contraction of distal musculature around the ankle providing increased joint stiffness (i.e. ankle strategy - Horak, 2006). This can be evidenced within the EMG profiles for standing-based postures in **Figure 5** and co-contraction indexes prior to finger onset (**Figure 7**). Inhibition in soleus prior to movement onset, and the reduction of tibialis anterior activity across postural configurations were also present. When the timing for clear inhibitions were examined (i.e., systematically reduced from baseline activity by 1SD), they represented stronger relationships with stimulus onset rather than movement onset. Based on their timing, muscle inhibitions therefore most likely reflect pAPA commands described by Schepens and Drew (2003). They may also represent an overlapping of a movement-based motor program on to the new reference (or baseline) activity required for balance. When postural adjustments have been examined across different postures there has been evidence that the functional organization of adjustments may be divided into two components (Forssberg and Hirschfeld, 1994; van der Fits, 1998). The first component produces a spatially tuned response, on which specific temporal and task-related features can be overlayed (Forssberg and Hirschfeld, 1994). This follows closely with the findings of the current study in which preservation of muscle tuning and greater co-contraction indexes for greater postural challenge prior to movement are seen. The specific changes in co-contraction indexes across the ipsilateral lower limbs, and contralateral trunk may reflect an underlying regulation of joint-based stiffness to provide rotational support based on the mechanics of the task (i.e., reaching across the body midline). Whether this aligns mechanistically with the notion by which an impedance controller may act in the refinement of a feedforward model (Franklin et al., 2003; Kadiallah et al., 2011; Osu et al., 2002), where the necessity for anterior displacement regardless of target is achieved by appropriate inhibitions on to which fine-tuned postural adjustments can then be enacted, remains to be confirmed.

Consistency in *p*PA production across postural configurations may also allow for the execution of accurate and stereotyped gaze patterns. In fact, comparing the timing of preparatory muscle onset with respect to the visuomotor responses previously reported from the current data set (Stamenkovic et al., 2018), postural activity precedes the initiation of gaze regardless of configuration. This further supports the notion that posture subserves gaze requirements necessary to produce a whole-body response when preparing to move (Scotto Di Cesare et al., 2013; Solomon et al., 2006) or reach.

It is also necessary to consider how consistency in preparatory postural adjustments and early CoM displacement align with current theories surrounding closed-loop theories of motor control, including optimal feedback control (or OFC, for review see, Todorov, 2002; Franklin and Wolpert, 2011). While a number of outcomes, including the influence of postural configuration on late-phase CoM displacement and similar endpoint precisions (as feedback is modulated differently depending on target distance - Liu and Todorov, 2007) can be explained through OFC, it is less clear as to why postural adjustments remain spatiotemporally preserved across postural configurations. Within this framework, preparatory postural adjustments should provide a reference to the motor prediction based on the efference copy for the upcoming reaching movement and accompanying whole body movements. Considering changes in state estimation that would occur due to changes in postural configuration, as well as uncertainty associated with sensory noise associated with the movement itself (Yeo et al., 2016) we might expect that the predictions upon which postural adjustments are organized would be modulated to account for the potential instability at final posture.

Conclusion

The current study has provided evidence that preparatory muscle activity with similar spatiotemporal characteristics persisted across postural changes that altered stability requirements. This occurred despite alterations to reaching kinematics and complemented displacement of the CoM in line with the desired target. This suggests that during voluntary reaching with the upper limb, postural adjustments are not always tied to balance constraints. Instead, postural adjustments are able to create the necessary dynamics for movement in spite of potential future instability, further supporting an alternative theory to their traditional role in posture and movement coordination.

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AS present address for correspondence: Motor Control Laboratory, Department of Physical Therapy, College of Health Professions, Virginia Commonwealth University, 900 East Leigh St, Box 980224, Richmond, VA, 23298

CONFLICT OF INTEREST

The authors state that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

AS, MAH and PJS conceived and designed the study. AS, RR collected the data. AS performed the analysis. AS produced the first draft of the manuscript. AS, MAH and PJS contributed to the interpretation of data, critical review of the manuscript and approval of the final version of this manuscript.

ABBREVIATIONS

APA – anticipatory postural adjustments
ADelt – anterior deltoid
BoS – base of support
CCI – co-contraction index
CoM – centre of mass
Contra – contralateral with respect to the reaching arm
*c*IOTrA – contralateral combined internal obliquus and transverse abdominis muscle
*c*Mult – contralateral multifidus muscle
*c*SCM – contralateral sternocleidomastoid muscle
*c*Sol – contralateral soleus muscle
*c*TA – contralateral tibialis anterior muscle
Ipsi – ipsilateral with respect to the reaching arm
*i*IOTrA – contralateral combined internal obliquus and transverse abdominis muscle
*i*Mult – ipsilateral multifidus muscle
*i*SCM – ipsilateral sternocleidomastoid muscle
*i*Sol – ipsilateral tibialis anterior muscle
*i*TA – ipsilateral tibialis anterior muscle
MT – movement time
*p*PA – preparatory postural adjustment
PVel – peak finger velocity

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Table 1: Finger kinematic variables across postural configuration and direction of reach

	Acceleration Phase (ms)		**Peak Velocity (m/s)**		**Inflexion point (ms)**		**Deceleration Phase (ms)**		**Movement Time (ms)**		**Symmetry Ratio (Acc:Inflex)**		**Symmetry Ratio (Acc:Dec)**		**Normalised reach distance[a]**	
	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
SIT																
contra38	256	74	2.4	0.49	290	110	675	181	931	224	0.93	0.17	0.42	0.1	1.18	0.16
contra23	245	64	2.52	0.49	265	70	658	198	903	211	0.97	0.17	0.42	0.11	1.19	0.14
centre	231	63	2.6	0.5	244	67	555	118	786	139	0.96	0.29	0.43	0.14	1.23	0.14
ipsi23	227	58	2.73	0.57	240	80	535	134	763	176	1	0.18	0.44	0.11	1.21	0.13
ipsi38	221	57	2.92	0.74	228	59	578	106	799	159	0.99	0.21	0.43	0.12	1.23	0.12
STAND																
contra38	257	56	2.52	0.5	289	84	776	399	1033	402	0.94	0.14	0.41	0.12	1.2	0.17
contra23	241	58	2.57	0.56	260	64	608	132	845	156	0.96	0.15	0.43	0.11	1.14	0.08
centre	221	59	2.56	0.54	240	47	561	158	782	173	0.95	0.26	0.43	0.16	0.15	0.12
ipsi23	219	53	2.69	0.56	247	49	568	160	787	170	0.91	0.13	0.43	0.1	1.12	0.08
ipsi38	213	40	2.9	0.55	229	53	550	101	764	123	0.96	0.13	0.41	0.09	1.21	0.09
NARROW																
contra38	270	97	2.53	0.62	276	93	623	232	892	254	1.07	0.46	0.5	0.24	1.17	0.1
contra23	249	62	2.47	0.59	248	43	676	293	926	287	1.03	0.23	0.45	0.13	1.1	0.13
centre	224	64	2.6	0.56	253	62	578	151	802	163	0.92	0.28	0.42	0.18	1.16	0.1
ipsi23	235	73	2.61	0.56	232	50	599	130	834	169	1.05	0.25	0.45	0.13	1.09	0.1
ipsi38	227	69	2.79	0.69	229	69	627	171	854	215	1.04	0.26	0.39	0.09	1.15	0.08
BEAM																
contra38	272	75	2.31	0.53	278	72	777	302	1049	356	1.01	0.2	0.41	0.1	1.09	0.11
contra23	256	56	2.34	0.55	250	53	752	208	1008	241	1.08	0.26	0.43	0.08	1.04	0.09
centre	240	80	2.35	0.54	236	132	556	170	797	205	0.96	0.45	0.45	0.14	1.08	0.06
ipsi23	228	54	2.47	0.53	255	54	661	220	889	264	0.92	0.16	0.41	0.09	1.05	0.07
ipsi38	230	57	2.72	0.58	239	51	666	301	896	338	0.98	0.19	0.42	0.1	1.14	0.07

[a] Normalized to arm reach distance (1 = 100% arm length)

Table 2: Finger accuracy measures across postural configuration and direction of reach

	Initial finger error (°)		**Endpoint finger error (°)**		**Finger trajectory curvature**[a]	
	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
SIT						
contra38	-4.05	11.36	1.66	7.65	0.068	0.033
contra23	-1.06	11.23	0.64	6.23	0.065	0.026
centre	8.51	5.07	4.3	3.84	0.056	0.023
ipsi23	-0.81	9.05	0.48	6.55	0.054	0.022
ipsi38	-3.64	7.39	1.03	5.32	0.05	0.026
STAND						
contra38	2.33	11.37	4.81	4.13	0.081	0.041
contra23	1.26	9.68	3.81	4	0.073	0.036
centre	7.65	4.34	3.75	2.61	0.065	0.031
ipsi23	3.19	8.92	5.02	4.17	0.056	0.028
ipsi38	2.19	8.17	8.15	4.79	0.059	0.029
NARROW						
contra38	-0.99	7.55	3.3	5.02	0.07	0.02
contra23	3.94	10.53	4.53	5.16	0.069	0.027
centre	8.14	5.75	3.94	3.39	0.064	0.028
ipsi23	0.9	9.77	1.73	5.97	0.06	0.022
ipsi38	-1.41	10.44	2.36	8.86	0.063	0.018
BEAM						
contra38	-1.06	8.06	1.03	3.57	0.072	0.024
contra23	2.77	11.72	5.64	7.53	0.063	0.02
centre	10.76	6.31	6.52	3.88	0.058	0.027
ipsi23	2.39	12.61	3.9	7.99	0.058	0.025
ipsi38	0.98	9.18	5.87	8.57	0.058	0.024

[a] Curvature = minor axis / major axis reach trajectory (see Figure 1c)

FIGURE LEGEND

Figure 1 Experimental (**a**) and postural (**b**) configurations with finger kinematic (**c**) and muscle (**d**) variables used in the current experimental study. **a**. Participants were instructed to reach to a remembered target position in space that aligned with one of five visual targets projected onto a wall-mounted screen. Targets were placed at two eccentricities (23° and 38°) on either side (contralateral and ipsilateral) of a central midline target (0°). **b**. Four postural configurations were assessed where participants either remained seated (SIT) or in one of three standing postures: feet a natural width apart (STAND), feet together (NARROW) or standing atop a reduced base of support (BEAM) **c**. Example of finger velocity and trajectory profile highlighting measures of finger kinematics accuracy calculated in the current study. **d**. Muscle onsets relative to light onset were determined if activity rose beyond 2 SD of the mean activity in the 500 ms preceding light onset (e.g. dashed line, asterisk).

Figure 2 Individual finger trajectories, velocity profiles (**a**), and finger accuracy distributions (**b**) for all participants (n = 11). **a**. Semicircle surrounding each set of trajectories represents 100% of reach distance. Virtual target positions (ellipse) are presented with contralateral targets to the left, and ipsilateral targets on the right of each panel. Trials representing greater eccentricities (i.e. 38°) are shown in grey, while smaller eccentricities (23°) are shown in black. The distance at which peak finger velocity occurred across trials is shaded overlying all trajectories. For velocity profiles, traces with the maximum and minimum peak velocity are shown in black, with all other trials in grey. **b**. Finger accuracy distributions plotted for each starting postural configuration for all participants (n = 11). For each target, 95% confidence ellipses were constructed for comparison of precision across postural configuration (SIT: dotted; STAND: filled; NARROW: large dash; BEAM: small dash). Crosses denote the centre position of the virtual target. Trials representing greater eccentricities (i.e. 38°) are shown in grey, while smaller eccentricities (23°) are shown in black.

Figure 3 Centre of Mass (CoM) displacement profiles for all participants (n =11) across each postural configuration. For each postural configuration, CoM displacement at peak finger velocity (filled circle) and movement termination (cross) is highlighted for each individual trial. Clear changes in the dispersion of CoM excursion were evident at movement termination for postures. Sections in **a-d** were expanded for each individual direction of reach to allow visualization of displacement prior to movement onset (**e-h**). The transition between displacement during the preparatory postural adjustment (*p*PA) period and following movement onset is delineated by the change in colour of traces from black (*p*PA) to grey.

Figure 4 Centre of Mass (CoM) displacements calculated for four distinct kinematic phases of reach, the *p*PA phase (open), acceleration phase (light grey), deceleration phase (dark grey), and to movement termination (filled). Significant differences were seen where standing postures showed greater CoM excursions than sitting (‘*p*PA phase’). Both SIT and STAND configurations allowed for greater CoM displacement compared to NARROW and BEAM. Values denote medians for each period, while error bars represent IQR. # $p < 0.05$.

Figure 5 Mean muscle activity profiles for the preparatory postural adjustment period (*p*PA) of selected postural muscles across four starting postural configurations for a single subject (S03). Muscle activity was evident in the 250 ms preparatory period (*p*PA: black, dashed) prior to finger movement initiation (black, solid) at time = 0. For each muscle, reaching movements to the ipsilateral target (grey) are positive whilst movements in the direction of the corresponding contralateral target (black) have been inverted for ease of comparison. Muscle naming conventions can be found within the Methods section of the text. All traces are represented by mean values (solid) ± 1 standard deviation (shaded).

Figure 6 Pooled spatial tuning curves for each epoch of the pPA period (n = 11) and the primary component (PC1) identified through principal component analysis (PCA) of *p*PA5 across all postural configurations. Individually coloured lines within each muscle-posture pairing represents sequential 50 ms time bins in the 250 ms period preceding finger initiation (e.g., *p*PA1: -250 ms : -200 ms prior to finger initiation to *p*PA5: -50 ms : 0 ms prior to finger initiation). Direction-dependent activity is seen for a number of muscles with evidence of similar tuning curves across postural configurations. *p*PA1 = black; *p*PA2 = dark blue; *p*PA3 = light blue; *p*PA4 = green; *p*PA5 = magenta) For PC1 (derived from *p*PA5), tuning curves that showed a directional preference for contralateral targets are represented in black, while curves with a preference for ipsilateral targets are in grey. Curves highlighted in blue represent tuning that was centrally biased. The total percentage of variability accounted for (VAF) provides a measure of similarity for spatial tuning across postural configurations. VAF measures denoted by an * represent PC2 tuning curves in blue for TA. Muscle naming conventions can be found within the Methods and Abbreviations sections of the text.

Figure 7 Spatial characterisation of muscle co-contraction indexes across the lower limb and trunk for each postural configuration prior to movement onset (pre-Fon) and movement termination (pre-Fend). Lines represent median changes across postural configurations (SIT – grey, STAND – blue, NARROW – red, BEAM – purple).

Figure 8 Boxplot distribution of muscle activation latencies with respect to finger initiation for the SIT (**a**), STAND (**b**), NARROW (**c**) and BEAM (**d**) postural configurations. Mean muscle activation (black line) for a number of muscles occurred during the *p*PA period (left of finger onset, dashed line). Medians are bounded by measures of the IQR (red) for movements to contralateral and ipsilateral targets respectively. Common timing can be seen for muscle activations of a particular muscle across postural configurations. Muscle naming conventions can be found within the Methods and Abbreviations sections of the text.

Figure 9 Comparison of coefficients of determination (r^2) for relationships of individual muscle activations with respect to stimulus (i.e., light onset) and movement onset. The reference line (dashed) indicates r^2 values that were identically correlated with both stimulus and movement, with values to the left favouring stimulus onset (shaded) and those to the right favouring movement onset. Regardless of posture (SIT: circle; STAND: square; NARROW: triangle; BEAM: cross) or direction of reach (contra = black; ipsi = grey), relationships tended to be more strongly aligned to movement rather than stimulus onset.

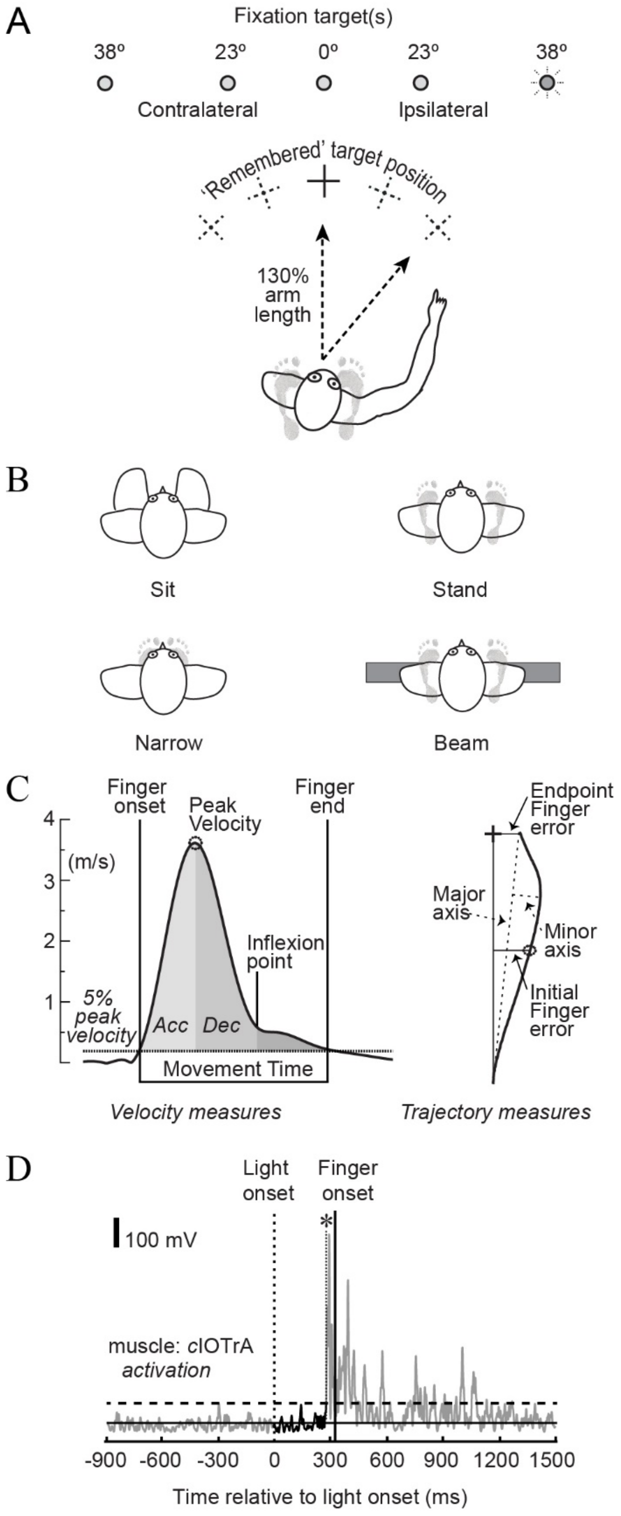
A
Fixation target(s)
38º
23º
0º
23º
38º
Contralateral
Ipsilateral
'Remembered' target position
130% arm length
B
Sit
Stand
Narrow
Beam
C
Finger onset
Peak Velocity
Finger end
4
(m/s)
3
2
1
Inflexion point
5% peak velocity
Acc
Dec
Movement Time
Velocity measures
Endpoint Finger error
Major axis
Minor axis
Initial Finger error
Trajectory measures
D
Light onset
Finger onset
*
100 mV
muscle: cIOTrA activation
-900
-600
-300
0
300
600
900
1200
1500
Time relative to light onset (ms)

FIGURE 1

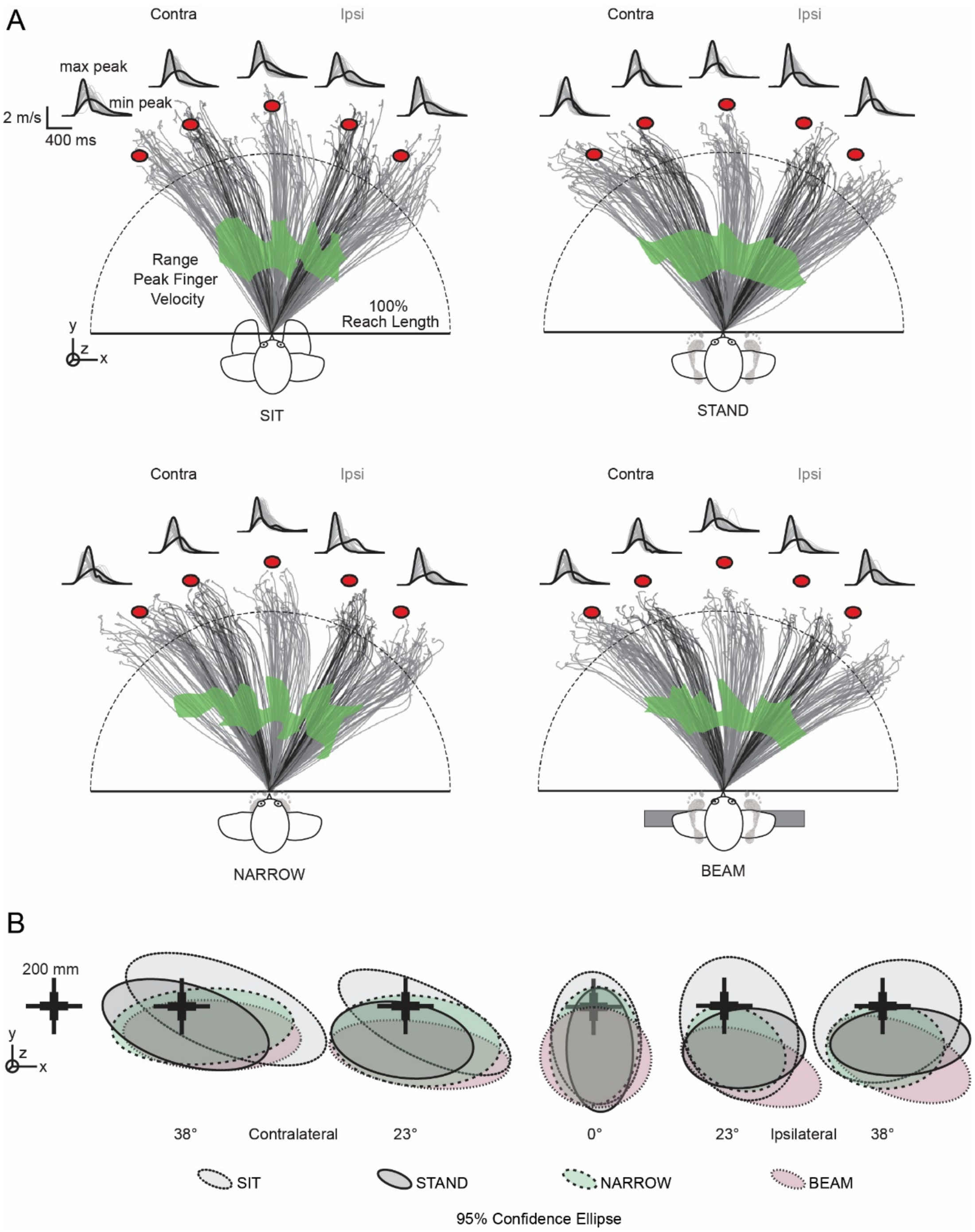
A
Contra
Ipsi
max peak
min peak
2 m/s
400 ms
Range
Peak Finger
Velocity
100%
Reach Length
y
z
x
SIT
STAND
NARROW
BEAM
B
200 mm
y
z
x
38°
Contralateral
23°
0°
23°
Ipsilateral
38°
SIT
STAND
NARROW
BEAM
95% Confidence Ellipse

FIGURE 2

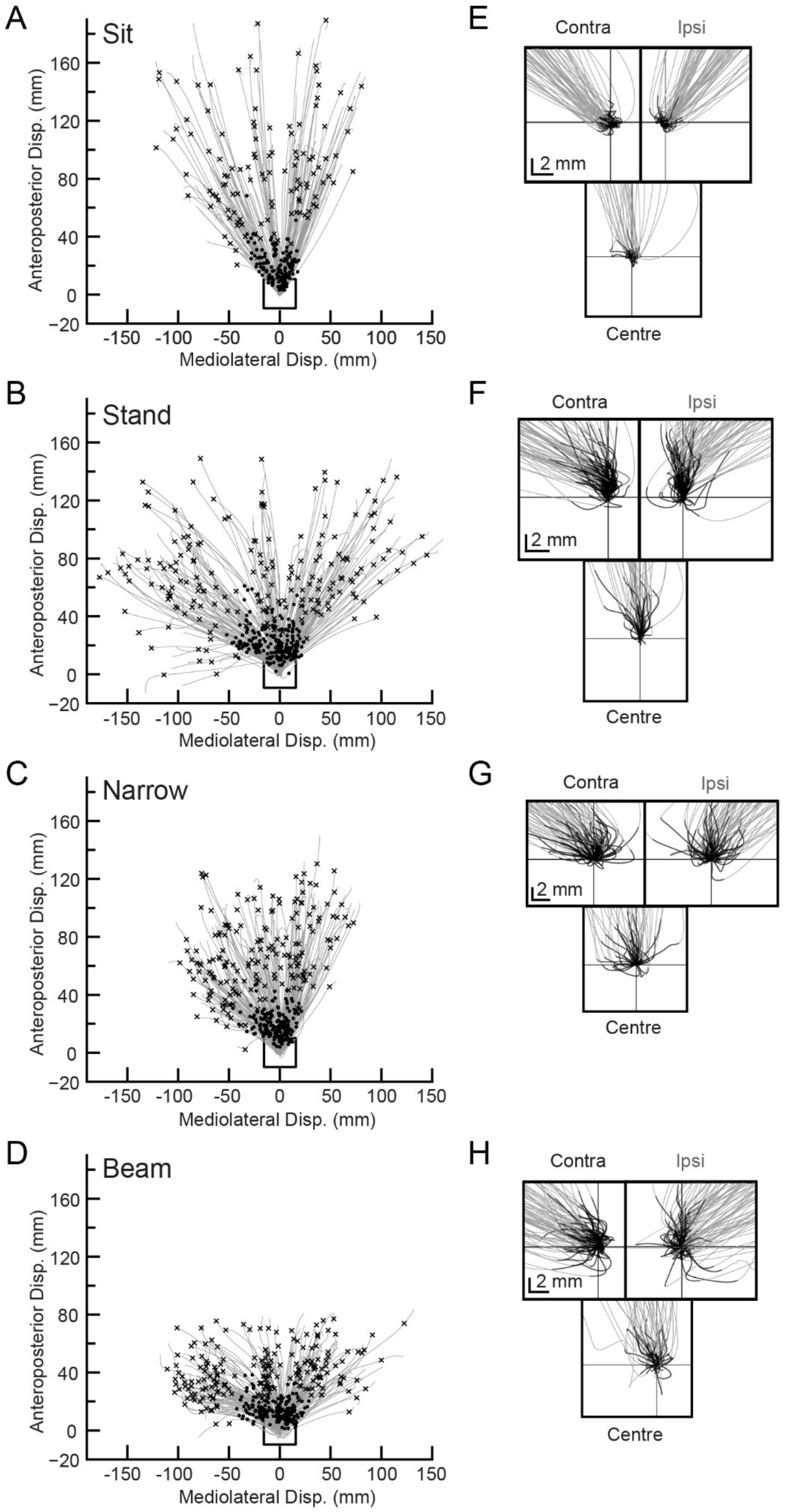
A
Sit
Anteroposterior Disp. (mm)
160
120
80
40
0
−20
-150
-100
-50
0
50
100
150
Mediolateral Disp. (mm)
E
Contra
Ipsi
2 mm
Centre
B
Stand
Anteroposterior Disp. (mm)
160
120
80
40
0
−20
-150
-100
-50
0
50
100
150
Mediolateral Disp. (mm)
F
Contra
Ipsi
2 mm
Centre
C
Narrow
Anteroposterior Disp. (mm)
160
120
80
40
0
−20
-150
-100
-50
0
50
100
150
Mediolateral Disp. (mm)
G
Contra
Ipsi
2 mm
Centre
D
Beam
Anteroposterior Disp. (mm)
160
120
80
40
0
−20
-150
-100
-50
0
50
100
150
Mediolateral Disp. (mm)
H
Contra
Ipsi
2 mm
Centre

FIGURE 3

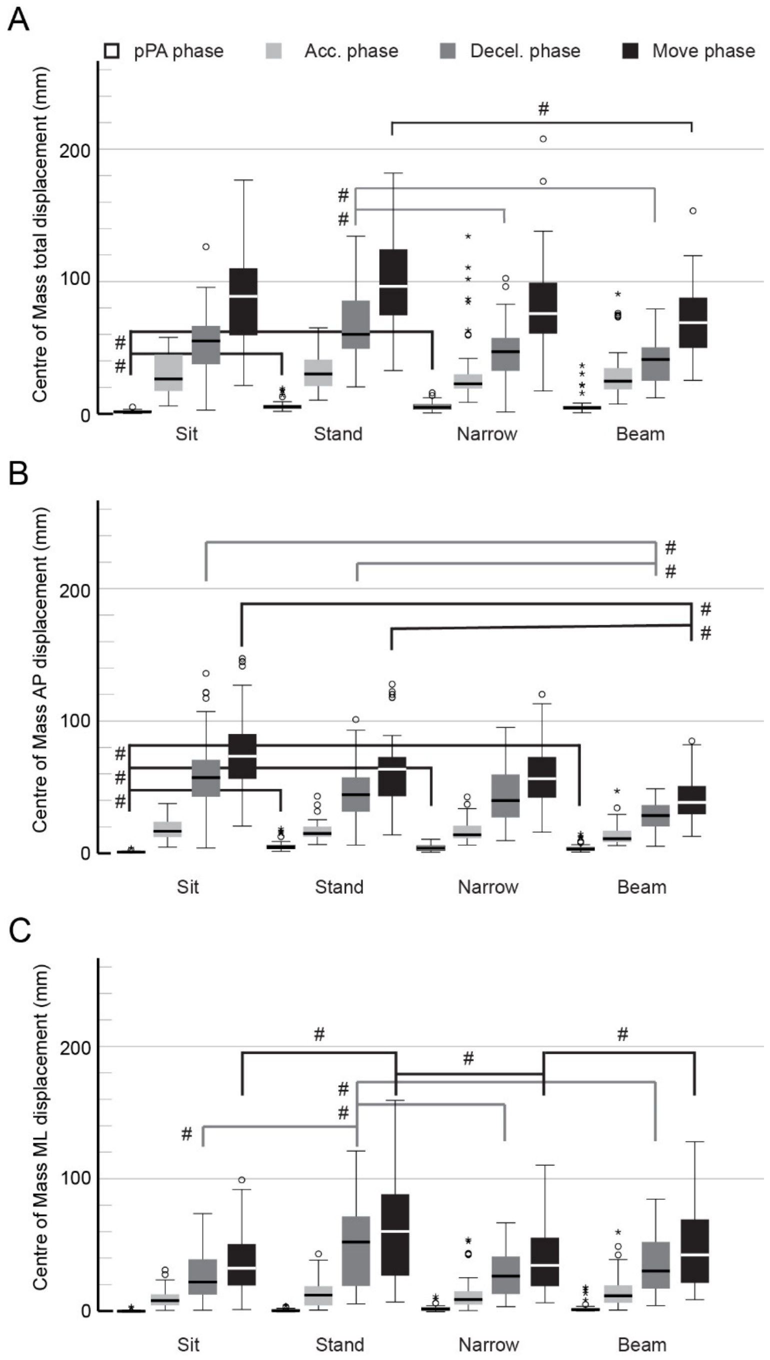
A
pPA phase
Acc. phase
Decel. phase
Move phase
Centre of Mass total displacement (mm)
0
100
200
#
Sit
Stand
Narrow
Beam
B
Centre of Mass AP displacement (mm)
0
100
200
#
Sit
Stand
Narrow
Beam
C
Centre of Mass ML displacement (mm)
0
100
200
#
Sit
Stand
Narrow
Beam

FIGURE 4

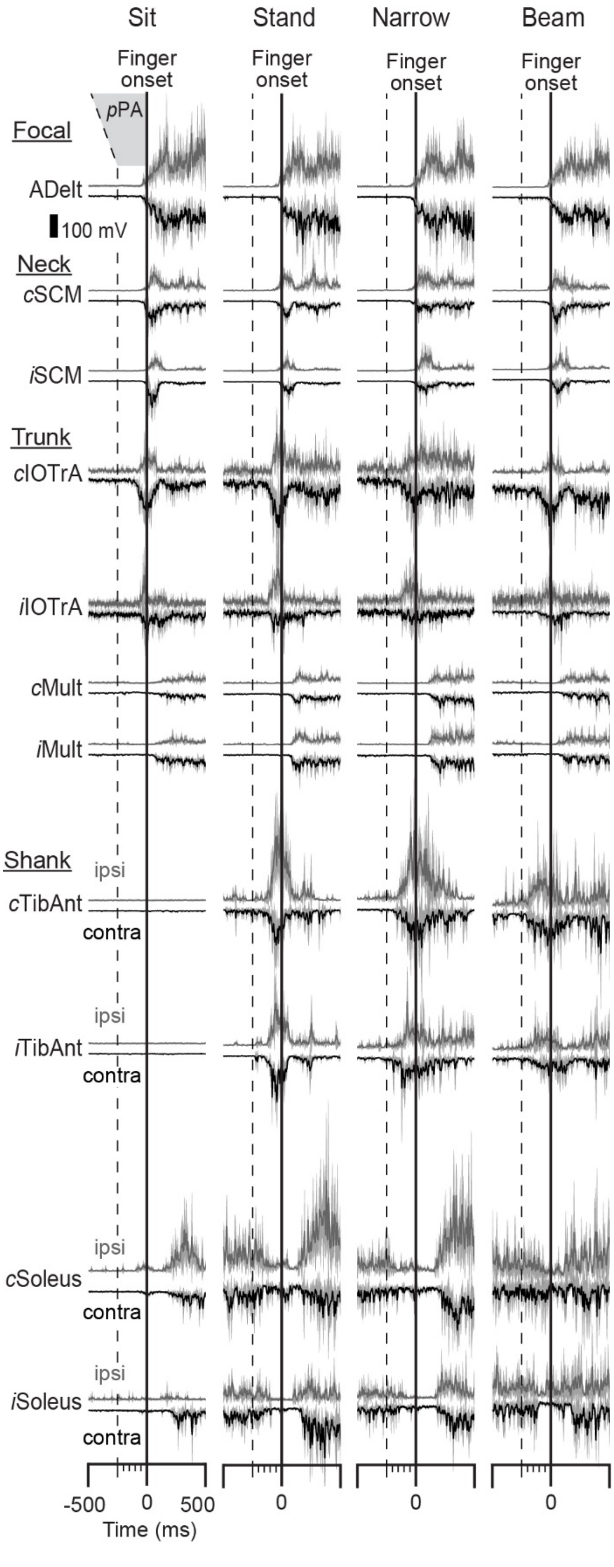
Sit
Stand
Narrow
Beam
Finger onset
Finger onset
Finger onset
Finger onset
pPA
Focal
ADelt
100 mV
Neck
cSCM
iSCM
Trunk
cIOTrA
iIOTrA
cMult
iMult
Shank
ipsi
cTibAnt
contra
ipsi
iTibAnt
contra
ipsi
cSoleus
contra
ipsi
iSoleus
contra
-500
0
500
0
0
0
Time (ms)

FIGURE 5

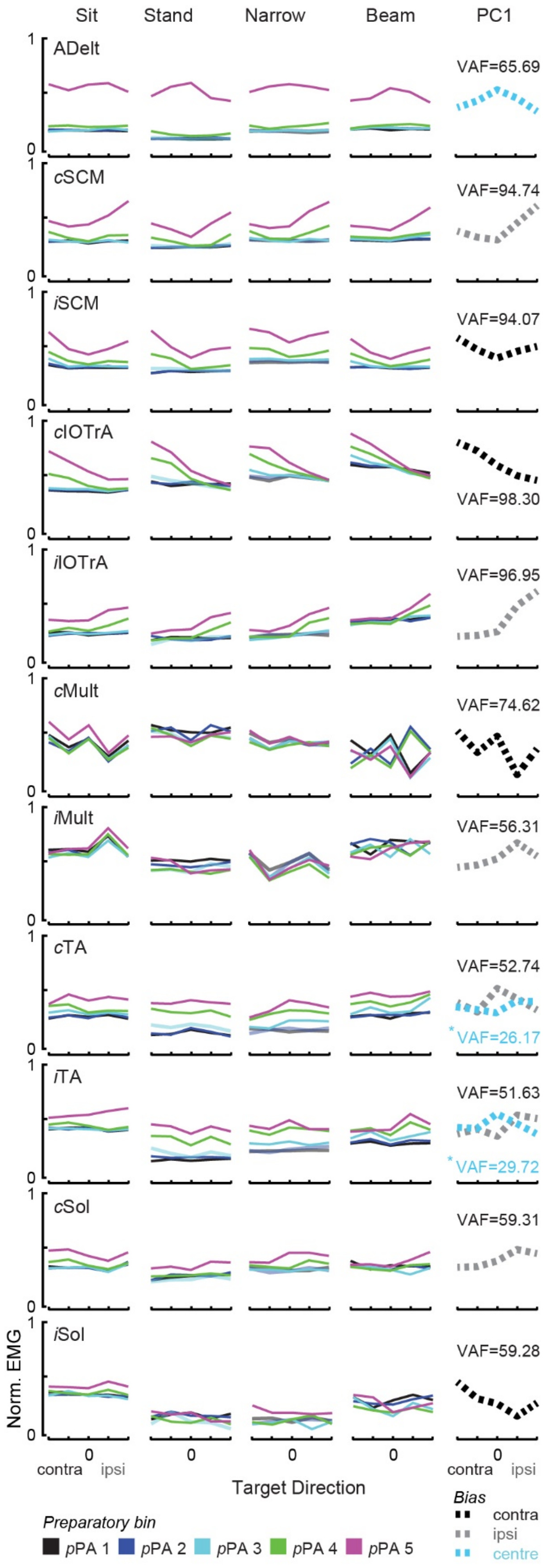
Sit
Stand
Narrow
Beam
PC1
ADelt
VAF=65.69
cSCM
VAF=94.74
iSCM
VAF=94.07
cIOTrA
VAF=98.30
iIOTrA
VAF=96.95
cMult
VAF=74.62
iMult
VAF=56.31
cTA
VAF=52.74
*VAF=26.17
iTA
VAF=51.63
*VAF=29.72
cSol
VAF=59.31
iSol
VAF=59.28
1
0
Norm. EMG
0
contra
ipsi
Target Direction
Preparatory bin
pPA 1
pPA 2
pPA 3
pPA 4
pPA 5
Bias
contra
ipsi
centre

FIGURE 6

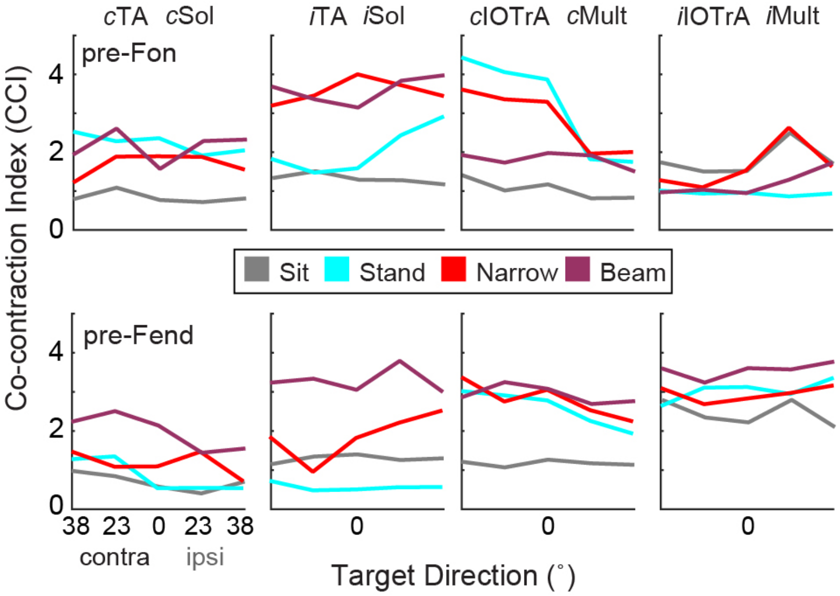
cTA cSol
iTA iSol
cIOTrA cMult
iIOTrA iMult
pre-Fon
pre-Fend
Co-contraction Index (CCI)
0
2
4
Sit
Stand
Narrow
Beam
38
23
0
23
38
contra
ipsi
0
0
0
Target Direction (˚)

FIGURE 7

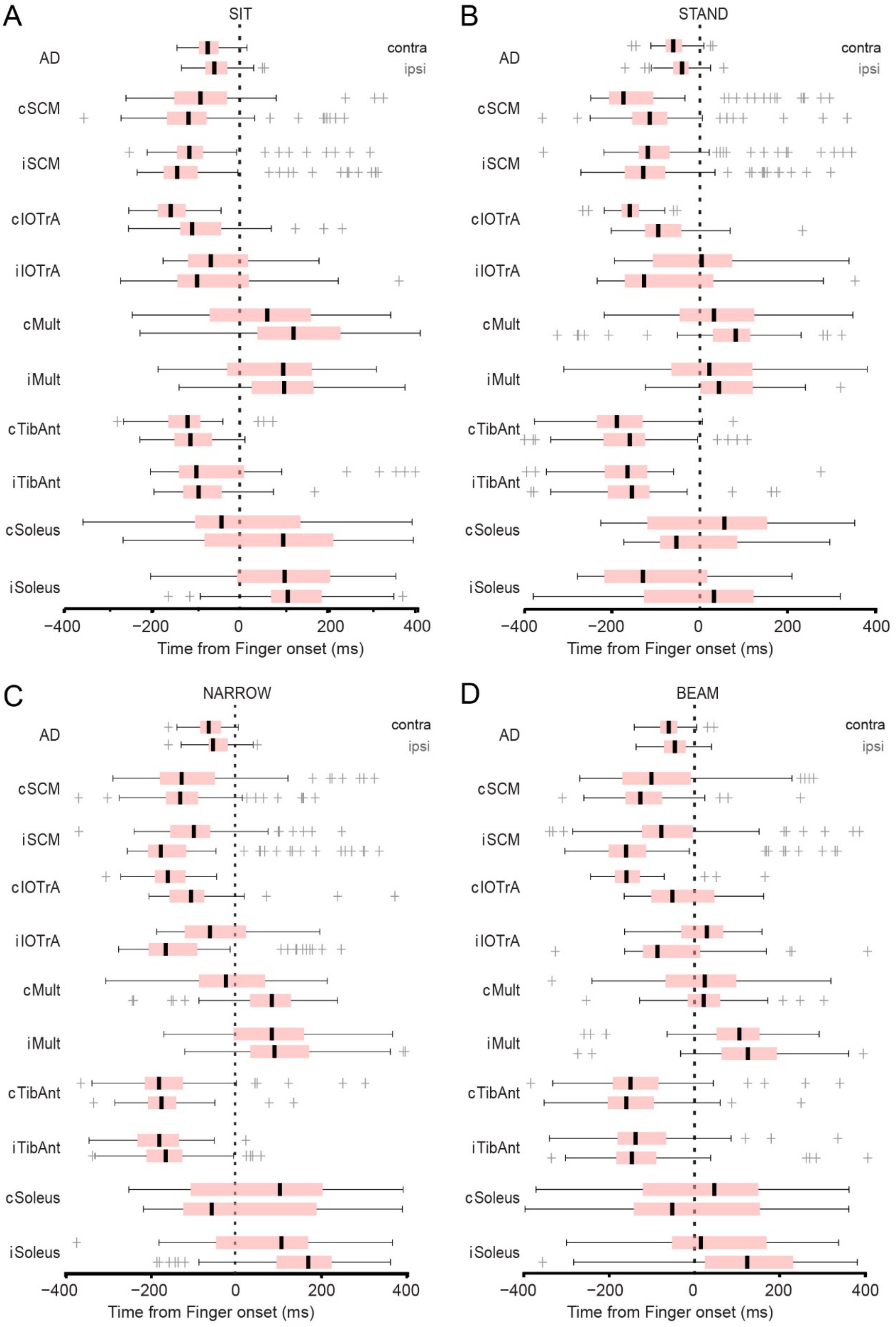
A
SIT
B
STAND
AD
cSCM
iSCM
cIOTrA
iIOTrA
cMult
iMult
cTibAnt
iTibAnt
cSoleus
iSoleus
contra
ipsi
−400
−200
0
200
400
Time from Finger onset (ms)
C
NARROW
D
BEAM

FIGURE 8

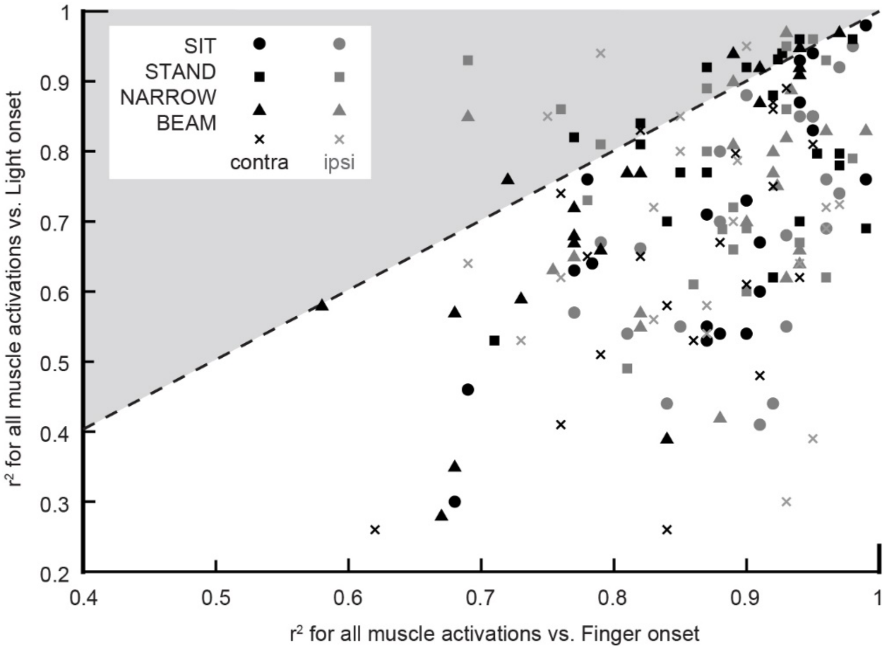
SIT ● ●
STAND ■ ■
NARROW ▲ ▲
BEAM × ×
contra
ipsi
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.4
0.5
0.6
0.7
0.8
0.9
1
r² for all muscle activations vs. Light onset
r² for all muscle activations vs. Finger onset

FIGURE 9