Stamenkovic, A, Stapley, P, Robins, R and Hollands, MA

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DO POSTURAL CONSTRAINTS AFFECT EYE, HEAD AND ARM COORDINATION?

Alexander STAMENKOVIC[1,2]
Paul J. STAPLEY[1,2]
Rebecca ROBINS[3]
Mark A. HOLLANDS[3]

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

[2] Illawarra Health & Medical Research Institute (IHMRI), Gerard Sutton Building
University of Wollongong
Northfields Avenue
Wollongong NSW 2522, AUSTRALIA

[3] 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

Address of corresponding author:
Mr. Alexander STAMENKOVIC
School of Medicine
Faculty of Science, Medicine & Health
University of Wollongong
Northfields Avenue
Wollongong NSW 2522
AUSTRALIA
Tel: +61-(02)-4221-4584
Fax: +61-(02)-4221-5945
Email: astamenk@uow.edu.au

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ABSTRACT

If a whole-body reaching task is produced when standing or adopting challenging postures, it is unclear whether changes in attentional demands or the sensorimotor integration necessary for balance control influence the interaction between visuomotor and postural components of the movement. Is gaze control prioritized by the CNS to produce coordinated eye movements with the head and whole-body regardless of movement context? Considering the coupled nature of visuomotor and whole-body postural control during action, this study aimed to understand how changing equilibrium constraints (in the form of different postural configurations) influenced the initiation of eye, head and arm movements. We quantified the eye-head metrics and segmental kinematics as participants executed either isolated gaze shifts or whole-body reaching movements to visual targets. In total, four postural configurations were compared: seated, natural stance, with the feet together (narrow stance), or while balancing on a wooden beam. Contrary to our initial predictions, the lack of distinct changes in: eye-head metrics, timing of eye, head and arm movement initiation, and gaze accuracy, in spite of kinematic differences, suggests that the CNS integrates postural constraints into the control necessary to initiate gaze shifts. This may be achieved by adopting a whole-body gaze strategy that allows for the successful completion of both gaze and reaching goals.

NEW AND NOTEWORTHY

Differences in sequence of movement between the eye, head and arm have been shown across various paradigms during reaching. Here we show that distinct changes in eye characteristics and movement sequence, coupled with stereotyped profiles of head and gaze movement are not observed when adopting postures requiring changes to balance constraints. This suggests that a whole-body gaze strategy is prioritized by the CNS with postural control subservient to gaze stability requirements.

KEYWORDS: visuomotor; eye head arm coordination; posture; balance; reach

INTRODUCTION

For visually-guided reaching, the central nervous system (CNS) must integrate visual, vestibular and proprioceptive sensory signals to produce an effective movement involving the eyes, head, body and the arm. For this, the CNS must consider well-established relationships between the eye-head, eye-arm and whole-body postural control. For example, reflexive mechanisms of eye-head control (in particular, the vestibulo-ocular reflex, VOR) are used to reduce retinal slip and maintain foveal vision, yet must be complemented by destabilizing gaze shifts (the combination of eye and head displacement in space) for the rapid fixation of stimuli that lie in the peripheral visual field. Such gaze shifts allow for accurate target foveation, underpinning mechanisms of eye-arm coordination including the necessary spatial transformation of stimuli from visual (eye-centered) coordinates into an appropriate frame of reference for movement to be initiated (e.g. body-centered, arm-centered or an intermediary coordinate reference frame – Crawford et al., 2004). When reaching is executed during standing, eye, head and limb coordination depends on the CNS providing a stable postural base.

Vision can also play a role in postural stability, although the precise mechanisms remain unclear (Guerraz and Bronstein, 2008). Initially, the retinal slip induced by postural sway (a central vision process) was thought to be the primary mechanism (Paulus et al., 1984). However, recent evidence has pointed to a greater role of proprioceptive extra-retinal signals, acting either through reafference or efference copy of extra-ocular motor signals (Glasauer et al., 2005; Guerraz and Bronstein, 2008; Strupp et al., 2003). Despite the general acceptance that vision impacts postural stability, whether postural demands can have a reciprocal effect upon vision, and more specifically, the execution of gaze shifts, is less clear. For example, when the head is stable vestibular signals encode movement of the body (as a function of postural sway) rather than head on body movements. These signals can be utilized for postural control (Strupp et al., 2003) with the maintenance of eye position (and visual stability) occurring via VOR. However, if postural instability is present in addition to an active head movement (much like during activities of daily living), eye-head stabilizing mechanisms such as the VOR are likely to interfere with the production of a correct gaze response (Daye et al., 2014; Haji-Abolhassani et al., 2016). Therefore, integration of whole-body posture with active eye and head movements must be required to ensure the timing of individual segment rotations provides accurate gaze shifts.

Research on visuomotor coordination has been predominantly restricted to the seated position, dramatically reducing any impact of postural instability on arm or gaze control. From this, two main theories of gaze control have been proposed: the first involves gaze being driven by feedback-mediated signals derived from a shared gaze motor error (Boulanger et al., 2012; Guitton et al., 2003), while the second proposes that feedback-mediated signals for the eye and head are modulated independently (Freedman and Sparks, 1997; Phillips et al., 1995). The latter has attempted to account for the changes that occur in the ‘main sequence’ characteristics of saccades when unrestrained head movements are incorporated into gaze (see Freedman, 2008). When gaze has been examined under greater freedom of movement (e.g. unrestrained whole-body movements such as turning), a top-down approach encompassing a coordinated whole-body contribution to gaze shift is observed (Anastasopoulos et al., 2015; Hollands et al., 2004; Scotto Di Cesare et al., 2013; Sklavos et al., 2008). Through scaling of head-in-space velocity gaze shifts are hypothesized to be driven by a separate head displacement controller in such conditions (Anastasopoulos et al., 2015). While the CNS is able to simplify this control through kinematic synergies (Anastasopoulos et al., 2009), a consequence is a subsequent delay in gaze shift initiation when posture is altered (Scotto Di Cesare et al., 2013). Such delays are suggested to allow additional time to incorporate anticipatory postural adjustments (APAs) and to reconcile more moving segments into the motor program (e.g. seated vs. standing axial rotations - Scotto Di Cesare et al., 2013).

If head-free gaze control comprises a separation of eye and head signals during whole-body movement then there lies a possibility that the addition of postural constraints and an arm movement could alter a preference for eye-head, eye-arm or head-arm coordination. Such is found when the sequence of eye, head and arm onsets are examined under a variety of experimental conditions (eye-head: Fuller, 1992; Zangermeister and Stark, 1982; eye-head-arm: Carnahan and Marteniuk, 1991; Pelz et al., 2001; Smeets et al., 1996). During coordinated reaching, modifications to this sequence are thought to reflect the reorganization of supraspinal postural control mechanisms (and a corresponding rise in corticospinal activity) associated with incorporating the arm movement (Herman et al., 1981). Whether altering posture and the requirement to incorporate balance delays the goals of target fixation and accompanying arm movement, or manifests itself through a dissociation of the eye and head movement for a more preferential head-arm coordination strategy seen during goal-directed reaching (Pelz et al., 2001) is unclear. Similarly, additional reliance on sensory drive associated with changes to posture may result in the release of pre-planned saccadic responses. This ensures that fixation occurs swiftly, allowing vision (and extra-retinal signals) to assist in postural control (Pacquette and Fung, 2007). Examples of this facilitation in saccade initiation are seen when performed during external perturbation (Pacquette and Fung, 2007) and in some instances, where reaching has been shown to reduce the onset latency of saccadic eye movements (Bekkering et al., 1994; Dean et al., 2011; Snyder et al., 2002).

Postural demand may also influence eye-head-arm coordination through the competition of attentional resources. Attention is important for the control of saccades (Kowler, 2011), and decrements in maintaining posture (e.g. an increase in postural sway) during dual-task paradigms suggest that re-allocation of attentional resources may be essential for balance control (Kerr et al., 1985; Lajoie et al., 1993). Importantly, regions within the posterior parietal cortex are associated with both spatial attention and reach planning, including the spatial transformation of a target from eye to arm centered coordinates (Crawford et al., 2004). If the cognitive control of balance increases with additional stability constraints (Kerr et al., 1985; Lajoie et al., 1993), these may manifest themselves in the production of eye movements. For example, increased eye onset latency may reflect changes akin to those seen when cognition is required for correct saccade production (e.g. during an anti-saccade task - Munoz and Everling, 2004). Further downstream, supraspinal centers within the brainstem integrate both descending and ascending signals during voluntary reaching (Schepens et al., 2008; Stapley et al., 2010) and other postural activities (Inglis et al., 1994; Stapley and Drew, 2009). In fact, specific nuclei of the reticular formation (pontine nucleus *pars* caudalis and *pars* oralis) are known to house neurons of the saccadic burst generators (e.g. short latency excitatory burst neurons - Haji-Abolhassani et al., 2016) and those which are modulated in the control of posture and movement (Schepens et al., 2008). These neuronal populations are responsible for the initiation of gaze shifts and are heavily linked to the production of feed-forward driven APAs (Sakai et al., 2009; Schepens and Drew, 2004). Therefore, by altering postural configuration for simple gaze shifts and coordinated whole-body reaching movements, we aimed to assess the role of posture upon the timing and sequence of eye, head and arm initiation. We predicted that if postural instability required greater sensorimotor integration, or resulted in the addition of attentional demands prior to movement initiation, such actions would delay the onset of the eye, head and arm until the postural component was rectified. Alternatively, if vision was required to assist postural control, the initiation of gaze shifts would be facilitated to ensure a rapid re-anchoring of gaze.

METHODS

Participants

Eleven healthy participants (8 male, 3 female; age: 24.3 ± 2.2 years), with normal (or corrected to normal) vision, and without any known neurological or orthopedic impairments were recruited from the Liverpool John Moores University student population. Participants gave their informed consent for all experimental procedures and local institutional ethical approval (14/SPS/021) was granted in accordance with the Declaration of Helsinki (1975). Hand dominance was self-reported with four of the 11 participants identifying as left-handed. All measures of direction are therefore reported in relation to the dominant (i.e. reaching) arm.

Experimental apparatus & configuration

The experimental configuration is shown in Figure 1a. Participants stood barefoot facing a blank screen on which five circular targets (diameter: ~3°) were projected. Targets were positioned at an eccentricity of 23° and 38° on either side of a central target situated 2.35m away from the participant. As the aim of this study was to assess the impact of different postural configurations on eye, head and arm sequencing, we asked participants to reach to a practiced and remembered distance in space as opposed to a physical target that may have provided support upon movement termination. Indeed, the effect of even light touch on balance is well documented (Clapp and Wing, 1999; Jeka, 1997) and so prior knowledge of a physical target could have influenced movement preparation strategies. The practiced target distance corresponded to 130% of each participant's outstretched arm length (measured from the xiphoid process to the tip of the reaching index finger, with the shoulder in neutral scapular retraction and arm extended), a distance adopted as it involves a significant postural component without placing a person beyond their limit of stability (Leonard et al. 2009).

A familiarization procedure for reaching to the practiced target distance was conducted on two separate occasions. Feedback was given during an initial anthropometric measurement and familiarization session the day before data collection and preceding each block of recorded postural trials during the main experimental period. A minimum of 5 reaching trials were conducted for each direction during the initial familiarization period and prior to the experimental recording period to ensure a whole body reaching movement was produced. No feedback was given relating to the accuracy of eye, head or arm movement with respect to the target eccentricity.

Three-dimensional kinematics were recorded using an 8 camera Bonita motion capture system (Vicon, Oxford, U.K) sampling at 200 Hz. Thirty-nine passive retro-reflective markers were attached to distinct anatomical landmarks as detailed in the Vicon "Plug-in-Gait" model. Horizontal eye movements were recorded using a wireless electrooculography (EOG) system (Bluegain, Cambridge Research Systems, U.K) sampling at 1,000 Hz. Silver/silver chloride (Ag/AgCl) electrodes (Neuroline 700, Ambu®) were aligned with the outer canthus of each eye and a ground electrode was positioned centrally on each participant's forehead. Target illumination parameters and synchronization signals for both EOG and Vicon data streams were controlled by a customized program written in LabVIEW (National Instruments, Austin, TX). The customised program delivered a 5V pulse that was recorded by the EOG system and activated an infrared strobe light visible within the motion capture volume to allow for synchronization of kinematic data with recorded EOG signals.

Experimental procedures

All target positions were visible throughout the experimental protocol and participants began by fixating upon the central target. They were asked to either look in the direction of a target that became illuminated on the screen ('LOOK' trials) or make a reaching movement with the dominant arm ('REACH' trials) under four separate postural configurations: 1) 'SIT', 2) 'STAND', 3) 'NARROW' stance, and 4) 'BEAM' (Fig. 1b). The order of task conditions (REACH vs. LOOK) within each postural configuration block was pseudo-randomized. Additionally, the order of postural configurations were also randomized between participants to nullify any differences due to blocked experiential learning.

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 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 center 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 antero-posterior plane.

For all conditions, trials began with the index finger of the reaching arm touching the xiphoid process and the shoulders parallel to the projection screen. The position of visually projected targets was adjusted to eye-level for all postural configurations with the center of the sternum aligned with the central target (see Fig. 1a). Initial quiet stance was monitored visually and stable eye position was checked using the real-time EOG signal. Participants were instructed about the type of upcoming trial ('LOOK' or 'REACH') just prior to trial onset. After a random time delay of 500 to 2000 ms, a target light illuminated and participants either reached or looked to the illuminated fixation target. For REACH trials, participants were instructed to move at a natural pace and to maintain the index finger at the perceived end point until instructed to return to the initial position. No other instructions were given as to how the movement should be conducted. A collection period totaling 5s captured all relevant data within each trial. Five repetitions for 'LOOK' and 'REACH' conditions were recorded for each target direction (including the central target), plus an additional 10 trials, for which no target illuminated (n = 50 trials + 10 'catch' per postural configuration). This reduced the possibility that movements were initiated before light onset. To counteract any fatiguing effects of the procedure, participants received 5 min rest periods between configuration-blocks.

Data analysis

All analyses were completed offline using customized scripts created within the MATLAB environment (ver. R2013b, The Mathworks, Natick, MA). Kinematics were low-pass filtered using a dual-pass second order Butterworth algorithm at 20 Hz. In line with eye position recordings during whole-body movement (Anastasopoulos et al., 2009; Scotto Di Cesare et al., 2013), eye position data was low-pass filtered with a 5th order polynomial Savitzy-Golay algorithm used to conserve the higher frequency aspects of the initial acceleration of the eye movement.

EOG calibration and movement onsets. Calibration of raw eye signals to a horizontal Eye-in-Head angular position was carried out using the vestibular-ocular reflex mechanism and was undertaken prior to each postural configuration block. Briefly, the head was rotated through a field of ± 30 - 40° while participants maintained visual fixation upon the central target. As the gain between the head movement and compensatory eye movements during the VOR is close to 1, a linear regression of the EOG signals (recorded as a change in voltage) and Head-in-space position (recorded as a change in angular displacement via kinematics) can be used to convert the analog EOG recording to an Eye-in-Head position (in degrees). The calculated regression coefficient (i.e. slope) can then be used to determine Eye-in-Head position during experimental trials (Hollands et al., 2004; Reed-Jones et al., 2009). When combined with Head-in-space position, a measure of gaze location (or, Eye-in-Space position) could be deduced. Figure 1c illustrates the absolute ('in-space') and relative ('on-Segment') segment angular rotations calculated for the eye, head, trunk and pelvis.

Eye onset was determined using an angular velocity threshold of 30°/s (Daye et al., 2014; Pélisson et al., 2001). This was compared to other velocity measures (e.g. 20°/s, 3% and 5% peak eye velocity) with minimal variation in onset detection (average difference = 2 ms). A velocity threshold of 15°/s was applied to determine head onset (Daye et al., 2014). All onsets were confirmed or adjusted based upon visual inspection of their respective position profiles (Teasdale et al., 1993). Trials with eye onsets which occurred within 100 ms from target illumination or after 800 ms were removed from further analysis (Munoz et al., 1998); this equated to the exclusion of ~4.8% of all trials, which closely aligned with a previous report for adult saccade latencies (Yang et al., 2002). Eye metrics including peak velocity and duration of the initial saccade, as well as its total contribution to the amplitude of gaze shift and final gaze accuracy (i.e. the gaze gain ratio, where values less than 1 indicate hypometric gaze shifts) were quantified to determine if the main sequence of gaze shifts altered with postural instability. This was complemented by measures of head alignment (i.e. final head position) and its respective contribution to the total amplitude of gaze shift.

Key kinematic events relating to the arm component of the reaching movement (within the 'REACH' trials) were determined using the bell-shaped tangential velocity profile of the index finger due to the curvilinear nature of the trajectory seen throughout the movement. Five percent of the peak velocity was chosen as an onset threshold, with movement initiation being the first sample with a value that exceeded this threshold and movement termination being the first sample with a value that reduced below this threshold following the movement. This allowed for a robust measure of finger movement onset (Sainburg and Schaefer, 2004). Finally, as an index of postural instability, head sway (or the mean standard deviation of head displacement) was calculated in the antero-posterior and medio-lateral axes for the time course of trials in which no active movement was required (i.e. central target, 'LOOK' condition).

Statistical analysis

Statistical analyses were conducted using the SPSS statistical package (ver. 21, IBM, OR, USA) or within the MATLAB environment (ver. R2013b, The Mathworks, Natick, MA). Data were assessed for normality using Shapiro-Wilk testing. Eye onsets were positively skewed and subsequently inversely transformed for all statistical analyses. It is well established that amplitude (or the absolute eccentricity of eye movements) influences eye-head metrics and was not a primary interest in this study; therefore, the dataset was split to compare all 38° and 23° degree trials. Eye-head metrics were examined using a 2x4x2 design repeated measures ANOVA (TASK x POSTURE x TARGET). For reaching trials, differences between postural configuration and direction of movement were analyzed using a 4x2 repeated measures ANOVA (POSTURE x TARGET). Greenhouse-Geisser adjustments to the degrees of freedom were used if violations of sphericity were observed. Additionally, to control for the potential increase in the familywise error rate present in undertaking multiple ANOVAs on related variables (e.g. eye-head metrics, kinematics), all reported *p*-values for main effects and interactions were adjusted using the sequential Bonferroni method (i.e. Bonferroni-Holm correction) before further post-hoc testing (Cramer et al., 2016). For effects and interactions that remained significant following the adjustments above, post-hoc analyses were conducted using pairwise comparisons with Bonferroni's adjustment.

Correlations between onsets for the eye-head, eye-finger and, head-finger were examined using a Type II major axis regression to account for the independent error within each measurement (when compared to the ordinary least squares regression - Smith, 2009). To test whether particular relationships between movement onsets (i.e. eye-head, eye-finger, head-finger) changed as a function of posture and direction (i.e. co-varied on a trial-by-trial basis), significance testing was undertaken on correlation and regression coefficients (i.e. slope). Coefficients were first normalized using Fisher's *z*-transformation, with the difference between *z*-transformed coefficients compared to a critical Z-score (Suzuki et al., 2008; Weaver and Wuensch, 2013). To account for multiple comparisons, Bonferroni adjustments were applied (such that $Z_{crit} = 3.20$, $p < 0.0007$) prior to significance being calculated according to the following formula:

$$Z_{calc} = \frac{Z_1 - Z_2}{\sqrt{\frac{1}{n_1 - 3} + \frac{1}{n_2 - 3}}}$$

$|Z_{calc}| < |Z_{(crit)}|$, H_0 accepted

RESULTS

While gaze shifts requiring both eye and head involvement were to be expected from both target eccentricities (Gresty, 1974), during the initial stages of analysis it became evident that the incorporation of a head movement into the gaze shift was not always produced. In fact, a purely saccadic eye movement was the primary strategy adopted by 3/11 participants for movements to the smaller eccentricity of 23° during the LOOK condition. As conclusions relating to the question of coordination between eye, head and arm movement initiation could not accurately be assessed for these trials the following section will focus on results pertaining to movements occurring to the greater eccentricity 38° targets only (Fig. 1a), which always required a combined eye and head response (despite being within the upper range for pure saccadic eye movements). Interpretations relating to the change in strategy will be raised within the Discussion (see *Whole-body gaze strategy*).

Effect of postural constraint on head sway

Total (n = 11) head displacement (Figure 2a) and mean head displacement variability (i.e. head sway) in the antero-posterior (AP, see Figure 2b) and medio-lateral axes (ML, see Figure 2c) were calculated to assess the influence of postural constraints on static balance. Qualitatively, the area of the 95% confidence ellipses tended to increase between seated and standing postures (Figure 2a). For the SIT, STAND and BEAM conditions, the 95% confidence ellipses were skewed to show greater AP displacement, with the NARROW condition showing the greatest ML displacement. When head sway was analyzed across postures (Figure 2b,c), a main effect of POSTURE was seen in both the AP ($F_{(1.709,17.095)} = 28.594$, $p < 0.001$, $\eta_p^2 = 0.741$) and ML axes ($F_{(3,30)} = 25.692$, $p < 0.001$, $\eta_p^2 = 0.720$). The SIT condition consistently produced less sway in both axes when compared to all standing postures (AP axis: SIT vs. STAND, $p = 0.009$; vs. NARROW, $p < 0.001$; vs. BEAM, $p = 0.009$; ML axis: SIT vs. STAND, $p < 0.001$; vs. NARROW, $p = 0.001$; vs. BEAM, $p < 0.001$). Significantly greater mean head sway was also seen between standing postures in the AP axis (STAND vs. NARROW, $p = 0.001$; NARROW vs. BEAM, $p = 0.004$).

Qualitative features of eye, head and gaze movements across postural configurations.

Figure 3 represents mean angular displacements and velocities of the eye, head and gaze (i.e. combined eye and head angular displacements) for a single representative participant (S01) to the ipsilateral 38° target. Between postural configurations, eye, head and gaze profiles showed a stereotyped pattern of progression during the initial period of movement, between eye initiation and its termination at the new fixation position (see Fig. 3, ~450 ms after light onset). In both tasks (LOOK and REACH), the eye showed a counter-rotatory deviation following peak eye displacement that allowed for the maintenance of a consistent gaze position profile.

Influence of reaching movements on eye-head metrics

Eye metrics. Population results (n = 11 subjects) for measures of eye-head metrics including eye onset latency (Fig. 4a), peak eye velocity (Fig. 4b), saccade duration (Fig. 4c) and eye amplitude contribution to gaze (Fig. 4d) did not differ statistically across task (REACH vs. LOOK) or postural configurations (see Supporting Table 1). This was despite reaching movements to targets generally eliciting slightly longer eye latencies compared to LOOK trials (Fig. 4a), an exception being during ipsilateral reaching in the SIT and BEAM configurations (see Fig. 4a SIT and BEAM). Also, the slightly increased eye onsets observed in the contralateral and ipsilateral reaching trials of the NARROW and BEAM configurations coincided with decreases in peak eye velocity compared to the stable seated (SIT) and natural stance (STAND) configurations. However, this did not seem to influence the duration of the saccade (Fig. 4c with the exception of NARROW, which may be due to its greater variability) or the contribution of eye movement to total gaze displacement (Fig. 4d). In fact, eye metrics for ipsilateral gaze shifts (i.e. LOOK) were fairly consistent across postures with the greatest changes occurring with eye onset while contralateral gaze shifts showed decreases in peak eye velocity and contribution to gaze amplitude across the standing postures. Analysis of gaze gain ratio (gaze amplitude : target amplitude) for all participants (Fig. 5, n = 11) showed that gaze shifts remained within the 3° boundary of the visual target. Despite evidence of an increase in gaze gain between ipsilateral NARROW and BEAM gaze shifts and across DIRECTION within BEAM trials, the interaction between POSTURE and TARGET was not significant ($F_{(3,30)} = 3.452$, $p = 1$, $\eta_p^2 = 0.257$).

Head metrics. From Figure 3, a clear difference was identified for final head position between tasks (LOOK vs. REACH). During simple gaze shifts (LOOK), final head position did not show a complete rotation of the eyes to be centered within the orbit and tended to align with peak eye displacement. REACH trials showed a better alignment of the head with peak gaze displacement and the corresponding target with the eye returning to its original position centered within the orbit after approximately 500 ms from movement initiation (Fig.

3; right side panels). As such, final head position and the contribution of its displacement to gaze amplitude were quantified for all participants. Figure 6 represents the mean changes that occurred for head displacement variables between TASK and DIRECTION across postural configurations. Changes seen in the representative participant (Figure 3) were reflective of all participants as a three-way repeated-measures ANOVA (see Supporting Table 2) revealed a significant interaction between TASK and DIRECTION ($F_{(1,10)} = 5.293$, $p = 0.044$, $\eta_p^2 = 0.346$) with reduced head rotation occurring within the LOOK task (Fig. 6a). This was more prominent for shifts to contralateral targets (REACH vs. LOOK mean difference ~8.5°, $p = 0.009$) compared to ipsilateral targets (REACH vs. LOOK mean difference ~5°, $p = 0.091$). In a similar vein, a three-way repeated measures ANOVA revealed that the contribution of the head to the initial gaze shift changed as a function of TASK and DIRECTION ($F_{(1,10)} = 11.294$, $p = 0.007$, $\eta_p^2 = 0.529$) across conditions (Fig. 6b). On average, the head contributed an additional 1.3° to gaze when reaching to contralateral targets ($p = 0.016$).

Eye, head, trunk and pelvis kinematics across postural configurations

Figure 7 shows absolute and relative angular displacement profiles for the eye, head, trunk and pelvis during reaching movements for a representative participant (S01). Typically, differences in kinematics were most obvious when examined between directions (i.e. ipsi- vs. contralateral). In particular, the difference in end positions of eye and head interactions (Fig. 7, Eye-in-Head, Head-in-space) between ipsi- and contralateral movements allowed for the maintenance of final gaze position (Fig. 7, Eye-in-space). Also, axial segments contributed differently to the extent of reaching, with movement of the trunk and pelvis showing little displacement for ipsilateral targets. Trunk and pelvis motion during the SIT and STAND postural configurations was often counter-rotatory in nature (i.e. rotating in the opposite direction from the specified target), especially when compared to the NARROW and BEAM configurations. However, their relative movement (i.e. Trunk-on-Pelvis; see Fig. 7) remained consistent across postural configurations despite changes in trunk displacement (Fig. 7, Trunk-in-space). While segment movement profiles remained qualitatively similar between postures, differences in the amplitude of final positions (most of which are reflected in our representative participant, Fig. 7) were also evident when analyzing the entire cohort.

For absolute ‘in-space’ displacements, a two-way repeated measures ANOVA (see Supporting Tables 3 and 4) revealed a significant main effect of POSTURE on final head position ($F_{(3,30)}$ = 13.819, p < 0.001, η_p^2 = 0.580) with greater head motion seen when all standing postures were compared to sitting during reaching (SIT vs. STAND, p = 0.020; vs. NARROW, p = 0.002; vs. BEAM, p = 0.005). Although this is equivocal in Figure 7 due to an increased displacement during the ipsilateral SIT condition, on average head displacement during standing postures was 3° - 5° greater than during the SIT condition. Also, greater Trunk-in-space and Pelvis-in-space contributions to whole-body movement were evident during contralateral reaching and varied significantly across postures (Trunk-in-space: POSTURE x DIRECTION $F_{(3,30)}$ = 12.316, p < 0.001, η_p^2 = 0.552; Pelvis-in-space: POSTURE x DIRECTION $F_{(3,30)}$ = 8.497, p = 0.007, η_p^2 = 0.459). Specifically, both STAND and NARROW postures were displaced significantly more than their SIT counterpart (Trunk-in-space: SIT vs. STAND, p = 0.001; SIT vs. NARROW, p = 0.003; Pelvis-in-space: SIT vs. STAND, p < 0.001; SIT vs. NARROW, p < 0.001; SIT vs. BEAM, p < 0.001); however, the decreases seen in trunk displacement during the BEAM configuration did not reach significance when compared to other standing postures (Trunk-in-space: STAND vs. BEAM, p = 0.077; NARROW vs. BEAM, p = 0.057).

Relative ‘on-Segment’ displacements only differed for the extent of counter-rotation between the head and trunk (Head-on-Trunk: POSTURE x DIRECTION $F_{(3,30)}$ = 11.021, p = 0.001, η_p^2 = 0.524). When reaching contralaterally, standing elicited a greater displacement between the head and trunk compared to both the SIT and BEAM configurations (Head-on-Trunk: SIT vs. STAND, p = 0.006; STAND vs. BEAM, p = 0.047), while the NARROW configuration showed greater displacement when compared to sitting (SIT vs. NARROW, p = 0.012).

Angular velocity profiles for the corresponding segments shown in Figure 7 are represented in Figure 8. Following light stimulus illumination (time = 0), the eye (Fig. 8; vertical black, dashed lines) and head preceded movement of the finger (Fig. 8; vertical black, solid lines). Generally, Eye-in-space velocities displayed similar bell-shaped profiles regardless of target direction or posture. For contralateral targets, Head-in-space and Head-on-Trunk profiles were positively skewed across all postures while the inferior segments returned to a more bell-shaped profile. Pelvis-in-space profiles tended to show greater qualitative changes across postures.

For all participants, mean minimum and maximum peak velocities and their timing (time to peak) were compared using two-way repeated measures ANOVA (see Supporting Tables 5 and 6). After adjustments (see *Statistical analysis*), significant interactions between POSTURE x DIRECTION remained for Head-on-Trunk peak minimum velocity ($F_{(3,30)}$ = 7.897, $p = 0.013$, $\eta_p^2 = 0.441$) and Trunk-in-space peak maximum velocity ($F_{(3,30)}$ = 16.855, $p < 0.001$, $\eta_p^2 = 0.628$). In particular, contralateral reaching produced greater counter-rotatory Head-on-Trunk velocities (i.e. negative values represent the speed of movement occurring towards the opposite direction with respect to the target) between the STAND and NARROW postures when compared to sitting (SIT vs. STAND, $p < 0.001$; vs. NARROW, $p < 0.001$). SIT and BEAM postural configurations also showed reduced contralateral peak Trunk-in-space maximum velocities when compared to the other standing postures (SIT vs. STAND, $p = 0.008$; vs. NARROW, $p = 0.001$; STAND vs. BEAM, $p = 0.013$; NARROW vs. BEAM, $p = 0.005$).

As evidenced by the differing strategies seen in segmental displacements, a number of segments also revealed a main effect of DIRECTION including greater ipsilateral Head-on-Trunk maximum velocity ($F_{(1,10)}$ = 100.939, $p < 0.001$, $\eta_p^2 = 0.910$), Trunk-in-space minimum velocity ($F_{(1,10)}$ = 24.794, $p = 0.014$, $\eta_p^2 = 0.713$) and Pelvis-in-space minimum velocity ($F_{(1,10)}$ = 18.698, $p = 0.038$, $\eta_p^2 = 0.652$). Greater contralateral Trunk-on-Pelvis maximum velocity ($F_{(1,10)}$ = 92.149, $p < 0.001$, $\eta_p^2 = 0.902$) and Pelvis-in-space maximum velocity ($F_{(1,10)}$ = 25.946, $p = 0.013$, $\eta_p^2 = 0.486$) were also seen. However, time to respective segmental minima and maxima velocity did not statistically differ across POSTURE or DIRECTION across all segments (see Supporting Tables 7 and 8).

Effect of posture on eye, head and finger sequencing

When reaching to ipsilateral targets, mean onset latencies (Figure 9a, n = 11 participants) for the eye, head and finger showed a similar sequence of initiation across each postural configuration. The eye consistently led the head and the finger; however, small relative changes in the timing between each onset were observed across postures. When reaching was executed contralaterally (Fig. 9b), a similar sequence was displayed for the SIT and STAND postural configurations, but shifted for the more challenging standing postures (i.e. NARROW and BEAM) to a sequence where the eye followed the head. Despite this, there were no significant interactions in the absolute timing of eye, head or finger onset across POSTURE or DIRECTION. As expected from the greater delay to finger initiation seen across all conditions in Figure 9, a main effect of SEGMENT ($F_{(2,20)} = 19.075$, $p = <0.001$, $\eta_p^2 = 0.656$) was present and was significant for both the eye (vs. FINGER, $p = 0.009$) and head onsets (vs. FINGER, $p < 0.001$).

Relationships between eye, head and finger onsets

In order to gain insight into how the eye, head and finger were coordinated at their initiation across postural configurations, correlations were calculated using Type II major axis regressions (see *Statistical analysis*). Figure 10 shows that positive correlations were observed for relationships between the eye-head (Fig. 10a and b), eye-finger (Fig. 10c and d) and head-finger onsets (Fig. 10e and f) regardless of posture. Relationships between the eye, head and finger for movement to the ipsilateral target reported high correlations (Fig. 10; right side panels, r^2 range: 0.714 - 0.932), while a number of relationships for contralateral target remained moderate (Fig. 10; left side panels, r^2 range: 0.473 - 0.929). Of note, the range of correlations between the head and finger showed little change across POSTURE and DIRECTION (Head-Finger STAND vs. BEAM; $r^2 = 0.60 – 0.64$ vs $r^2 = 0.68 – 0.75$), with coupling of eye and head onsets weakening in their correlations as postural configurations increased in their stability requirements (Eye-Head STAND vs. BEAM: $r^2 = 0.75 – 0.84$ vs $r^2 = 0.35 – 0.67$).

When correlation coefficients (*r*) were *z*-transformed (Fig. 11a) to allow statistical comparisons to be made across conditions, eye-finger and head-finger interactions showed smaller changes in their relationship when compared to eye-head interactions. A weaker relationship for the BEAM configuration (vs. STAND, $p = 0.034$) was found during reaching to the contralateral target. Comparison of regression slopes (i.e. regression coefficients, Fig. 11b) revealed a change between the SIT and BEAM postural configurations ($p = 0.043$) for the eye-head interaction during contralateral reaching.

DISCUSSION

Considering the coupled nature of visuomotor and whole-body postural control during action, this study aimed to understand how changing equilibrium constraints (in the form of different postural configurations) influenced the initiation of eye, head and arm movements. In contrast to our predictions, a lack of statistical differences were revealed in eye-head metrics, initiation of eye, head and arm movement, and gaze accuracy across conditions in spite of kinematic differences suggesting that postural control was likely incorporated into the initiating gaze shift. Although the tight coupling of the eye and head can be altered under a variety of conditions (Freedman, 2008; Fuller, 1992; Zangermeister and Stark, 1982), including when arm movements are incorporated into a visually-guided reaching task (Carnahan and Martenuik, 1991; Pelz et al., 2001; Smeets et al., 1996), we did not find evidence to support this in the present study. We discuss how our results fit into models of gaze and postural control mechanisms based on the premise that posture constraints revealed little change in gaze behavior.

Eye-head metrics

Despite latencies of eye shifts being longer than those generally seen for pure saccadic eye movements (approx. 200 - 250 ms, Gaveau et al., 2014), values remained within the bounds reported for recordings of whole-body movements, including whole-body turning and reaching (310-460 ms, Carnahan and Martenuik, 1991; 310–320 ms, Scotto Di Cesare et al., 2013; 312.5 – 406 ms Vercher et al., 1994). A number of factors may have been responsible for the longer latencies which we discuss below;

First, the distance of the fixation targets may have influenced the latency of the required gaze shift. Often, visual targets are situated within peri-personal space (i.e. within arm’s reach) and nearer targets are known to elicit shorter saccadic latencies than those farther from the body (Yang et al., 2002). Also, for the REACH instruction, initial gaze shifts were made to fixation positions further away from the participant, when compared to the closer and ‘remembered’ reaching positions. While unlikely, we cannot directly assess the role that vergence may have played in visuomotor control in the current study (as eye measures were recorded via EOG). If a combined gaze shift and convergence task to the remembered position in space occurred, we would expect that latencies would have increased by ~20 ms (Yang et al., 2002). Considering the implications above, the facilitation of gaze shifts seen with the addition of a reaching movement may have been masked for some conditions (Bekkering et al., 1994; Dean et al., 2011; Snyder et al., 2002) as mean differences were ~10 ms (range:. -14 ms : 25 ms). Interestingly, such facilitation was only evident during ipsilateral reaching when seated and balanced upon the BEAM (Fig. 4a). This is despite the BEAM condition eliciting the longest eye latencies (observed previously when postural constraint is increased - Legrand et al., 2016).

Second, the cognitive demand placed upon motor planning may have been increased as task instructions (i.e. LOOK or REACH) occurred just prior to the visual cue (~2,000 ms). However, if this was the case we would have expected that the cognitive demand of task interpretation would interact with those of maintaining stability in an additive fashion, similar to that shown during dual-task paradigms (Woollacott and Shumway-Cook, 2002). Based on the lack of statistical differences in onset times across postures and tasks in the present study, it does not appear that this occurred. Whether this is a reflection upon postural challenge within the current experimental design (i.e. whether the changes in postural stability index shown in Figure 2 were sufficient to elicit an increase in cognitive control), or whether attentional processes in postural control are not as involved as originally thought (Genoves et al., 2016) is unclear. However, dual-task paradigms have shown that increased cognitive loads influence whole-body postural responses during the later phases of balance control (Maki and McIlroy, 2007). Therefore, we would not expect cognitive demands to interfere with the planning and initiation of eye and arm movements in the current study. Similar evidence is also found during reaching, when paradigms known to generate feedback-mediated responses (e.g. soleus stretch reflex, Vedula et al., 2010; external perturbation, Trivedi et al., 2010) are produced during the execution of the voluntary arm movement. When a surface perturbation is delivered *during* an ongoing reach movement, modulation of postural responses only occurs for long-latency components (Trivedi et al., 2010). This would suggest that responses based on long-latency cortical loops are more susceptible to attentional delays or changes caused by sensorimotor integration and occur too late to influence gaze initiation.

Finally, the constant availability of target information (i.e. targets were always present and task initiation was indicated by illumination of a single target) may have elicited longer latencies through the production of volitional rather than reflexive gaze shifts. This becomes an important distinction as it would help explain the greater average latencies that occur with gaze shifts in the standard control of visuomotor experiments, i.e., the seated position (Fig. 3a

SIT LOOK) and the lack of statistical differences when compared to standing postures. In fact, eye (and arm) latencies from our study align with findings reported for a similar task of visual scanning (Sailer et al., 2000 eye: 283 ± 71 ms; hand: 376 ± 105 ms). Based on the correlation of latencies across a number of different eye-arm coordination tasks, Sailer and colleagues posited that the signals required to initiate movement rely on similar streams of information for volitional rather than reflexive movements. Therefore, the resulting eye metrics across postures in the current study would suggest that the required sensorimotor integration for posture and gaze execution are well accounted for by the CNS in a volitional context. While the current study cannot deduce where this is occurring (whether cortical or subcortical in nature), the basal ganglia and reticular formation (via the superior colliculus) would appear to be two ideal neural candidates as they are implicated in volitional saccadic pathways, postural control and sensorimotor integration.

Eye-head-finger sequencing during movement preparation

In the current study, the eye generally led a sequence of onsets, with the head and finger following. However, the mean delay between the eye and head became less prominent under the constraints of the NARROW and BEAM postures and even altered when reaching across the midline (see Fig. 9a, contralateral). It is possible that such changes in sequence simply reflect a greater propensity for earlier head movement that can occur under predictable gaze scenarios (Fuller, 1992). The rationale as to why this seems to occur only for the more challenging balance conditions in the current study is unknown. One thought is that the active head movement may be required to delineate from the interference associated with postural sway. This is thought to occur early in vestibular processing whereby accurate gaze control can be maintained by subtracting the efference copy of the upcoming active head movement from passive movements due to postural sway and subsequent activity from vestibular-only neurons within the brainstem (McCrea et al., 1999).

Despite this alteration in the initial sequence, when saccade initiation and duration are taken into account, the eye was always the first to terminate. This lends further evidence to a generalized preparation of movement, where gaze fixation (and the subsequent visual information it provides) is necessary before a plan to *end* the arm movement is executed (Gribble et al., 2002; Rand and Stelmach, 2011).

However, our findings suggest that even with an increased requirement for sensorimotor integration (theoretically induced by postural changes), stored visuospatial information is sufficient to initiate a generalized whole-body reaching response. As the arm starts before the end of a gaze shift, initial reach motor planning must be coarsely programmed with peripherally stored retinal information gathered prior to a gaze shift and corrected online once fixation of the target is made (Desmurget et al., 1998). As target information was constantly available, the spatial predictability of targets provides a potential source for the coordination observed in the current study. Generally, visuomotor planning from peripheral signals is linked to processes arising from the dorsal visual stream, requiring the posterior parietal cortex (Desmurget et al., 1998) and sub-cortical structures of the brainstem, including the superior colliculus (Gaveau et al., 2014), to integrate spatial representations of the surrounding environment in an eye-centered (or intermediary) coordinate frame of reference (Crawford et al., 2004). While target position can be encoded in eye, head or body-centered coordinates (Henriques et al., 1998), recent evidence points towards such sensorimotor transformations occurring early during visual processing in eye centered coordinates (Crawford et al., 2004; Beurze et al., 2006). If movements were planned purely from a stored spatial representation then a minimization of the difference between a body or head-centered frame of reference and the eye-centered frame of reference (i.e. an alignment of visual and motor space representations) might prevail (Batista et al., 1999). The alignment of final head position with the target, predominantly present during REACH trials could aim to reduce the complexity in the transformation from a visual to a proprioceptive-based frame of reference for the arm movement in such a way (Sober and Sabes, 2005). This would explain why differences in planned head movements between LOOK and REACH conditions, depicted by the changes in final total head displacement occurred and aligns with the ‘conversion-on-demand’ model of visuomotor control (Henriques et al., 1998). This model suggests that multiple targets are encoded globally in eye-centered coordinates and further transformed into appropriate head or body-centered frames prior to motor planning. Whether the same holds true under paradigms specifically investigating various frames of reference during reaching is unknown as active head movements are often limited (Beurze et al., 2006; Dessing et al., 2012, Henriques et al., 1998). Such examples are also adopted *during* reaching with evidence stemming from online corrections during double-step paradigms (Pélisson et al., 1986; Prablanc and Martin, 1992; Soetching and Lacquaniti 1983), where short motor delays (~90 - 150ms) are seen for movement adjustments. As such, the eye and finger might be linked, with the head involved in a synergy with either. In the current study, the strength of correlations relating to the head and finger (Fig. 10) provide further evidence that head control is a necessity in achieving oculomotor goals in a combined whole body task (Anastasopoulos et al., 2015). Whether this coordination of gaze and reaching is driven by control of eye, head or gaze parameters is still of debate (Daye et al., 2014; Freedman, 2008; Guitton et al., 2003; Haji-Abolhassani et al., 2016).

Whole-body gaze strategy

The consistent patterns of gaze trajectory and accuracy (see the standard deviations in Figure 5 and 7), coupled with the greater variability of eye and head components (in particular the variable counter-rotation of the eye once at fixation, see Figure 3) strengthen the notion that gaze is a controlled variable in the execution of visuomotor tasks. This seems in competition to models that have often been used to describe head-free gaze shifts (Freedman et al., 2008). In fact, models of feedback-mediated gaze position error have previously been shown to describe the spatiotemporal coupling of the eye and head during long torque head perturbations, resulting in gaze trajectories that are invariant to their non-perturbed counterparts (Boulanger et al., 2012). More recently, gaze modelling incorporating both neuroanatomical and classic behavioral findings (e.g. main sequence) has used gaze position error to simulate eye and head trajectories despite a difference in gaze and head goals (Haji-Abolhassani et al., 2016). Such a mechanism may easily account for the differences in head movement strategy based on target eccentricity, whereby a purely saccadic eye movement was produced during gaze shifts to the smaller eccentricity of 23°. While models of gaze control often limit themselves to the interactions between the eye, head and gaze components, some have also considered the necessity of whole-body coordination during gaze shifts (Daye et al., 2014). Daye and colleagues suggested that a hierarchical model controls linked segments via a number of feedback loops. In doing so, proximal segments may serve differing goals but are coupled to the goals of the most distal segment (in this case, gaze) whose feedback is dictated by a global goal. If head and gaze position are controlled variables (rather than eye position), this might explain the stronger relationships seen in eye-head and head-finger onsets in the current study. A hierarchical model may also account for the interactions between posture and direction seen across a number of axial segments while gaze trajectories and accuracy were maintained. This includes the Clear changes in strategy used to coordinate body segments that occurred between movements made to ipsilateral and contralateral targets. In particular, greater involvement of the large segments of the trunk and (to a lesser extent) pelvis were necessary for target attainment to the contralateral target yet their movement was minimized for ipsilateral reaching (Fig. 7, 'in-space' displacements). The movement patterns in the current study aligned with descriptions of predictable, 'return-bound' turning (Scotto Di Cesare et al., 2013). These authors postulated that changes in coordination (alongside oculomotor delays) are introduced for predictable targets to allow for the integration of appropriate muscle activity to produce APAs. Whether this represents a reduction in the discrepancy between head-centered vestibular coordinates and body-centered trunk coordinates, which may be useful in reducing the processing costs of such APAs (for movement generation - Solomon et al., 2006) is unclear; however, it would align with a gaze model that requires an explicit head goal (and the efference copy that accompanies it – Daye et al., 2014).

The lack of significant differences in eye and head metrics across postural configurations would further suggest that a coordinated whole-body gaze shift occurs, such that postural control (for stability) is subservient to gaze control (Flanders et al., 1999). Further evidence from supra-postural dual-task scenarios has shown that more complex oculomotor strategies (i.e. double step visuomotor task) utilize tighter control of head movements, aimed to reduce postural instability (Boulanger et al., 2017). While unable to directly assess the postural component during active head movements, this is difficult to reconcile with the increases in head displacement that accompany reaching, rather than the simple gaze shift task, seen in the current study. Considering that reaching errors can be accounted for by changes in head-in-space displacement (Flanders et al., 1999) and the strong evidence of gaze-arm coordination within a number of cortical regions (in particular, the posterior parietal cortex), arm control (for goal-directed movement) may still be somewhat subservient to gaze control, but via signals derived from head displacement during whole-body movements. This would also align with the arguments set forth above for the transformation of visuomotor goals to an actionable task (Henriques et al., 1998).

While we have made interpretations based upon a number of negative findings, it may be that our methodological approach was insufficient to result in postural effects upon visuomotor control. In particular, the longer absolute latency of eye onsets across all tasks and postural conditions (see *Eye-head metrics*), suggestive of a volitional rather than reflexive approach to gaze initiation, may mask any interaction between posture and visuomotor control despite differences in postural instability across configurations (Figure 2).

Therefore, while a generalized preparation and execution of the initial motor program is supported for volitional gaze shifts in the current study, challenges to equilibrium and the accompanying increased cognitive load may instead be prominent under reflexive or more complex visuomotor tasks. This aligns with previous discussion highlighting the greater postural control during complex double-step saccades (Boulanger et al., 2017). Also, an influence of posture on saccade initiation in younger adults was not evident for simple single-step saccades but accelerated the onset of a secondary saccade when standing under certain circumstances (Jimenez et al., 2016). Further insights into the role of cognition on postural and visuomotor control could also be examined using the Linear Approach to Threshold with Ergodic Rate (LATER) model (Noorani and Carpenter, 2016). Briefly, by compiling a large sample of eye onset latencies (or theoretically any segment reaction time) across a range of conditions, their cumulative reciprocal distributions (which are linear when plotted on a reciprobit scale) can be easily compared. Based on changes in the slope, intercept or pivot point of the regression line, specific alterations within the decision signal that dictates reaction time can be hypothesized (see Figure 5, Noorani and Carpenter, 2016). Changes in these parameters have been shown in a number of experimental and clinical settings relating to cognition (Burrell et al., 2012; Carpenter and Williams, 1995) and could be applied to our paradigm.

Based upon the premise that descending corticospinal and other supraspinal commands are required to execute a goal-directed arm movement, it was expected that when combined with additional neuro-mechanical constraints (i.e. different postural configurations) that the timing and sequence of eye, head and arm initiation may become altered. As such, it was initially thought that if posture had the potential to influence the saccadic premotor circuits, it may occur in two ways: First, a facilitation of gaze shift initiation may have occurred through the priming of the excitatory burst neurons (EBNs) and/or early release of inhibitory burst neurons (IBNs) to allow for the fast re-anchoring of gaze. This is seen when additional sensory modalities are concurrent with saccade initiation (termed ‘sensory fusion’ - Pacquette and Fung, 2007), and is evident during eye-arm coordination tasks in head-restrained individuals (Bekkering et al., 1994; Dean et al., 2011; Snyder et al., 2002). Second, it was thought that if additional processing is required by higher cortical structures to integrate visuomotor and postural outcomes, a delay in gaze shift initiation may occur. If this influenced the entire mechanism (eye-head-arm), it may further implicate common areas within the posterior parietal cortex associated with the planning and execution of eye and arm movements, and the re-allocation of attentional resources.

Conclusion:

In conclusion, our results revealed that changing posture did not produce consistent or distinct alterations to eye-head metrics, or the movement sequence, despite changes to kinematic contributions of other axial body segments. This suggests that the CNS is able to adequately account for instability arising from differing postural configurations. The constancy of coordination between head and gaze signals would further suggest that their ‘in-space’ position is a controlled variable by the CNS, to produce a whole-body gaze strategy that can account for postural instability. Whether this occurs through the determination of an explicit and independent head goal (Daye et al., 2014) or can be achieved purely through gaze feedback and passive mechanisms (Haji-Abolhassani et al., 2016) is undetermined.

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CONFLICT OF INTEREST

The authors state that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

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

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FIGURE LEGEND

Figure 1. Apparatus (**a**), postural configurations (**b**) and angle conventions used within the current experimental configuration. **a** Participants were placed in front of a wall-mounted projection screen upon which five visual targets were displayed: a central fixation target and a target located 23° and 38° on the same side (***ipsi***lateral) and opposite side (***contra***lateral) to the reaching arm. (**b**) Participants were either seated (SIT) or standing (STAND, NARROW, BEAM) with their midline aligned perpendicular to the central 'fixation' target. Targets were aligned with eye-level and illuminated in a pseudo-randomized order. For LOOK trials, participants made gaze shifts to fixate upon the illuminated target. For REACH trials, participants were made to reach to, and hold a 'remembered target' position in space aligned with the illuminated target (distance = 130% reaching arm length). (**c**) Schematic representation of the absolute '*in-space*' and relative '*on-segment*' rotations calculated for interactions of the eye, head trunk and pelvis segments during the experimental procedure.

Figure 2. Mean total head displacement (**a**) and mean head sway measures in the antero-posterior (**b**) and medio-lateral axes (**c**) across four postural configurations (SIT, STAND, NARROW, BEAM). Measures were taken from the central target LOOK condition to provide an index of postural stability. Clear changes in total head displacement and the area of 95% confidence ellipses across postures (**a**) were confirmed by the greater head sway present in both axes (**b**, **c**) when standing postures were compared to the seated configuration. Error bars indicate variability as standard deviation (**b**, **c**).

Figure 3. Mean angular displacement and velocity profiles for the eye (black, solid), head (black, dashed) and gaze (black, dotted) for a representative participant (S01). Differences between simple gaze fixations (LOOK, left panels) and whole-body reaching movements (REACH, right side panels) to the 38° ***ipsi***lateral target are shown for each postural configuration and are relative to light onset (Time = 0). Shaded areas surrounding mean traces represent inter-trial variability (± 1 standard deviation).

Figure 4. Mean (n=11) changes in eye metrics between simple gaze fixations (LOOK) and whole-body reaching movements (REACH) across each postural configuration. Bounded boxes represent values for movements to either the ***contra***lateral (black) or ***ipsi***lateral (grey) 38° target for measures of (**a**) eye onset, (**b**) peak eye velocity, (**c**) duration of saccade, and (**d**) eye contribution to gaze amplitude. Comparisons of means show that regardless of task, direction or postural configuration, measures of eye metrics were not significantly altered. Error bars indicate variability as standard deviation.

Figure 5. Comparison of gaze gain ratio (gaze amplitude : target amplitude) for movements to ***contra***lateral and ***ipsi***lateral across the four postural configurations. A value of 1 indicates that the primary saccade was aligned with the center of the visual target while dashed lines represent the boundaries of the visual target. Values less than one would represent saccades that tended to be hypometric while values greater than one hypermetric. Regardless of posture or direction, mean gaze gain remained within the bounds of the visual target. Error bars indicate variability as ± 1 standard deviation.

Figure 6. Mean (n=11) changes in final head position (**a**) and head contribution to gaze (**b**) between simple gaze fixations (LOOK) and whole-body reaching movements (REACH) across each postural configuration. Bounded boxes represent values for movements to either the ***contra***lateral (black) or ***ipsi***lateral (grey) 38° target. Comparisons of means show that final head position was reduced for **contra**lareral gaze shifts (LOOK) compared to reaching ($^{*}p = 0.009$) with a similar trend for ***ipsi***lateral movements ($^{\#}p = 0.091$).Head contributions to gaze followed a similar reduction during simple gaze shifts (LOOK) towards ***contra***lateral targets ($^{*}p = 0.016$). Error bars indicate variability as ± 1 standard deviation for individual postures and 95% confidence intervals when postural configurations were pooled.

Figure 7. Mean kinematic changes, including absolute and relative axial angular displacements, for a representative subject (S01) across four postural configurations during reaching. Traces are aligned to initial light stimulus onset for each posture (time = 0) preceding eye (*E*) and finger movement initiation (*F*). For absolute or, '*in-space*' measures, positive values are indicative of segmental displacements or velocities towards the target of interest, i.e. reaching movements producing ***contra***lateral segment movements are positive for the ***contra***lateral target. For relative or, '*on-segment*' measures, positive values indicate movement of the anatomically superior segment upon the inferiorly placed segment. All traces are represented by mean values (solid) ± 1 standard deviation (shaded).

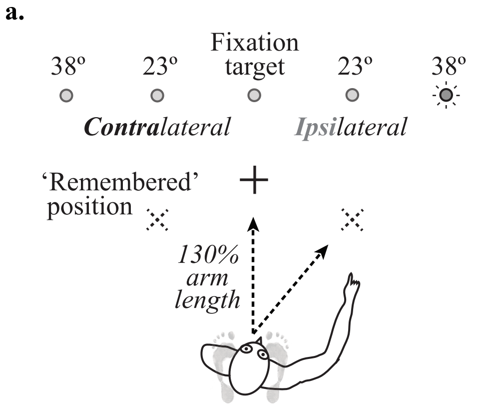
Figure 8. Mean absolute and relative angular velocity profiles for a representative subject (S01) across four postural configurations during reaching. Traces are aligned to initial light stimulus onset for each posture (time = 0) preceding eye (*E*) and finger movement initiation (*F*). The head often proceeded movement of the eye (black, dashed) and preceded finger movement. Segmental velocities across the four postural configurations have been scaled similarly for ease of comparison. All traces are represented by mean values (solid) ± 1 standard deviation (shaded).

Figure 9. Eye, head and finger movement initiation from light stimulus illumination across postural configurations for ***contra***lateral (**a**) and ***ipsi***lateral (**b**) reaching movements. While ***ipsi***lateral reaching movements showed a distinct sequence of initiation with the eye preceding both the head and finger regardless of postural configuration, ***contra***lateral reaching saw a preference for 'head-first' movement initiation for the NARROW and BEAM configurations. Error bars indicate variability as ± 1 standard deviation.

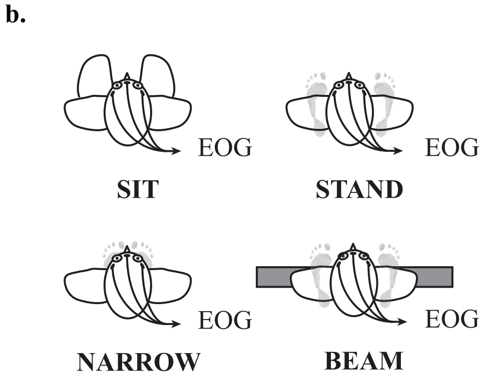
Figure 10. Major axis regression analyses and coefficients of determination (r^2) for relationships between eye-head (**a**-**b**), eye-finger (**c**-**d**), and head-finger onsets (**e**-**f**) grouped by target direction (***contra***lateral, left panels; ***ipsi***lateral, right panels). Coefficients of determination for the head and finger exhibited a more consistent relationship across postural configurations and direction compared to the eye and head or, eye and hand. ***Ipsi***lateral targets (**b, d, f**) showed stronger correlations regardless of postural configuration, which began to diverge when reaching to ***contra***lateral targets (**a, c, e**).

Figure 11. Comparison of *z*-transformed correlation coefficients (**a**) and regression coefficients (**b**) for eye-head, eye-finger, and head-finger onset relationships across the four

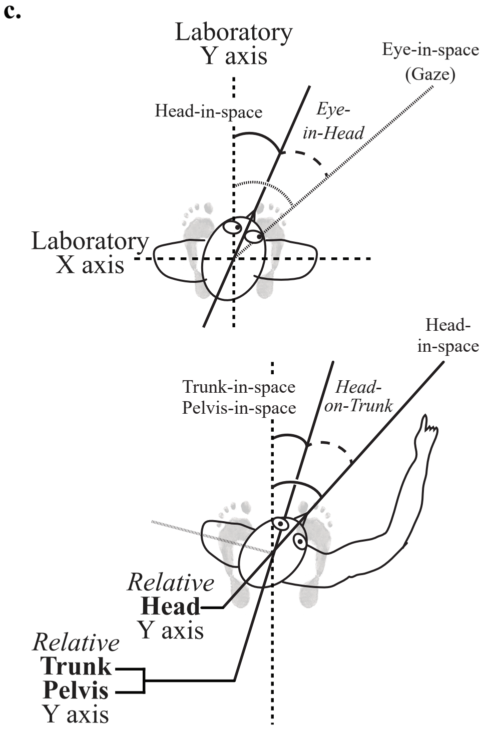
postural configurations. While interactions were generally weaker for reaching to ***contra***lateral targets (black, solid bars) when compared to ***ipsi***lateral reaching (grey, solid bars), significantly weaker correlations were only seen between the eye and head (STAND vs. BEAM; $^{*}p_{adj} = 0.034$). Error bars indicate variability as ± 1 standard deviation.



Experimental Configuration



Postural Configuration



Angle conventions

Figure 1
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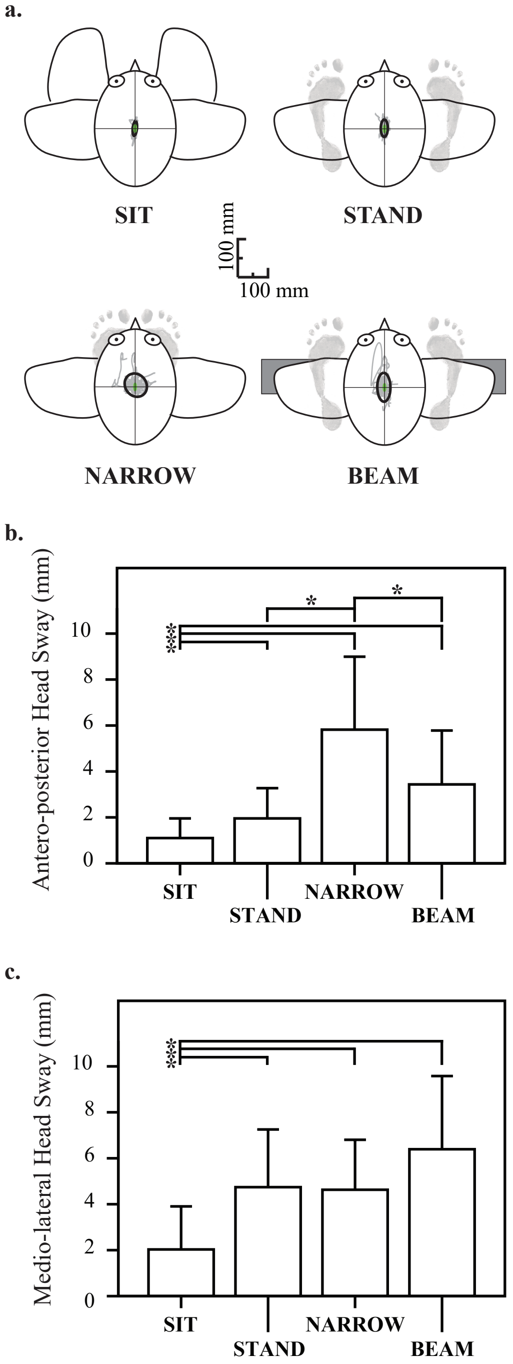

Figure 2
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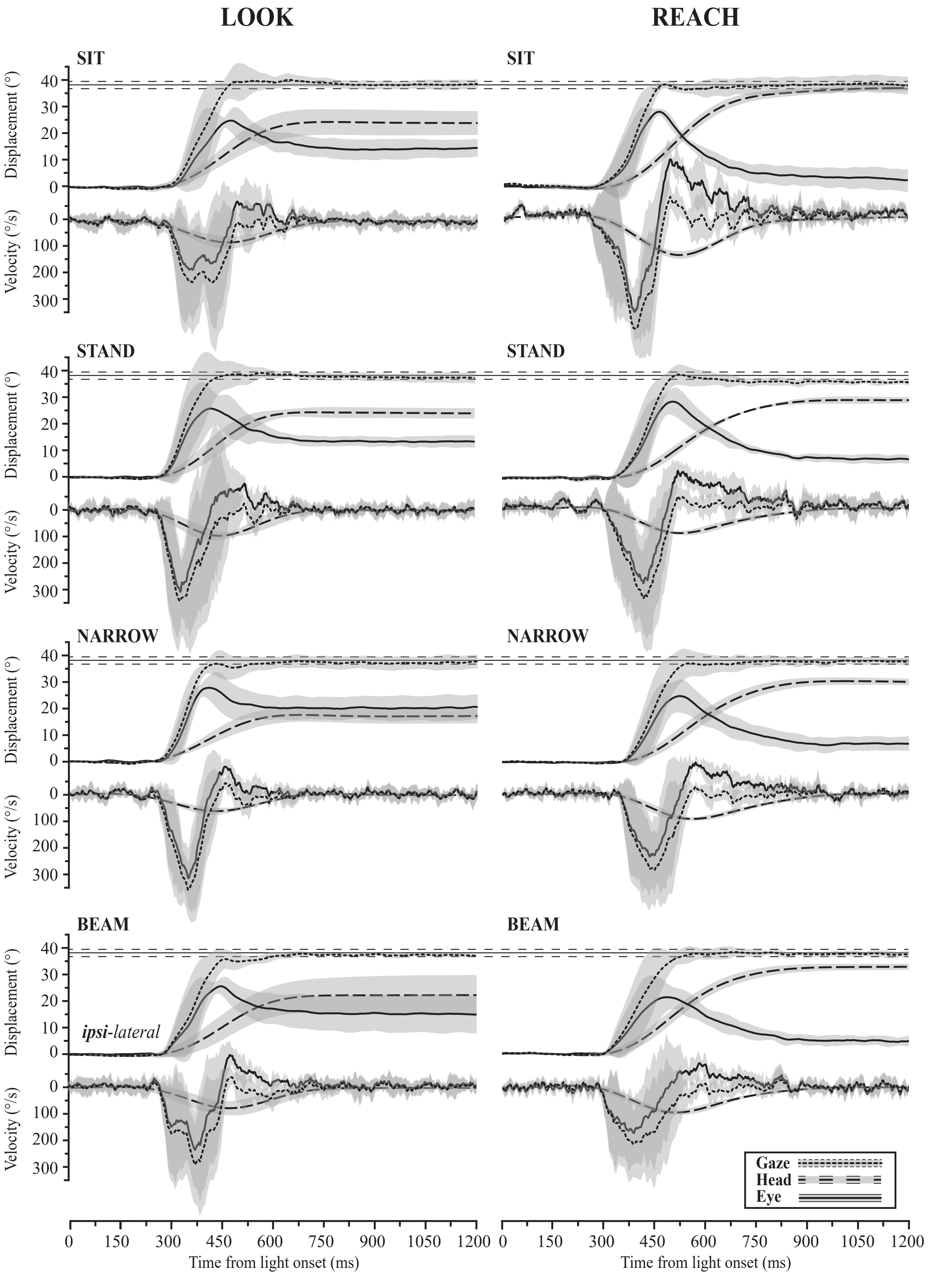

Figure 3
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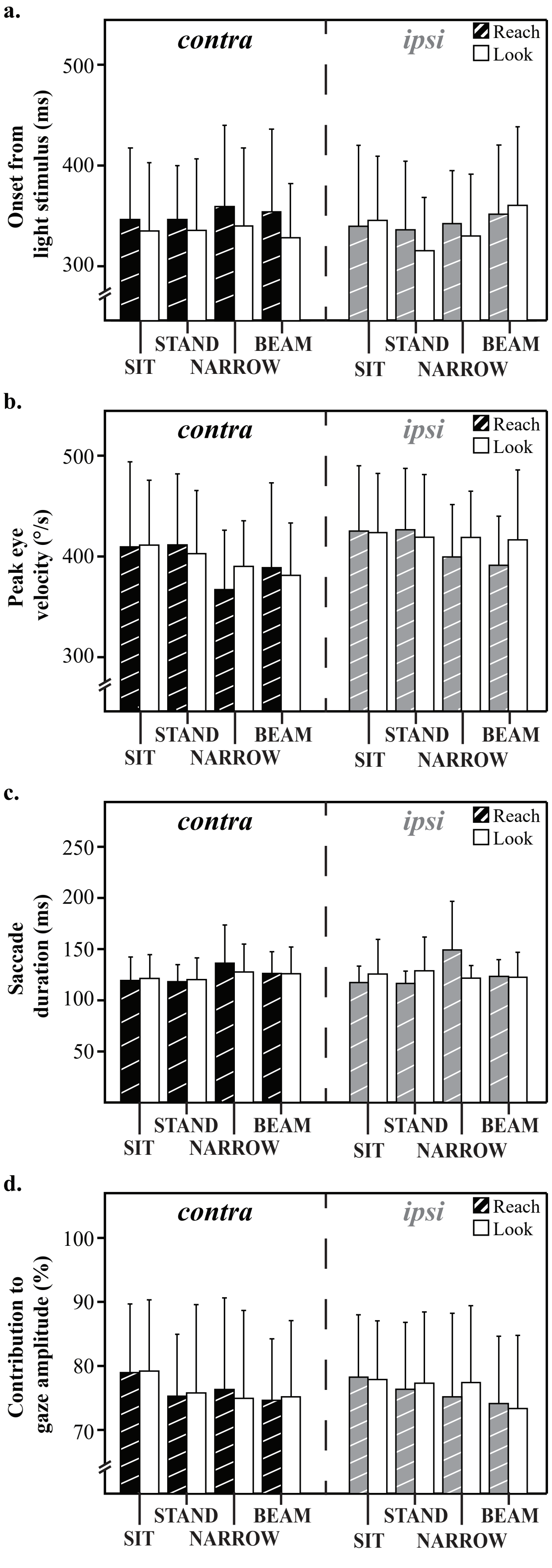

Figure 4
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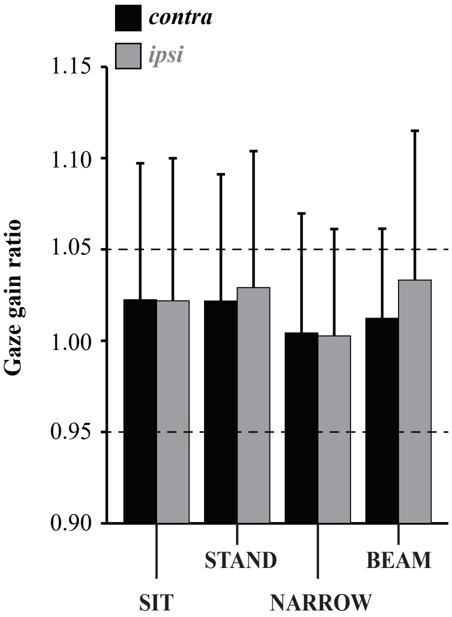

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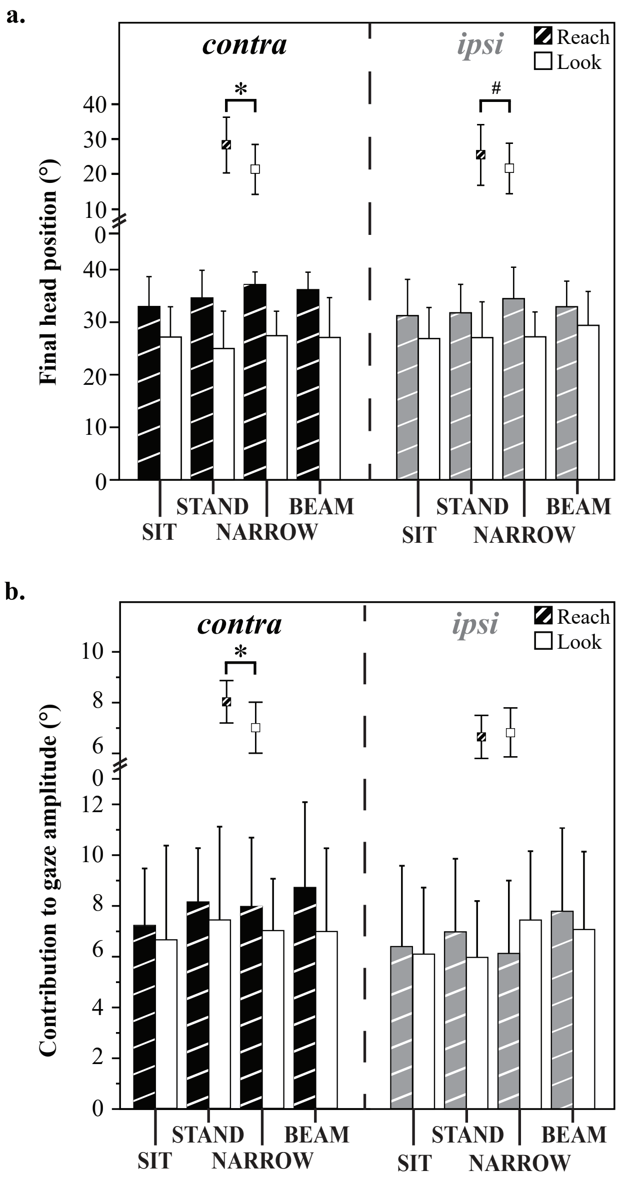

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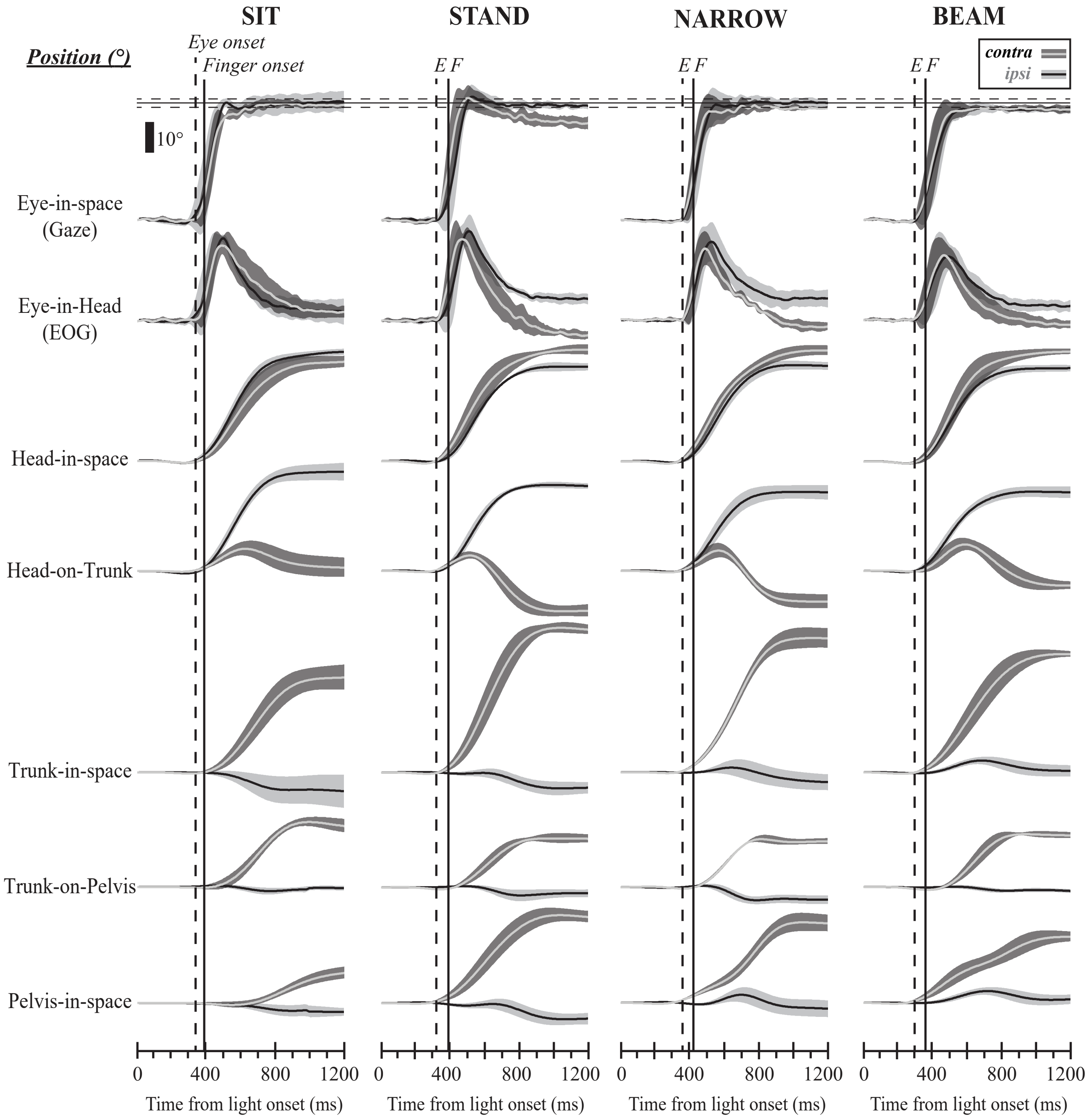

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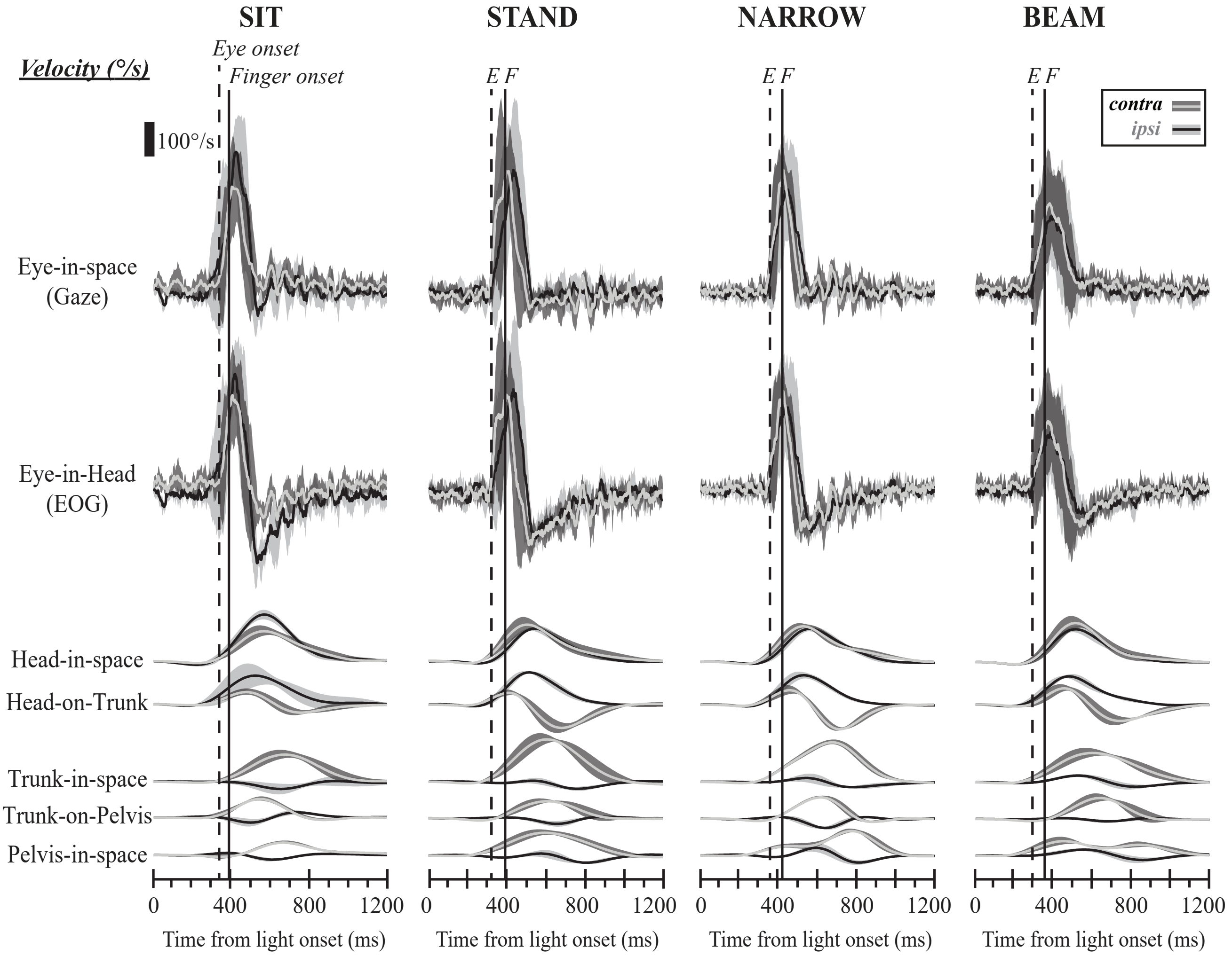

Figure 8

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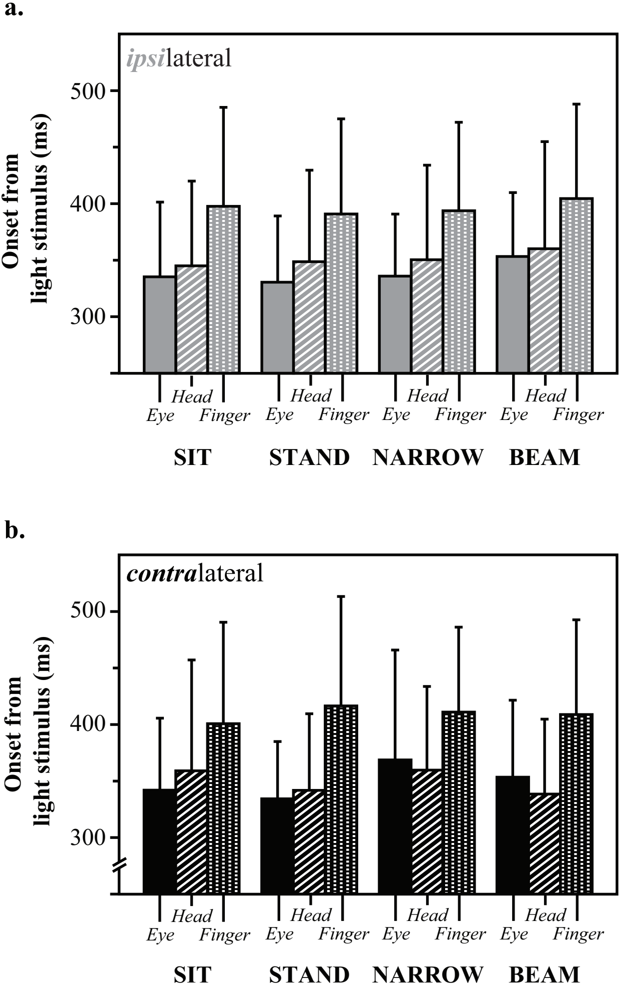

Figure 9
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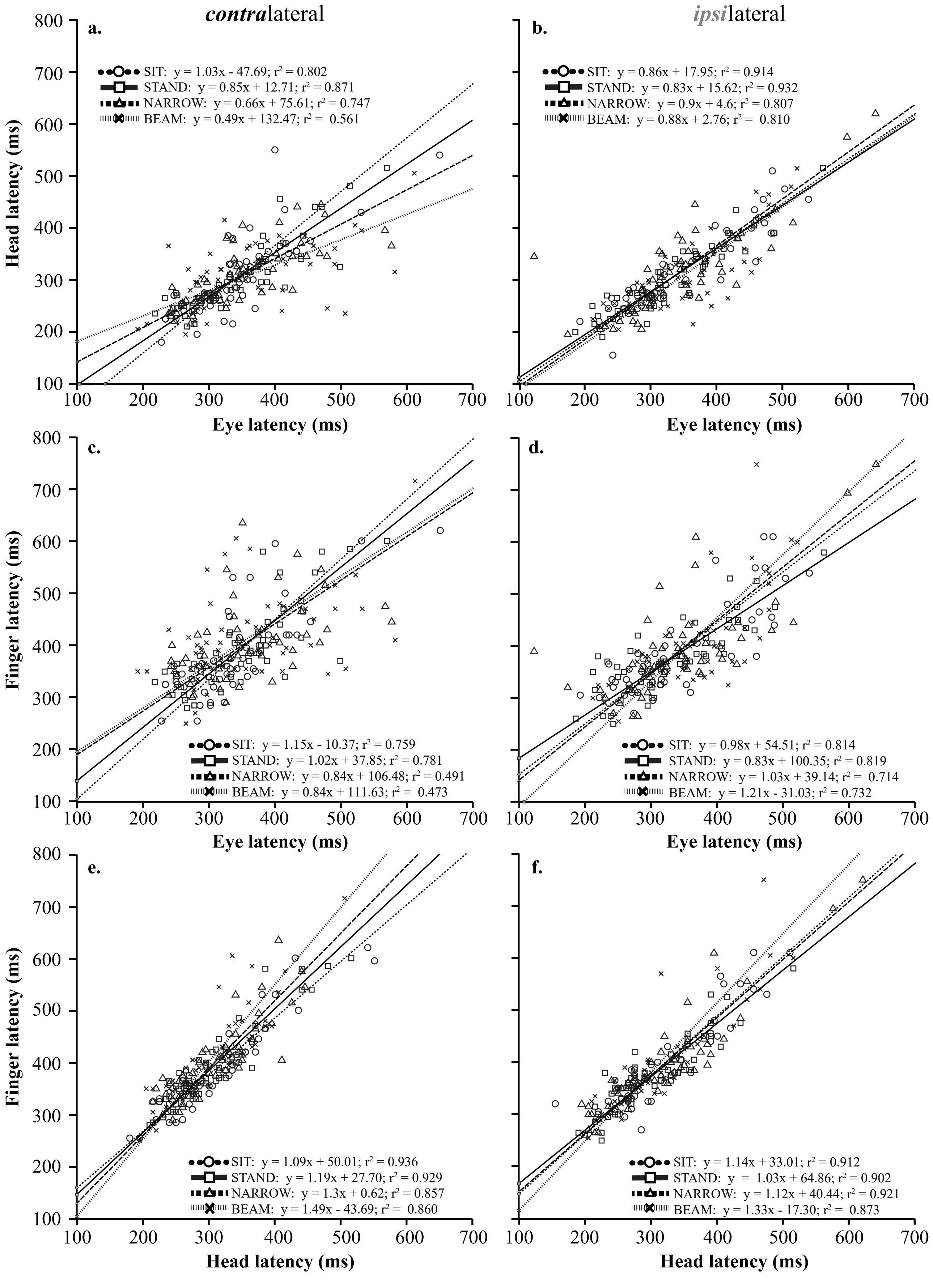

Figure 10
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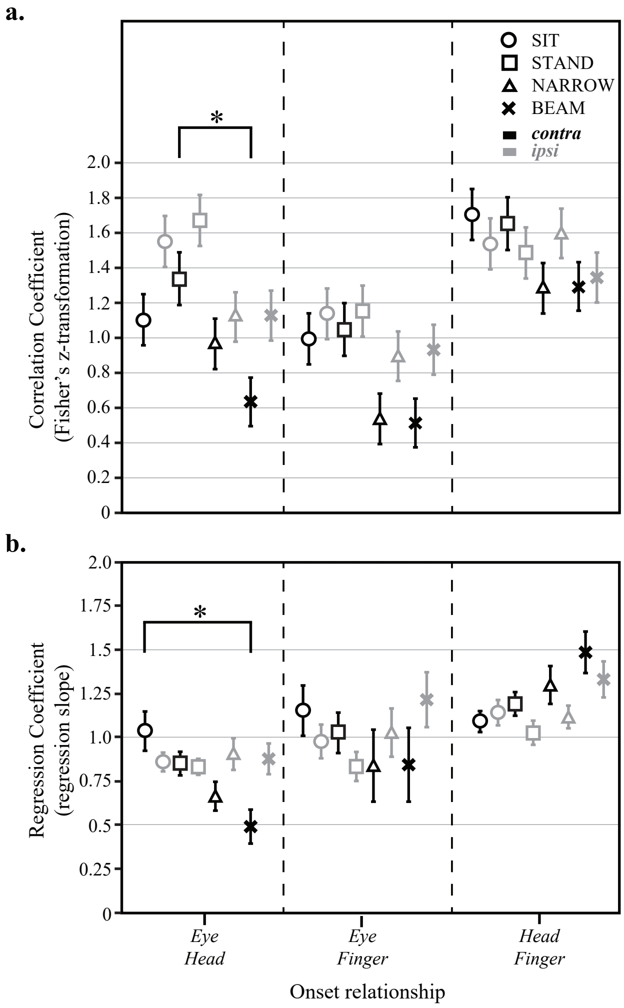

Figure 11
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