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**Do Postural Constraints Affect Eye, Head and Arm Coordination?**

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### Article

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3  
4 DO POSTURAL CONSTRAINTS AFFECT EYE, HEAD AND ARM COORDINATION?

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47 Running Head: *Postural influences on visuomotor coordination*

48 **ABSTRACT**

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

65

66 **NEW AND NOTEWORTHY**

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

73

74

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

76 **INTRODUCTION**

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

91 Vision can also play a role in postural stability, although the precise mechanisms  
92 remain unclear (Guerraz and Bronstein, 2008). Initially, the retinal slip induced by postural  
93 sway (a central vision process) was thought to be the primary mechanism (Paulus et al.,  
94 1984). However, recent evidence has pointed to a greater role of proprioceptive extra-retinal  
95 signals, acting either through reafference or efference copy of extra-ocular motor signals  
96 (Glasauer et al., 2005; Guerraz and Bronstein, 2008; Strupp et al., 2003). Despite the general  
97 acceptance that vision impacts postural stability, whether postural demands can have a  
98 reciprocal effect upon vision, and more specifically, the execution of gaze shifts, is less clear.  
99 For example, when the head is stable vestibular signals encode movement of the body (as a  
100 function of postural sway) rather than head on body movements. These signals can be utilized  
101 for postural control (Strupp et al., 2003) with the maintenance of eye position (and visual  
102 stability) occurring via VOR. However, if postural instability is present in addition to an  
103 active head movement (much like during activities of daily living), eye-head stabilizing  
104 mechanisms such as the VOR are likely to interfere with the production of a correct gaze  
105 response (Daye et al., 2014; Haji-Abolhassani et al., 2016). Therefore, integration of whole-  
106 body posture with active eye and head movements must be required to ensure the timing of  
107 individual segment rotations provides accurate gaze shifts.



108 Research on visuomotor coordination has been predominantly restricted to the seated  
109 position, dramatically reducing any impact of postural instability on arm or gaze control.  
110 From this, two main theories of gaze control have been proposed: the first involves gaze  
111 being driven by feedback-mediated signals derived from a shared gaze motor error  
112 (Boulanger et al., 2012; Guitton et al., 2003), while the second proposes that feedback-  
113 mediated signals for the eye and head are modulated independently (Freedman and Sparks,  
114 1997; Phillips et al., 1995). The latter has attempted to account for the changes that occur in  
115 the ‘main sequence’ characteristics of saccades when unrestrained head movements are  
116 incorporated into gaze (see Freedman, 2008). When gaze has been examined under greater  
117 freedom of movement (e.g. unrestrained whole-body movements such as turning), a top-  
118 down approach encompassing a coordinated whole-body contribution to gaze shift is  
119 observed (Anastasopoulos et al., 2015; Hollands et al., 2004; Scotto Di Cesare et al., 2013;  
120 Sklavos et al., 2008). Through scaling of head-in-space velocity gaze shifts are hypothesized  
121 to be driven by a separate head displacement controller in such conditions (Anastasopoulos et  
122 al., 2015). While the CNS is able to simplify this control through kinematic synergies  
123 (Anastasopoulos et al., 2009), a consequence is a subsequent delay in gaze shift initiation  
124 when posture is altered (Scotto Di Cesare et al., 2013). Such delays are suggested to allow  
125 additional time to incorporate anticipatory postural adjustments (APAs) and to reconcile  
126 more moving segments into the motor program (e.g. seated vs. standing axial rotations -  
127 Scotto Di Cesare et al., 2013).

128 If head-free gaze control comprises a separation of eye and head signals during whole-  
129 body movement then there lies a possibility that the addition of postural constraints and an  
130 arm movement could alter a preference for eye-head, eye-arm or head-arm coordination.  
131 Such is found when the sequence of eye, head and arm onsets are examined under a variety of  
132 experimental conditions (eye-head: Fuller, 1992; Zangermeister and Stark, 1982; eye-head-  
133 arm: Carnahan and Marteniuk, 1991; Pelz et al., 2001; Smeets et al., 1996). During  
134 coordinated reaching, modifications to this sequence are thought to reflect the reorganization  
135 of supraspinal postural control mechanisms (and a corresponding rise in corticospinal  
136 activity) associated with incorporating the arm movement (Herman et al., 1981). Whether  
137 altering posture and the requirement to incorporate balance delays the goals of target fixation  
138 and accompanying arm movement, or manifests itself through a dissociation of the eye and  
139 head movement for a more preferential head-arm coordination strategy seen during goal-  
140 directed reaching (Pelz et al., 2001) is unclear. Similarly, additional reliance on sensory drive

141 associated with changes to posture may result in the release of pre-planned saccadic  
142 responses. This ensures that fixation occurs swiftly, allowing vision (and extra-retinal  
143 signals) to assist in postural control (Pacquette and Fung, 2007). Examples of this facilitation  
144 in saccade initiation are seen when performed during external perturbation (Pacquette and  
145 Fung, 2007) and in some instances, where reaching has been shown to reduce the onset  
146 latency of saccadic eye movements (Bekkering et al., 1994; Dean et al., 2011; Snyder et al.,  
147 2002).

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

174 if vision was required to assist postural control, the initiation of gaze shifts would be  
175 facilitated to ensure a rapid re-anchoring of gaze.

176 **METHODS**177 *Participants*

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

186 *Experimental apparatus & configuration*

187           The experimental configuration is shown in Figure 1a. Participants stood barefoot  
188 facing a blank screen on which five circular targets (diameter:  $\sim 3^\circ$ ) were projected. Targets  
189 were positioned at an eccentricity of  $23^\circ$  and  $38^\circ$  on either side of a central target situated  
190 2.35m away from the participant. As the aim of this study was to assess the impact of  
191 different postural configurations on eye, head and arm sequencing, we asked participants to  
192 reach to a practiced and remembered distance in space as opposed to a physical target that  
193 may have provided support upon movement termination. Indeed, the effect of even light  
194 touch on balance is well documented (Clapp and Wing, 1999; Jeka, 1997) and so prior  
195 knowledge of a physical target could have influenced movement preparation strategies. The  
196 practiced target distance corresponded to 130% of each participant's outstretched arm length  
197 (measured from the xiphoid process to the tip of the reaching index finger, with the shoulder  
198 in neutral scapular retraction and arm extended), a distance adopted as it involves a  
199 significant postural component without placing a person beyond their limit of stability  
200 (Leonard et al. 2009).

201           A familiarization procedure for reaching to the practiced target distance was  
202 conducted on two separate occasions. Feedback was given during an initial anthropometric  
203 measurement and familiarization session the day before data collection and preceding each  
204 block of recorded postural trials during the main experimental period. A minimum of 5  
205 reaching trials were conducted for each direction during the initial familiarization period and  
206 prior to the experimental recording period to ensure a whole body reaching movement was

207 produced. No feedback was given relating to the accuracy of eye, head or arm movement  
208 with respect to the target eccentricity.

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

### 221 *Experimental procedures*

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

230 Mediolateral stance width remained identical for three of the four configurations (SIT,  
231 STAND and BEAM) and was determined by taking the average distance between medial  
232 malleoli of the ankles after three 15 m walking trials at the participant’s preferred walking  
233 speed. For the NARROW posture, the feet were placed together such that the medial malleoli  
234 of the two ankles touched. For SIT trials, a stool with no back support was used to allow for  
235 neutral vertebral and shoulder position and a constant 90° knee flexion. During the BEAM  
236 configuration, participants stood on a wooden beam (dimensions: 800 mm length x 80 mm  
237 height x 80 mm width) aligned with the approximate center of the ankle joint (line between

238 the medial and lateral malleoli). This was to ensure that the feet did not touch the ground for  
239 support throughout the entirety of the reaching movement and that the base of support was  
240 reduced in the antero-posterior plane.

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

#### 258 *Data analysis*

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

266 *EOG calibration and movement onsets.* Calibration of raw eye signals to a horizontal  
267 Eye-in-Head angular position was carried out using the vestibular-ocular reflex mechanism  
268 and was undertaken prior to each postural configuration block. Briefly, the head was rotated

269 through a field of  $\pm 30 - 40^\circ$  while participants maintained visual fixation upon the central  
270 target. As the gain between the head movement and compensatory eye movements during the  
271 VOR is close to 1, a linear regression of the EOG signals (recorded as a change in voltage)  
272 and Head-in-space position (recorded as a change in angular displacement via kinematics)  
273 can be used to convert the analog EOG recording to an Eye-in-Head position (in degrees).  
274 The calculated regression coefficient (i.e. slope) can then be used to determine Eye-in-Head  
275 position during experimental trials (Hollands et al., 2004; Reed-Jones et al., 2009). When  
276 combined with Head-in-space position, a measure of gaze location (or, Eye-in-Space  
277 position) could be deduced. Figure 1c illustrates the absolute ('in-space') and relative ('on-  
278 Segment') segment angular rotations calculated for the eye, head, trunk and pelvis.

279 Eye onset was determined using an angular velocity threshold of  $30^\circ/\text{s}$  (Daye et al.,  
280 2014; Pélişson et al., 2001). This was compared to other velocity measures (e.g.  $20^\circ/\text{s}$ , 3%  
281 and 5% peak eye velocity) with minimal variation in onset detection (average difference = 2  
282 ms). A velocity threshold of  $15^\circ/\text{s}$  was applied to determine head onset (Daye et al., 2014).  
283 All onsets were confirmed or adjusted based upon visual inspection of their respective  
284 position profiles (Teasdale et al., 1993). Trials with eye onsets which occurred within 100 ms  
285 from target illumination or after 800 ms were removed from further analysis (Munoz et al.,  
286 1998); this equated to the exclusion of  $\sim 4.8\%$  of all trials, which closely aligned with a  
287 previous report for adult saccade latencies (Yang et al., 2002). Eye metrics including peak  
288 velocity and duration of the initial saccade, as well as its total contribution to the amplitude of  
289 gaze shift and final gaze accuracy (i.e. the gaze gain ratio, where values less than 1 indicate  
290 hypometric gaze shifts) were quantified to determine if the main sequence of gaze shifts  
291 altered with postural instability. This was complemented by measures of head alignment (i.e.  
292 final head position) and its respective contribution to the total amplitude of gaze shift.

293 Key kinematic events relating to the arm component of the reaching movement  
294 (within the 'REACH' trials) were determined using the bell-shaped tangential velocity profile  
295 of the index finger due to the curvilinear nature of the trajectory seen throughout the  
296 movement. Five percent of the peak velocity was chosen as an onset threshold, with  
297 movement initiation being the first sample with a value that exceeded this threshold and  
298 movement termination being the first sample with a value that reduced below this threshold  
299 following the movement. This allowed for a robust measure of finger movement onset  
300 (Sainburg and Schaefer, 2004). Finally, as an index of postural instability, head sway (or the

301 mean standard deviation of head displacement) was calculated in the antero-posterior and  
302 medio-lateral axes for the time course of trials in which no active movement was required  
303 (i.e. central target, 'LOOK' condition).

#### 304 *Statistical analysis*

305 Statistical analyses were conducted using the SPSS statistical package (ver. 21, IBM,  
306 OR, USA) or within the MATLAB environment (ver. R2013b, The Mathworks, Natick, MA).  
307 Data were assessed for normality using Shapiro-Wilk testing. Eye onsets were positively  
308 skewed and subsequently inversely transformed for all statistical analyses. It is well  
309 established that amplitude (or the absolute eccentricity of eye movements) influences eye-  
310 head metrics and was not a primary interest in this study; therefore, the dataset was split to  
311 compare all 38° and 23° degree trials. Eye-head metrics were examined using a 2x4x2 design  
312 repeated measures ANOVA (TASK x POSTURE x TARGET). For reaching trials,  
313 differences between postural configuration and direction of movement were analyzed using a  
314 4x2 repeated measures ANOVA (POSTURE x TARGET). Greenhouse-Geisser adjustments  
315 to the degrees of freedom were used if violations of sphericity were observed. Additionally,  
316 to control for the potential increase in the familywise error rate present in undertaking  
317 multiple ANOVAs on related variables (e.g. eye-head metrics, kinematics), all reported  $p$ -  
318 values for main effects and interactions were adjusted using the sequential Bonferroni method  
319 (i.e. Bonferroni-Holm correction) before further post-hoc testing (Cramer et al., 2016). For  
320 effects and interactions that remained significant following the adjustments above, post-hoc  
321 analyses were conducted using pairwise comparisons with Bonferroni's adjustment.

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



333

$$334 \quad Z_{calc} = \frac{Z_1 - Z_2}{\sqrt{\frac{1}{n_1 - 3} + \frac{1}{n_2 - 3}}}$$

335

$$336 \quad |Z_{calc}| < |Z_{(crit)}|, H_0 \text{ accepted}$$

337

338

339 **RESULTS**

340 While gaze shifts requiring both eye and head involvement were to be expected from  
341 both target eccentricities (Gresty, 1974), during the initial stages of analysis it became  
342 evident that the incorporation of a head movement into the gaze shift was not always  
343 produced. In fact, a purely saccadic eye movement was the primary strategy adopted by 3/11  
344 participants for movements to the smaller eccentricity of 23° during the LOOK condition. As  
345 conclusions relating to the question of coordination between eye, head and arm movement  
346 initiation could not accurately be assessed for these trials the following section will focus on  
347 results pertaining to movements occurring to the greater eccentricity 38° targets only (Fig.  
348 1a), which always required a combined eye and head response (despite being within the  
349 upper range for pure saccadic eye movements). Interpretations relating to the change in  
350 strategy will be raised within the Discussion (see *Whole-body gaze strategy*).

351 *Effect of postural constraint on head sway*

352 Total (n = 11) head displacement (Figure 2a) and mean head displacement variability  
353 (i.e. head sway) in the antero-posterior (AP, see Figure 2b) and medio-lateral axes (ML, see  
354 Figure 2c) were calculated to assess the influence of postural constraints on static balance.  
355 Qualitatively, the area of the 95% confidence ellipses tended to increase between seated and  
356 standing postures (Figure 2a). For the SIT, STAND and BEAM conditions, the 95%  
357 confidence ellipses were skewed to show greater AP displacement, with the NARROW  
358 condition showing the greatest ML displacement. When head sway was analyzed across  
359 postures (Figure 2b,c), a main effect of POSTURE was seen in both the AP ( $F_{(1,709,17.095)} =$   
360  $28.594, p < 0.001, \eta_p^2 = 0.741$ ) and ML axes ( $F_{(3,30)} = 25.692, p < 0.001, \eta_p^2 = 0.720$ ). The  
361 SIT condition consistently produced less sway in both axes when compared to all standing  
362 postures (AP axis: SIT vs. STAND,  $p = 0.009$ ; vs. NARROW,  $p < 0.001$ ; vs. BEAM,  $p =$   
363  $0.009$ ; ML axis: SIT vs. STAND,  $p < 0.001$ ; vs. NARROW,  $p = 0.001$ ; vs. BEAM,  $p <$   
364  $0.001$ ). Significantly greater mean head sway was also seen between standing postures in the  
365 AP axis (STAND vs. NARROW,  $p = 0.001$ ; NARROW vs. BEAM,  $p = 0.004$ ).

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

367 Figure 3 represents mean angular displacements and velocities of the eye, head and  
368 gaze (i.e. combined eye and head angular displacements) for a single representative  
369 participant (S01) to the ipsilateral 38° target. Between postural configurations, eye, head and

370 gaze profiles showed a stereotyped pattern of progression during the initial period of  
371 movement, between eye initiation and its termination at the new fixation position (see Fig. 3,  
372 ~450 ms after light onset). In both tasks (LOOK and REACH), the eye showed a counter-  
373 rotatory deviation following peak eye displacement that allowed for the maintenance of a  
374 consistent gaze position profile.

### 375 *Influence of reaching movements on eye-head metrics*

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

396 *Head metrics.* From Figure 3, a clear difference was identified for final head position  
397 between tasks (LOOK vs. REACH). During simple gaze shifts (LOOK), final head position  
398 did not show a complete rotation of the eyes to be centered within the orbit and tended to  
399 align with peak eye displacement. REACH trials showed a better alignment of the head with  
400 peak gaze displacement and the corresponding target with the eye returning to its original  
401 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  $\sim 8.5^\circ$ ,  $p = 0.009$ ) compared to ipsilateral targets (REACH vs. LOOK mean difference  $\sim 5^\circ$ ,  $p = 0.091$ ). 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  $1.3^\circ$  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

433 position ( $F_{(3,30)} = 13.819, p < 0.001, \eta_p^2 = 0.580$ ) with greater head motion seen when all  
434 standing postures were compared to sitting during reaching (SIT vs. STAND,  $p = 0.020$ ; vs.  
435 NARROW,  $p = 0.002$ ; vs. BEAM,  $p = 0.005$ ). Although this is equivocal in Figure 7 due to  
436 an increased displacement during the ipsilateral SIT condition, on average head displacement  
437 during standing postures was  $3^\circ - 5^\circ$  greater than during the SIT condition. Also, greater  
438 Trunk-in-space and Pelvis-in-space contributions to whole-body movement were evident  
439 during contralateral reaching and varied significantly across postures (Trunk-in-space:  
440 POSTURE x DIRECTION  $F_{(3,30)} = 12.316, p < 0.001, \eta_p^2 = 0.552$ ; Pelvis-in-space:  
441 POSTURE x DIRECTION  $F_{(3,30)} = 8.497, p = 0.007, \eta_p^2 = 0.459$ ). Specifically, both  
442 STAND and NARROW postures were displaced significantly more than their SIT  
443 counterpart (Trunk-in-space: SIT vs. STAND,  $p = 0.001$ ; SIT vs. NARROW,  $p = 0.003$ ;  
444 Pelvis-in-space: SIT vs. STAND,  $p < 0.001$ ; SIT vs. NARROW,  $p < 0.001$ ; SIT vs. BEAM,  $p$   
445  $< 0.001$ ); however, the decreases seen in trunk displacement during the BEAM configuration  
446 did not reach significance when compared to other standing postures (Trunk-in-space:  
447 STAND vs. BEAM,  $p = 0.077$ ; NARROW vs. BEAM,  $p = 0.057$ ).

448 Relative 'on-Segment' displacements only differed for the extent of counter-rotation  
449 between the head and trunk (Head-on-Trunk: POSTURE x DIRECTION  $F_{(3,30)} = 11.021, p =$   
450  $0.001, \eta_p^2 = 0.524$ ). When reaching contralaterally, standing elicited a greater displacement  
451 between the head and trunk compared to both the SIT and BEAM configurations (Head-on-  
452 Trunk: SIT vs. STAND,  $p = 0.006$ ; STAND vs. BEAM,  $p = 0.047$ ), while the NARROW  
453 configuration showed greater displacement when compared to sitting (SIT vs. NARROW,  $p$   
454  $= 0.012$ ).

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

463 For all participants, mean minimum and maximum peak velocities and their timing  
 464 (time to peak) were compared using two-way repeated measures ANOVA (see Supporting  
 465 Tables 5 and 6). After adjustments (see *Statistical analysis*), significant interactions between  
 466 POSTURE x DIRECTION remained for Head-on-Trunk peak minimum velocity ( $F_{(3,30)} =$   
 467  $7.897, p = 0.013, \eta_p^2 = 0.441$ ) and Trunk-in-space peak maximum velocity ( $F_{(3,30)} = 16.855,$   
 468  $p < 0.001, \eta_p^2 = 0.628$ ). In particular, contralateral reaching produced greater counter-  
 469 rotatory Head-on-Trunk velocities (i.e. negative values represent the speed of movement  
 470 occurring towards the opposite direction with respect to the target) between the STAND and  
 471 NARROW postures when compared to sitting (SIT vs. STAND,  $p < 0.001$ ; vs. NARROW,  $p$   
 472  $< 0.001$ ). SIT and BEAM postural configurations also showed reduced contralateral peak  
 473 Trunk-in-space maximum velocities when compared to the other standing postures (SIT vs.  
 474 STAND,  $p = 0.008$ ; vs. NARROW,  $p = 0.001$ ; STAND vs. BEAM,  $p = 0.013$ ; NARROW vs.  
 475 BEAM,  $p = 0.005$ ).

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

#### 485 *Effect of posture on eye, head and finger sequencing*

486 When reaching to ipsilateral targets, mean onset latencies (Figure 9a,  $n = 11$   
 487 participants) for the eye, head and finger showed a similar sequence of initiation across each  
 488 postural configuration. The eye consistently led the head and the finger; however, small  
 489 relative changes in the timing between each onset were observed across postures. When  
 490 reaching was executed contralaterally (Fig. 9b), a similar sequence was displayed for the SIT  
 491 and STAND postural configurations, but shifted for the more challenging standing postures  
 492 (i.e. NARROW and BEAM) to a sequence where the eye followed the head. Despite this,

493 there were no significant interactions in the absolute timing of eye, head or finger onset  
494 across POSTURE or DIRECTION. As expected from the greater delay to finger initiation  
495 seen across all conditions in Figure 9, a main effect of SEGMENT ( $F_{(2,20)} = 19.075$ ,  $p =$   
496  $<0.001$ ,  $\eta_p^2 = 0.656$ ) was present and was significant for both the eye (vs. FINGER,  $p =$   
497  $0.009$ ) and head onsets (vs. FINGER,  $p < 0.001$ ).

#### 498 *Relationships between eye, head and finger onsets*

499 In order to gain insight into how the eye, head and finger were coordinated at their  
500 initiation across postural configurations, correlations were calculated using Type II major  
501 axis regressions (see *Statistical analysis*). Figure 10 shows that positive correlations were  
502 observed for relationships between the eye-head (Fig. 10a and b), eye-finger (Fig. 10c and d)  
503 and head-finger onsets (Fig. 10e and f) regardless of posture. Relationships between the eye,  
504 head and finger for movement to the ipsilateral target reported high correlations (Fig. 10;  
505 right side panels,  $r^2$  range: 0.714 - 0.932), while a number of relationships for contralateral  
506 target remained moderate (Fig. 10; left side panels,  $r^2$  range: 0.473 - 0.929). Of note, the  
507 range of correlations between the head and finger showed little change across POSTURE and  
508 DIRECTION (Head-Finger STAND vs. BEAM;  $r^2 = 0.60 - 0.64$  vs  $r^2 = 0.68 - 0.75$ ), with  
509 coupling of eye and head onsets weakening in their correlations as postural configurations  
510 increased in their stability requirements (Eye-Head STAND vs. BEAM:  $r^2 = 0.75 - 0.84$  vs  $r^2$   
511  $= 0.35 - 0.67$ ).

512 When correlation coefficients ( $r$ ) were  $z$ -transformed (Fig. 11a) to allow statistical  
513 comparisons to be made across conditions, eye-finger and head-finger interactions showed  
514 smaller changes in their relationship when compared to eye-head interactions. A weaker  
515 relationship for the BEAM configuration (vs. STAND,  $p = 0.034$ ) was found during reaching  
516 to the contralateral target. Comparison of regression slopes (i.e. regression coefficients, Fig.  
517 11b) revealed a change between the SIT and BEAM postural configurations ( $p = 0.043$ ) for  
518 the eye-head interaction during contralateral reaching.

519

**DISCUSSION**

520  
521       Considering the coupled nature of visuomotor and whole-body postural control during  
522 action, this study aimed to understand how changing equilibrium constraints (in the form of  
523 different postural configurations) influenced the initiation of eye, head and arm movements.  
524 In contrast to our predictions, a lack of statistical differences were revealed in eye-head  
525 metrics, initiation of eye, head and arm movement, and gaze accuracy across conditions in  
526 spite of kinematic differences suggesting that postural control was likely incorporated into the  
527 initiating gaze shift. Although the tight coupling of the eye and head can be altered under a  
528 variety of conditions (Freedman, 2008; Fuller, 1992; Zangermeister and Stark, 1982),  
529 including when arm movements are incorporated into a visually-guided reaching task  
530 (Carnahan and Martenuik, 1991; Pelz et al., 2001; Smeets et al., 1996), we did not find  
531 evidence to support this in the present study. We discuss how our results fit into models of  
532 gaze and postural control mechanisms based on the premise that posture constraints revealed  
533 little change in gaze behavior.

*Eye-head metrics*

535       Despite latencies of eye shifts being longer than those generally seen for pure saccadic  
536 eye movements (approx. 200 - 250 ms, Gaveau et al., 2014), values remained within the  
537 bounds reported for recordings of whole-body movements, including whole-body turning and  
538 reaching (310-460 ms, Carnahan and Martenuik, 1991; 310–320 ms, Scotto Di Cesare et al.,  
539 2013; 312.5 – 406 ms Vercher et al., 1994). A number of factors may have been responsible  
540 for the longer latencies which we discuss below;

541       First, the distance of the fixation targets may have influenced the latency of the  
542 required gaze shift. Often, visual targets are situated within peri-personal space (i.e. within  
543 arm's reach) and nearer targets are known to elicit shorter saccadic latencies than those  
544 farther from the body (Yang et al., 2002). Also, for the REACH instruction, initial gaze shifts  
545 were made to fixation positions further away from the participant, when compared to the  
546 closer and 'remembered' reaching positions. While unlikely, we cannot directly assess the  
547 role that vergence may have played in visuomotor control in the current study (as eye  
548 measures were recorded via EOG). If a combined gaze shift and convergence task to the  
549 remembered position in space occurred, we would expect that latencies would have increased  
550 by ~20 ms (Yang et al., 2002). Considering the implications above, the facilitation of gaze  
551 shifts seen with the addition of a reaching movement may have been masked for some



552 conditions (Bekkering et al., 1994; Dean et al., 2011; Snyder et al., 2002) as mean differences  
553 were ~10 ms (range: -14 ms : 25 ms). Interestingly, such facilitation was only evident during  
554 ipsilateral reaching when seated and balanced upon the BEAM (Fig. 4a). This is despite the  
555 BEAM condition eliciting the longest eye latencies (observed previously when postural  
556 constraint is increased - Legrand et al., 2016).

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

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

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

596 *Eye-head-finger sequencing during movement preparation*

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

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

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

648 study, the strength of correlations relating to the head and finger (Fig. 10) provide further  
649 evidence that head control is a necessity in achieving oculomotor goals in a combined whole  
650 body task (Anastasopoulos et al., 2015). Whether this coordination of gaze and reaching is  
651 driven by control of eye, head or gaze parameters is still of debate (Daye et al., 2014;  
652 Freedman, 2008; Guitton et al., 2003; Haji-Abolhassani et al., 2016).

### 653 Whole-body gaze strategy

654 The consistent patterns of gaze trajectory and accuracy (see the standard deviations in  
655 Figure 5 and 7), coupled with the greater variability of eye and head components (in  
656 particular the variable counter-rotation of the eye once at fixation, see Figure 3) strengthen  
657 the notion that gaze is a controlled variable in the execution of visuomotor tasks. This seems  
658 in competition to models that have often been used to describe head-free gaze shifts  
659 (Freedman et al., 2008). In fact, models of feedback-mediated gaze position error have  
660 previously been shown to describe the spatiotemporal coupling of the eye and head during  
661 long torque head perturbations, resulting in gaze trajectories that are invariant to their non-  
662 perturbed counterparts (Boulangier et al., 2012). More recently, gaze modelling incorporating  
663 both neuroanatomical and classic behavioral findings (e.g. main sequence) has used gaze  
664 position error to simulate eye and head trajectories despite a difference in gaze and head  
665 goals (Haji-Abolhassani et al., 2016). Such a mechanism may easily account for the  
666 differences in head movement strategy based on target eccentricity, whereby a purely  
667 saccadic eye movement was produced during gaze shifts to the smaller eccentricity of 23°.  
668 While models of gaze control often limit themselves to the interactions between the eye, head  
669 and gaze components, some have also considered the necessity of whole-body coordination  
670 during gaze shifts (Daye et al., 2014). Daye and colleagues suggested that a hierarchical  
671 model controls linked segments via a number of feedback loops. In doing so, proximal  
672 segments may serve differing goals but are coupled to the goals of the most distal segment (in  
673 this case, gaze) whose feedback is dictated by a global goal. If head and gaze position are  
674 controlled variables (rather than eye position), this might explain the stronger relationships  
675 seen in eye-head and head-finger onsets in the current study. A hierarchical model may also  
676 account for the interactions between posture and direction seen across a number of axial  
677 segments while gaze trajectories and accuracy were maintained. This includes the Clear  
678 changes in strategy used to coordinate body segments that occurred between movements  
679 made to ipsilateral and contralateral targets. In particular, greater involvement of the large

680 segments of the trunk and (to a lesser extent) pelvis were necessary for target attainment to  
681 the contralateral target yet their movement was minimized for ipsilateral reaching (Fig. 7, ‘in-  
682 space’ displacements). The movement patterns in the current study aligned with descriptions  
683 of predictable, ‘return-bound’ turning (Scotto Di Cesare et al., 2013). These authors  
684 postulated that changes in coordination (alongside oculomotor delays) are introduced for  
685 predictable targets to allow for the integration of appropriate muscle activity to produce  
686 APAs. Whether this represents a reduction in the discrepancy between head-centered  
687 vestibular coordinates and body-centered trunk coordinates, which may be useful in reducing  
688 the processing costs of such APAs (for movement generation - Solomon et al., 2006) is  
689 unclear; however, it would align with a gaze model that requires an explicit head goal (and  
690 the efference copy that accompanies it – Daye et al., 2014).

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

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

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

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

744 within the posterior parietal cortex associated with the planning and execution of eye and arm  
745 movements, and the re-allocation of attentional resources.

746 Conclusion:

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

756

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760 **CONFLICT OF INTEREST**

761 The authors state that they have no conflict of interest.

762 **AUTHOR CONTRIBUTIONS**

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

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957 **FIGURE LEGEND**

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

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

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

983 **Figure 4.** Mean (n=11) changes in eye metrics between simple gaze fixations (LOOK) and  
984 whole-body reaching movements (REACH) across each postural configuration. Bounded  
985 boxes represent values for movements to either the *contralateral* (black) or *ipsilateral* (grey)  
986 38° target for measures of (**a**) eye onset, (**b**) peak eye velocity, (**c**) duration of saccade, and  
987 (**d**) eye contribution to gaze amplitude. Comparisons of means show that regardless of task,  
988 direction or postural configuration, measures of eye metrics were not significantly altered.  
989 Error bars indicate variability as standard deviation.

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

997 **Figure 6.** Mean (n=11) changes in final head position (**a**) and head contribution to gaze (**b**)  
 998 between simple gaze fixations (LOOK) and whole-body reaching movements (REACH)  
 999 across each postural configuration. Bounded boxes represent values for movements to either  
 1000 the *contralateral* (black) or *ipsilateral* (grey) 38° target. Comparisons of means show that  
 1001 final head position was reduced for *contralateral* gaze shifts (LOOK) compared to reaching  
 1002 ( $p = 0.009$ ) with a similar trend for *ipsilateral* movements ( $p = 0.091$ ). Head contributions to  
 1003 gaze followed a similar reduction during simple gaze shifts (LOOK) towards *contralateral*  
 1004 targets ( $p = 0.016$ ). Error bars indicate variability as  $\pm 1$  standard deviation for individual  
 1005 postures and 95% confidence intervals when postural configurations were pooled.

1006 **Figure 7.** Mean kinematic changes, including absolute and relative axial angular  
 1007 displacements, for a representative subject (S01) across four postural configurations during  
 1008 reaching. Traces are aligned to initial light stimulus onset for each posture (time = 0)  
 1009 preceding eye (*E*) and finger movement initiation (*F*). For absolute or, ‘*in-space*’ measures,  
 1010 positive values are indicative of segmental displacements or velocities towards the target of  
 1011 interest, i.e. reaching movements producing *contralateral* segment movements are positive  
 1012 for the *contralateral* target. For relative or, ‘*on-segment*’ measures, positive values indicate  
 1013 movement of the anatomically superior segment upon the inferiorly placed segment. All  
 1014 traces are represented by mean values (solid)  $\pm 1$  standard deviation (shaded).

1015 **Figure 8.** Mean absolute and relative angular velocity profiles for a representative subject  
 1016 (S01) across four postural configurations during reaching. Traces are aligned to initial light  
 1017 stimulus onset for each posture (time = 0) preceding eye (*E*) and finger movement initiation  
 1018 (*F*). The head often preceded movement of the eye (black, dashed) and preceded finger  
 1019 movement. Segmental velocities across the four postural configurations have been scaled  
 1020 similarly for ease of comparison. All traces are represented by mean values (solid)  $\pm 1$   
 1021 standard deviation (shaded).

1022 **Figure 9.** Eye, head and finger movement initiation from light stimulus illumination across  
 1023 postural configurations for *contralateral* (**a**) and *ipsilateral* (**b**) reaching movements. While  
 1024 *ipsilateral* reaching movements showed a distinct sequence of initiation with the eye  
 1025 preceding both the head and finger regardless of postural configuration, *contralateral*  
 1026 reaching saw a preference for ‘head-first’ movement initiation for the NARROW and BEAM  
 1027 configurations. Error bars indicate variability as  $\pm 1$  standard deviation.

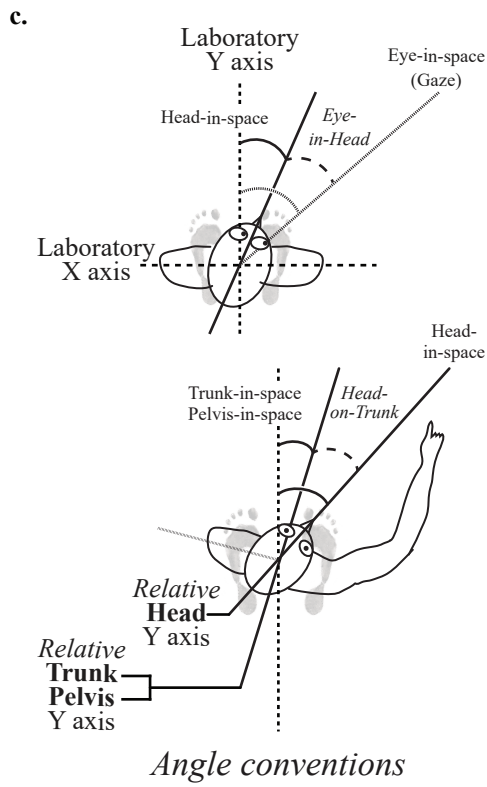
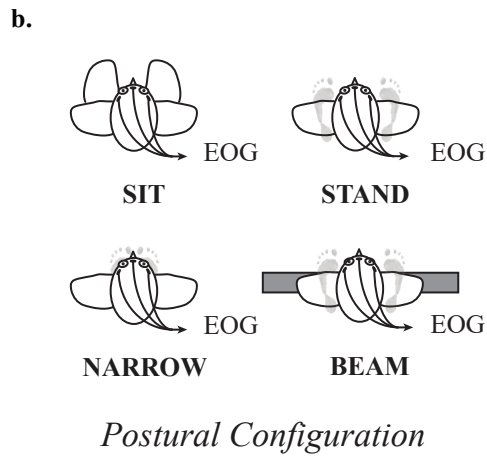
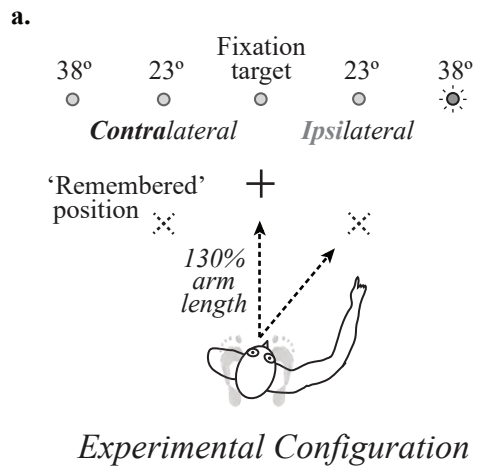
1028 **Figure 10.** Major axis regression analyses and coefficients of determination ( $r^2$ ) for  
 1029 relationships between eye-head (**a-b**), eye-finger (**c-d**), and head-finger onsets (**e-f**) grouped  
 1030 by target direction (*contralateral*, left panels; *ipsilateral*, right panels). Coefficients of  
 1031 determination for the head and finger exhibited a more consistent relationship across postural  
 1032 configurations and direction compared to the eye and head or, eye and hand. *Ipsilateral*  
 1033 targets (**b, d, f**) showed stronger correlations regardless of postural configuration, which  
 1034 began to diverge when reaching to *contralateral* targets (**a, c, e**).

1035 **Figure 11.** Comparison of *z*-transformed correlation coefficients (**a**) and regression  
 1036 coefficients (**b**) for eye-head, eye-finger, and head-finger onset relationships across the four

1037 postural configurations. While interactions were generally weaker for reaching to  
1038 **contra**lateral targets (black, solid bars) when compared to **ipsi**lateral reaching (grey, solid  
1039 bars), significantly weaker correlations were only seen between the eye and head (STAND  
1040 vs. BEAM;  $p_{adj} = 0.034$ ). Error bars indicate variability as  $\pm 1$  standard deviation.

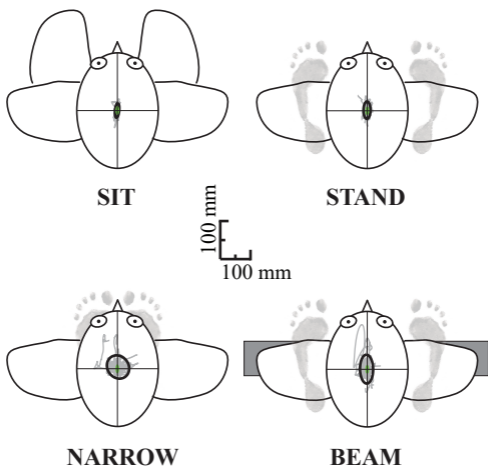
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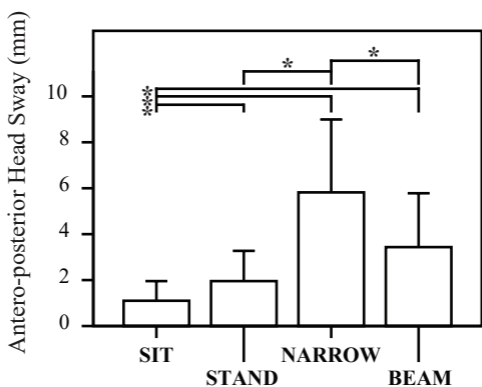


**Figure 1**  
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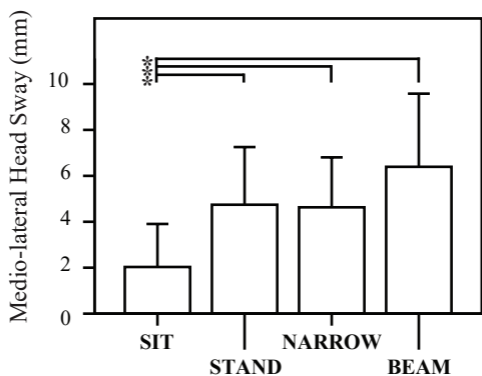
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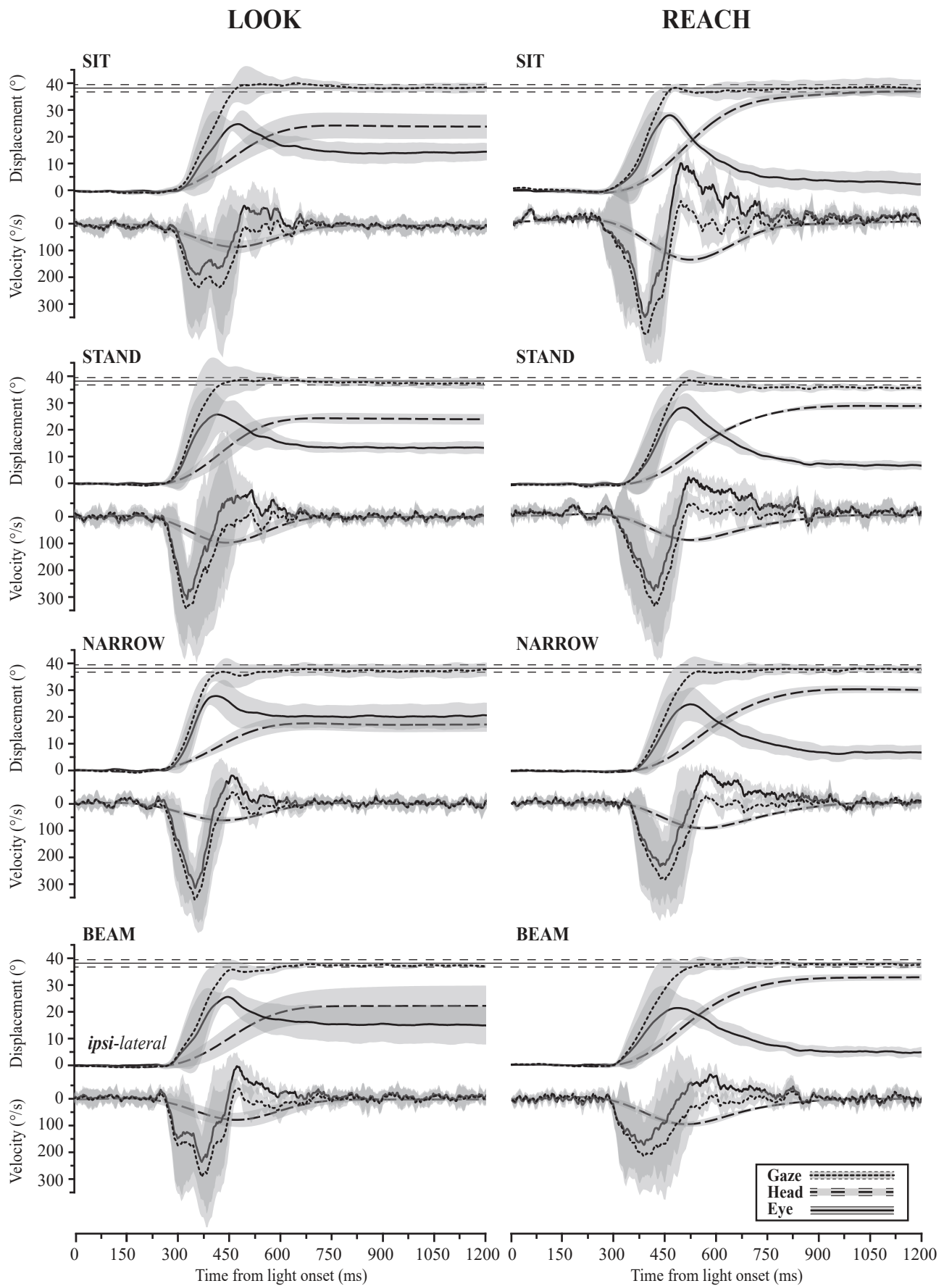


c.

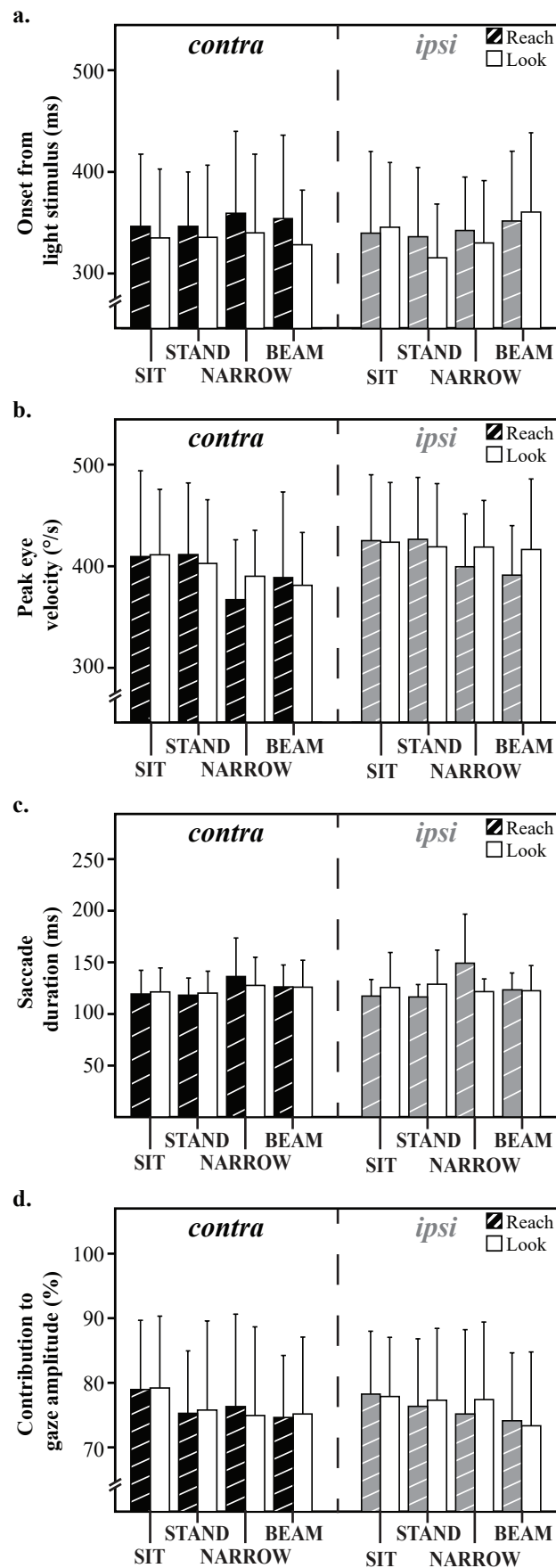


**Figure 2**

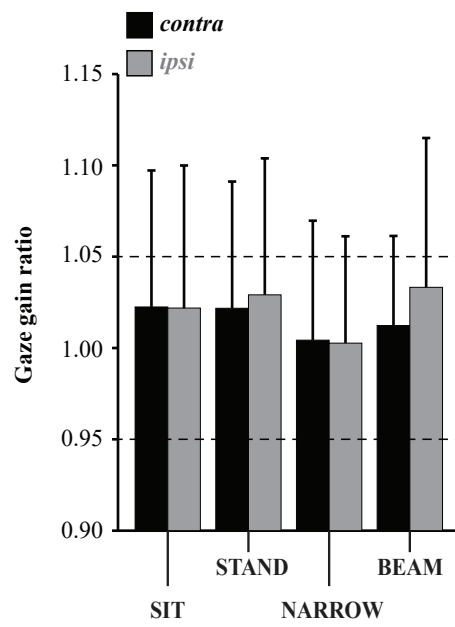
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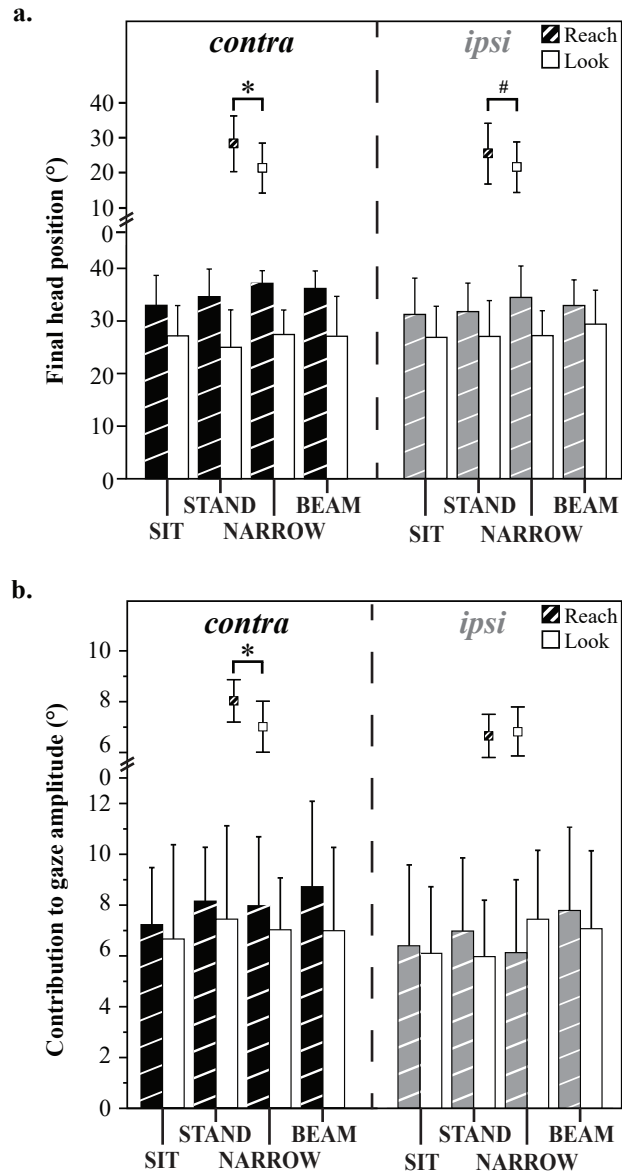
**Figure 3**  
**Stamenkovic et al., 2018**



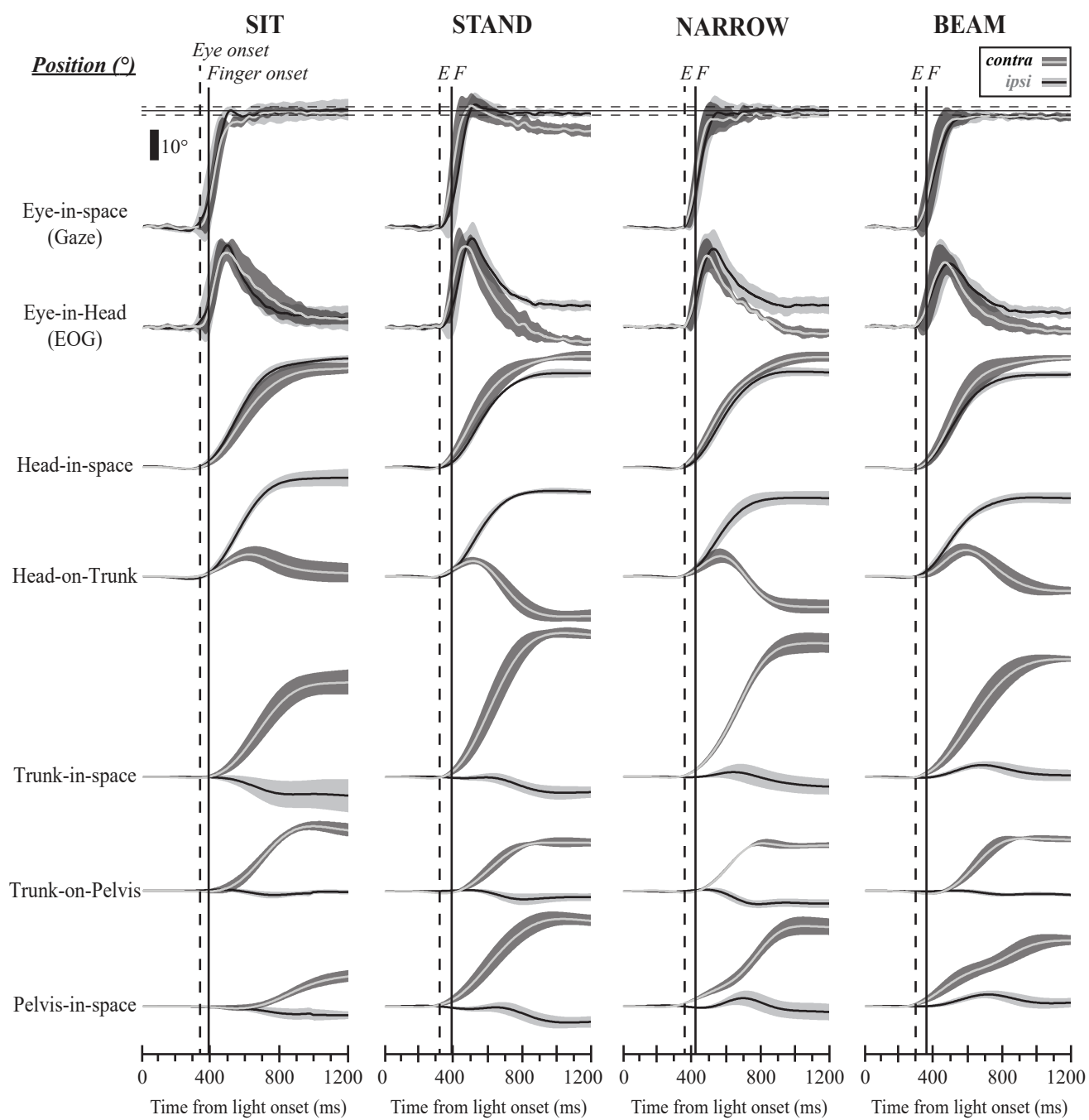
**Figure 4**  
**Stamenkovic et al., 2018**



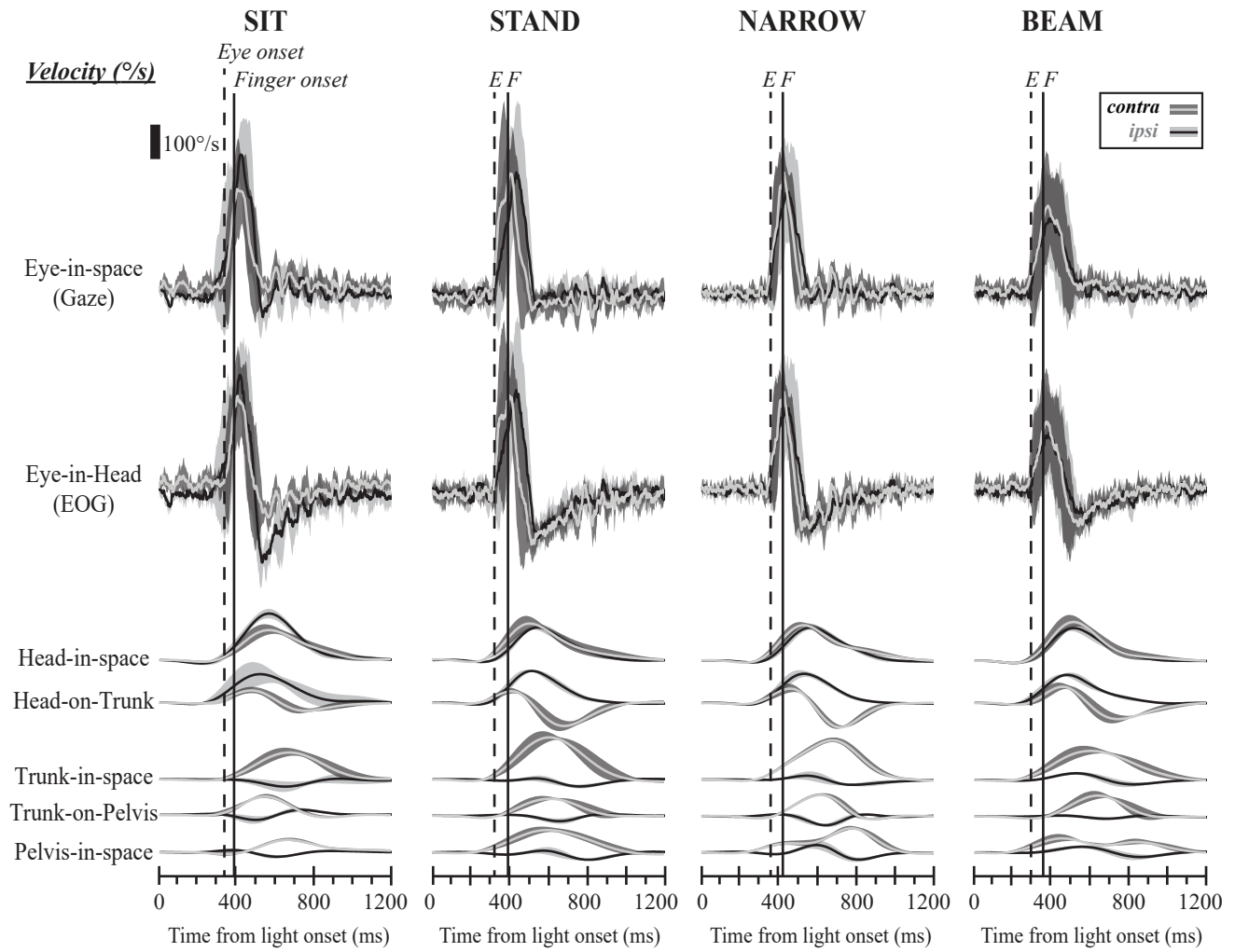
**Figure 5**  
**Stamenkovic et al., 2018**



**Figure 6**  
**Stamenkovic et al., 2018**

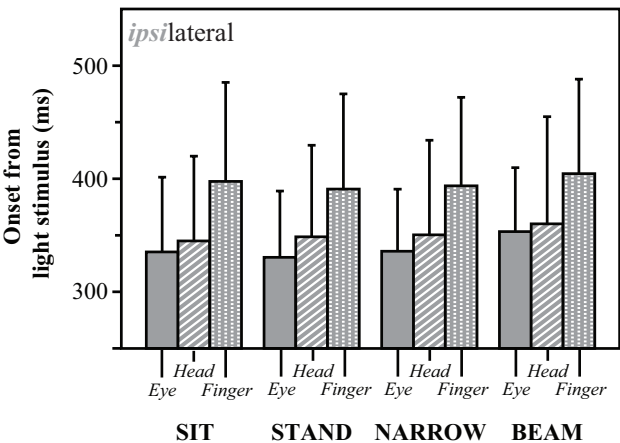
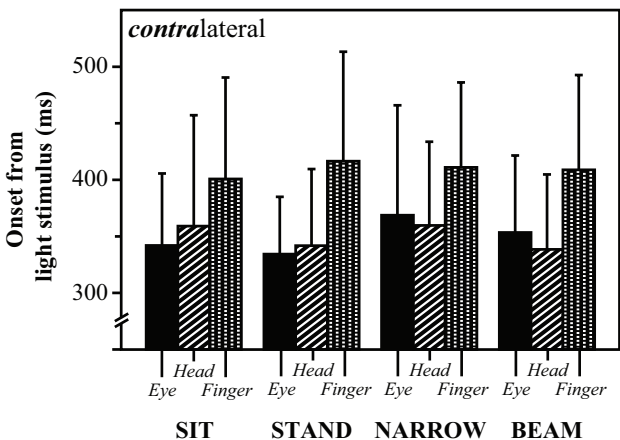


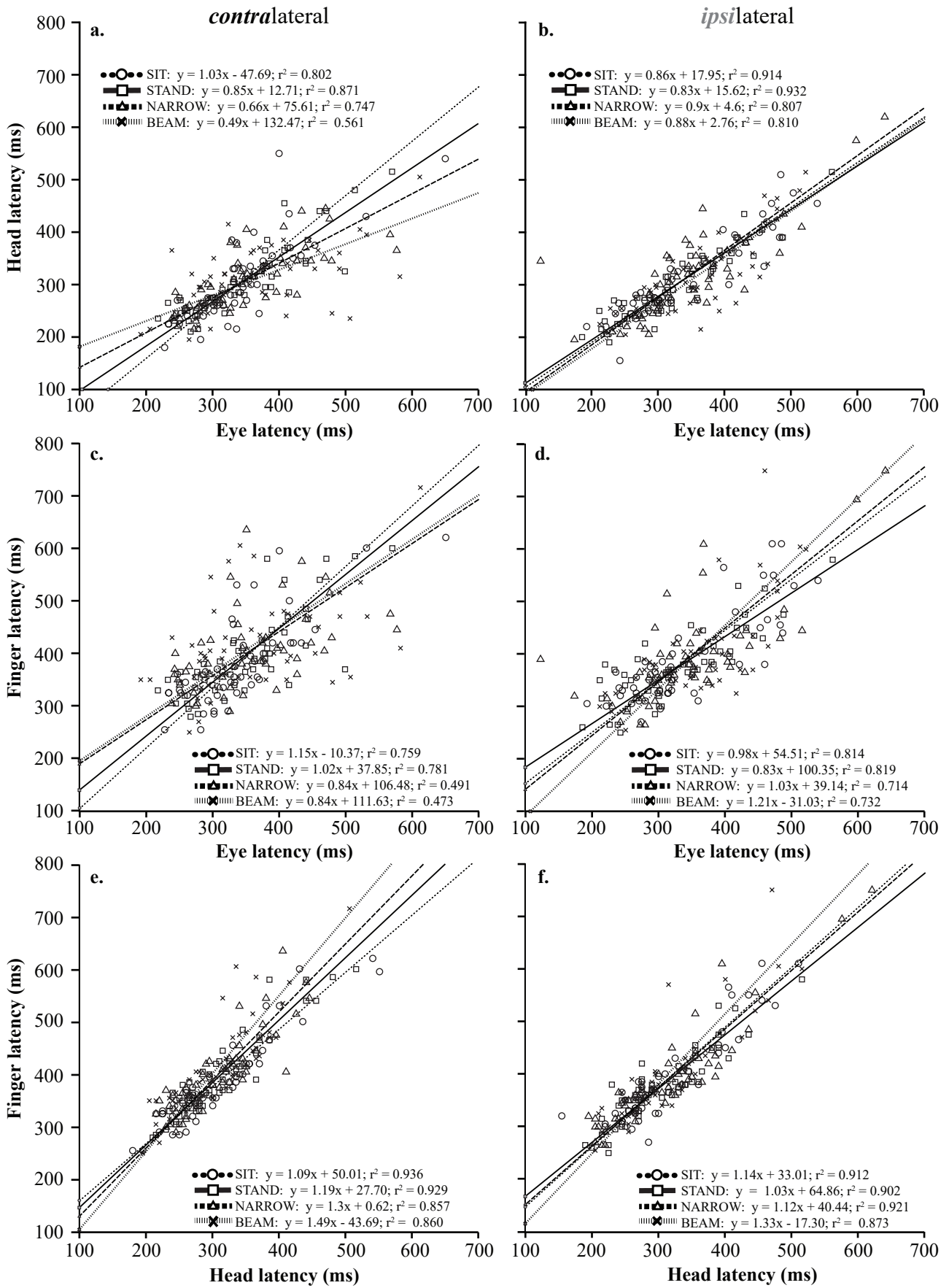
**Figure 7**  
**Stamenkovic et al., 2018**



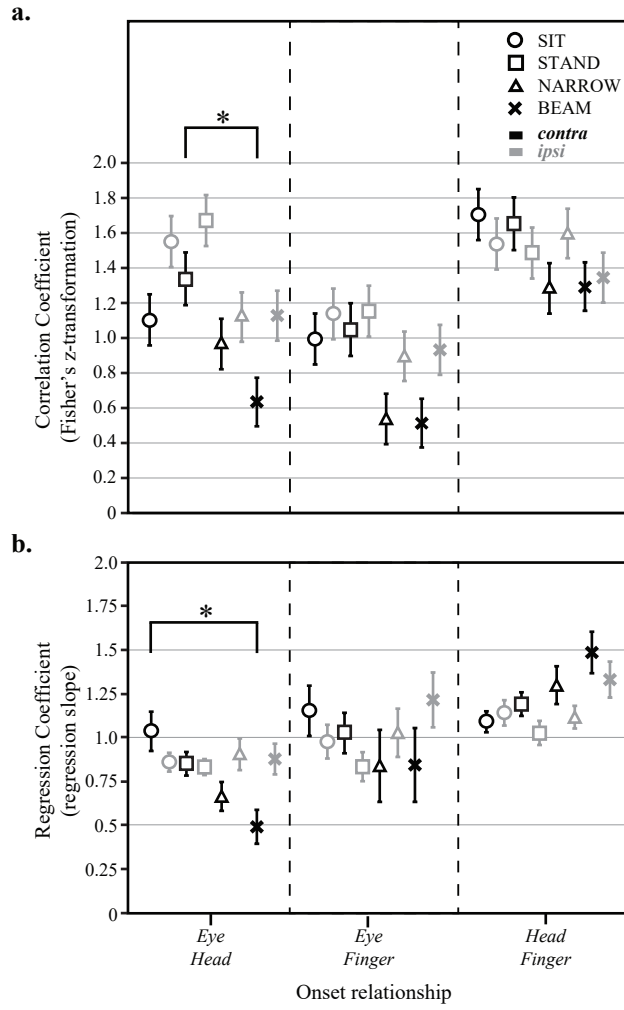
**Figure 8**  
**Stamenkovic et al., 2018**



**a.****b.****Figure 9****Stamenkovic et al., 2018**



**Figure 10**  
**Stamenkovic et al., 2018**



**Figure 11**  
**Stamenkovic et al., 2018**