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3
4 DO POSTURAL CONSTRAINTS AFFECT EYE, HEAD AND ARM COORDINATION?
5
6 Alexander STAMENKOVIC [1,2]
7 Paul J. STAPLEY [1,2]
8 Rebecca ROBINS [3]
9 Mark A. HOLLANDS [3]
10
11 [1] Neural Control of Movement Laboratory
12 School of Medicine, Faculty of Science, Medicine & Health
13 University of Wollongong
14 Northfields Avenue
15 Wollongong NSW 2522, AUSTRALIA
16
17 [2] Illawarra Health & Medical Research Institute (IHMRI), Gerard Sutton Building
18 University of Wollongong
19 Northfields Avenue
20 Wollongong NSW 2522, AUSTRALIA
21
22 [3] Research Institute for Sports and Exercise Sciences (RISES)
23 Tom Reilly Building
24 School of Sport and Exercise Sciences, Faculty of Science
25 Liverpool John Moores University
26 Byrom Street
27 Liverpool L3 3AF, UNITED KINGDOM
28
29 Address of corresponding author:
30 Mr. Alexander STAMENKOVIC
31 School of Medicine
32 Faculty of Science, Medicine & Health
33 University of Wollongong
34 Northfields Avenue
35 Wollongong NSW 2522
36 AUSTRALIA
37 Tel: +61-(02)-4221-4584
38 Fax: +61-(02)-4221-5945
39 Email: astamenk@uow.edu.au
40
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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.

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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,

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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 ± 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: ~3°) were projected. Targets

189 were positioned at an eccentricity of 23° and 38° 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 5th order polynomial

264   Savitzy-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 ± 30 - 40° 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°/s (Daye et al.,

280 2014; Pélisson et al., 2001). This was compared to other velocity measures (e.g. 20°/s, 3%

281 and 5% peak eye velocity) with minimal variation in onset detection (average difference = 2

282 ms). A velocity threshold of 15°/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 ~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).

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 $Z_{crit} = 3.20$, $p < 0.0007$) prior to significance being calculated

332 according to the following formula:

333

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

335

336 $\left| Z_{calc} \right| < \left| Z_{(crit)} \right|$, H_0 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° 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, η_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.

402   3; right side panels). As such, final head position and the contribution of its displacement to

403   gaze amplitude were quantified for all participants. Figure 6 represents the mean changes that

404   occurred for head displacement variables between TASK and DIRECTION across postural

405   configurations. Changes seen in the representative participant (Figure 3) were reflective of all

406   participants as a three-way repeated-measures ANOVA (see Supporting Table 2) revealed a

407   significant interaction between TASK and DIRECTION ($F_{(1,10)}$ = 5.293, p = 0.044, η_p^2 =

408   0.346) with reduced head rotation occurring within the LOOK task (Fig. 6a). This was more

409   prominent for shifts to contralateral targets (REACH vs. LOOK mean difference ~8.5°, p =

410   0.009) compared to ipsilateral targets (REACH vs. LOOK mean difference ~5°, p = 0.091).

411   In a similar vein, a three-way repeated measures ANOVA revealed that the contribution of

412   the head to the initial gaze shift changed as a function of TASK and DIRECTION ($F_{(1,10)}$ =

413   11.294, p = 0.007, η_p^2 = 0.529) across conditions (Fig. 6b). On average, the head contributed

414   an additional 1.3° to gaze when reaching to contralateral targets (p = 0.016).

415   *Eye, head, trunk and pelvis kinematics across postural configurations*

416   Figure 7 shows absolute and relative angular displacement profiles for the eye, head,

417   trunk and pelvis during reaching movements for a representative participant (S01). Typically,

418   differences in kinematics were most obvious when examined between directions (i.e. ipsi- vs.

419   contralateral). In particular, the difference in end positions of eye and head interactions (Fig.

420   7, Eye-in-Head, Head-in-space) between ipsi- and contralateral movements allowed for the

421   maintenance of final gaze position (Fig. 7, Eye-in-space). Also, axial segments contributed

422   differently to the extent of reaching, with movement of the trunk and pelvis showing little

423   displacement for ipsilateral targets. Trunk and pelvis motion during the SIT and STAND

424   postural configurations was often counter-rotatory in nature (i.e. rotating in the opposite

425   direction from the specified target), especially when compared to the NARROW and BEAM

426   configurations. However, their relative movement (i.e. Trunk-on-Pelvis; see Fig. 7) remained

427   consistent across postural configurations despite changes in trunk displacement (Fig. 7,

428   Trunk-in-space). While segment movement profiles remained qualitatively similar between

429   postures, differences in the amplitude of final positions (most of which are reflected in our

430   representative participant, Fig. 7) were also evident when analyzing the entire cohort.

431   For absolute 'in-space' displacements, a two-way repeated measures ANOVA (see

432   Supporting Tables 3 and 4) revealed a significant main effect of POSTURE on final head

433   position ($F_{(3,30)}$ = 13.819, $p < 0.001$, η_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° - 5° 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, $p < 0.001$, η_p^2 = 0.552; Pelvis-in-space:

441   POSTURE x DIRECTION $F_{(3,30)}$ = 8.497, $p = 0.007$, η_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, η_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, η_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

520   **DISCUSSION**

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.

534   *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 ± 71 ms; hand: 376 ± 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 (Boulanger 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   reciprobit 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

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 (*ipsi*lateral) and opposite side (***contra***lateral) 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° *ipsi*lateral 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 (± 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 ***contra***lateral (black) or *ipsi*lateral (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 ***contra***lateral and *ipsi*lateral 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 ± 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 *contra*lateral (black) or *ipsi*lateral (grey) 38° target. Comparisons of means show that
1001 final head position was reduced for **contra**lareral gaze shifts (LOOK) compared to reaching
1002 ($^*p = 0.009$) with a similar trend for *ipsi*lateral movements ($^\#p = 0.091$).Head contributions to
1003 gaze followed a similar reduction during simple gaze shifts (LOOK) towards *contra*lateral
1004 targets ($^*p = 0.016$). Error bars indicate variability as ± 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 *contra*lateral segment movements are positive
1012 for the *contra*lateral 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) ± 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 proceeded 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) ± 1
1021 standard deviation (shaded).

1022 *Figure 9.* Eye, head and finger movement initiation from light stimulus illumination across
1023 postural configurations for *contra*lateral (**a**) and *ipsi*lateral (**b**) reaching movements. While
1024 *ipsi*lateral reaching movements showed a distinct sequence of initiation with the eye
1025 preceding both the head and finger regardless of postural configuration, *contra*lateral
1026 reaching saw a preference for 'head-first' movement initiation for the NARROW and BEAM
1027 configurations. Error bars indicate variability as ± 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 (*contra*lateral, left panels; *ipsi*lateral, 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. *Ipsi*lateral
1033 targets (**b, d, f**) showed stronger correlations regardless of postural configuration, which
1034 began to diverge when reaching to *contra*lateral 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.
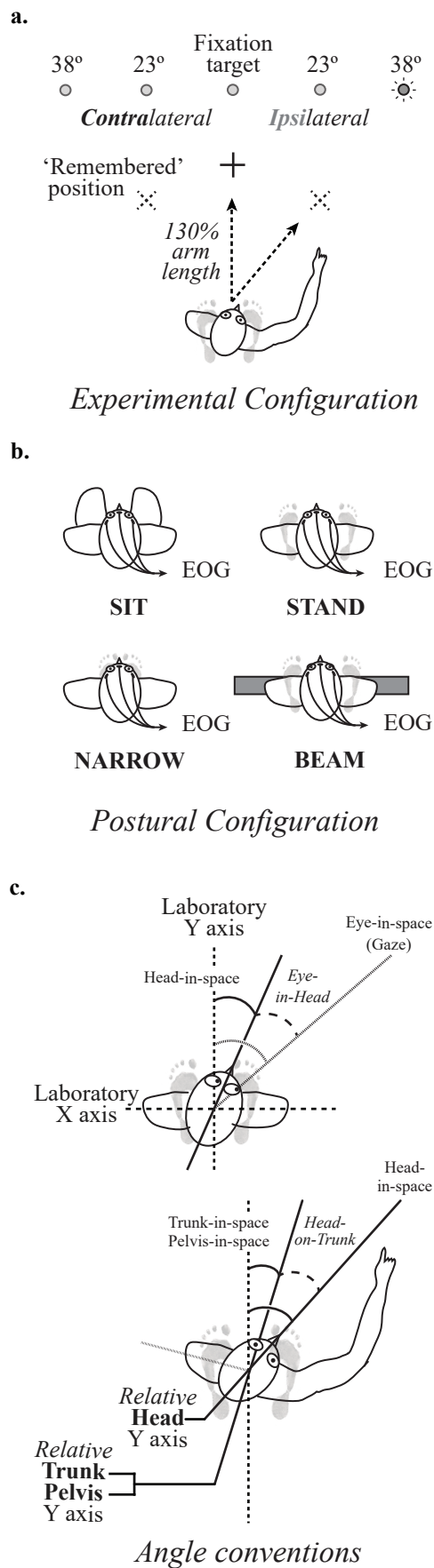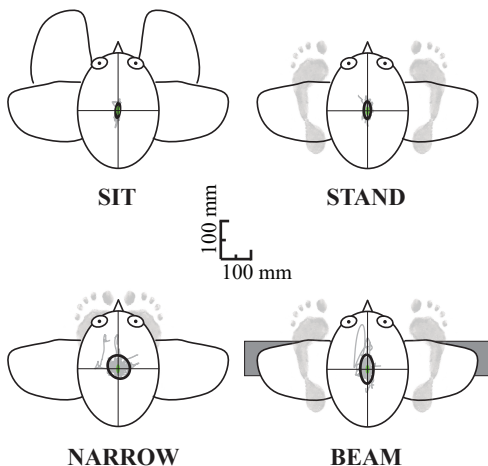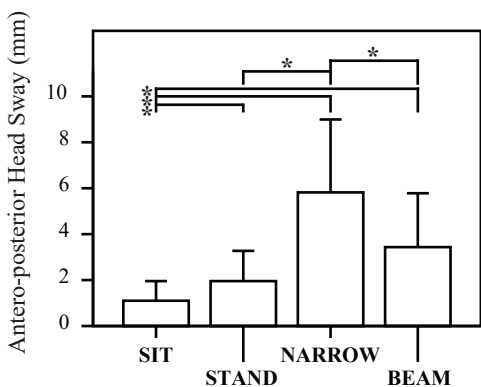
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a.

Fixation target

38º   23º   Fixation target   23º   38º

*Contra*lateral   *Ipsi*lateral

'Remembered' position

130% arm length

Experimental Configuration

b.

SIT — EOG   STAND — EOG

NARROW — EOG   BEAM — EOG

Postural Configuration

c.

Laboratory Y axis

Eye-in-space (Gaze)

Head-in-space   *Eye-in-Head*

Laboratory X axis

Head-in-space

Trunk-in-space Pelvis-in-space   *Head-on-Trunk*

Relative **Head** Y axis

Relative **Trunk** **Pelvis** Y axis

Angle conventions

Figure 1
Stamenkovic et al., 2018
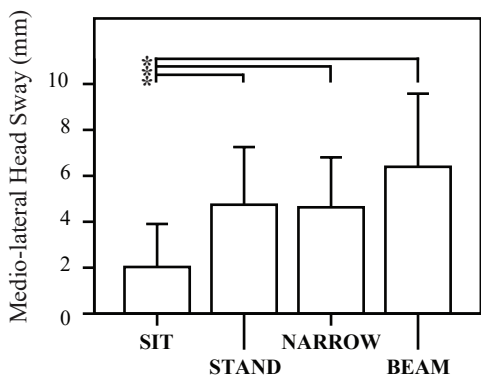
Figure 2
Stamenkovic et al., 2018

LOOK

SIT

STAND

NARROW

BEAM

ipsi-lateral

REACH

SIT

STAND

NARROW

BEAM

Gaze
Head
Eye

Time from light onset (ms)
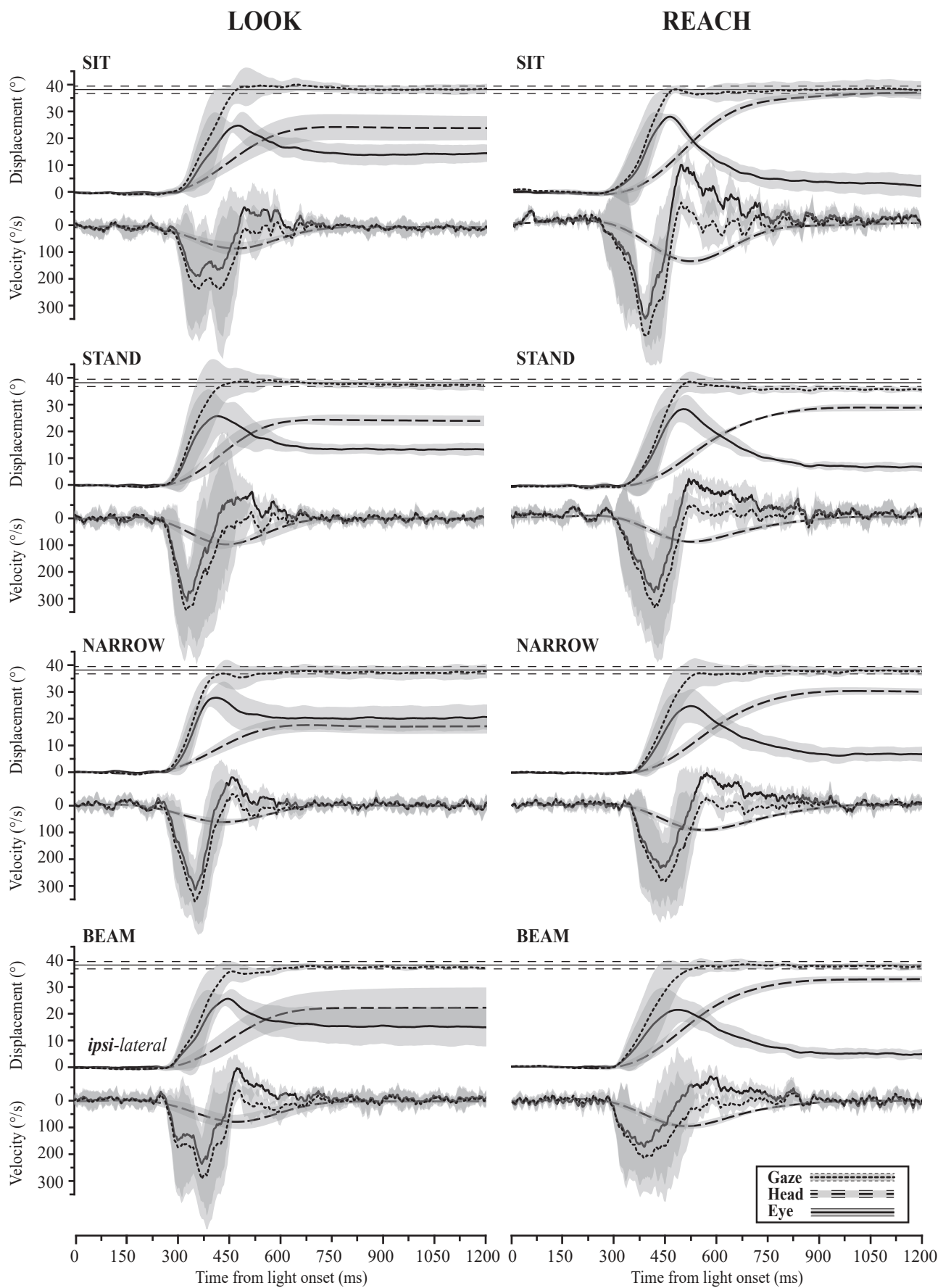
Displacement (°)

Velocity (°/s)

Figure 3
Stamenkovic et al., 2018
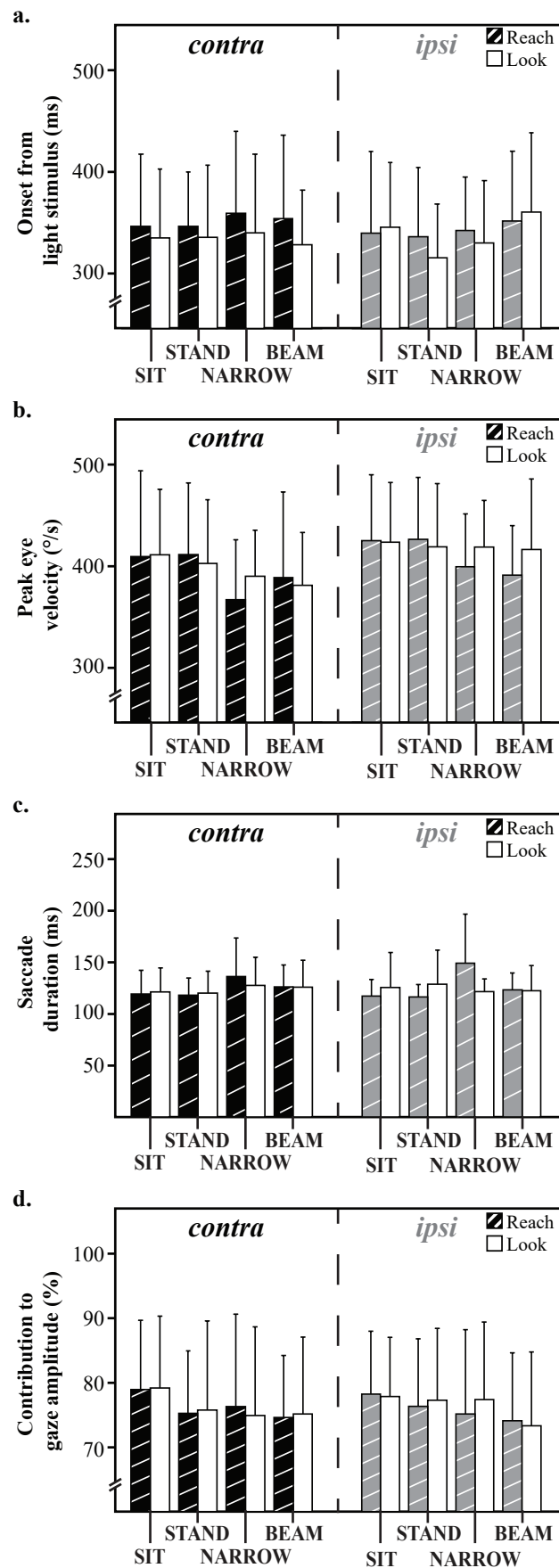
Figure 4
Stamenkovic et al., 2018
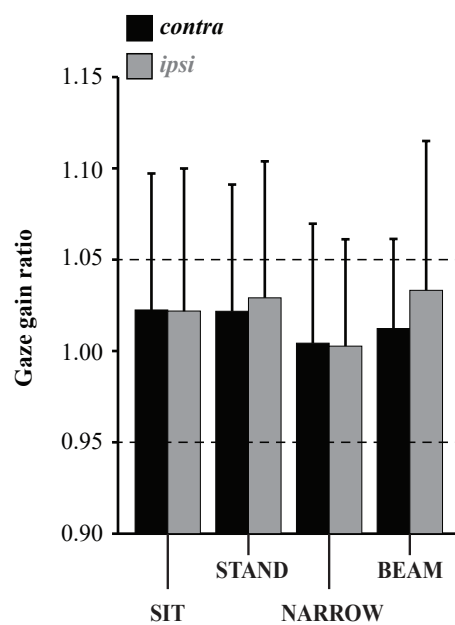
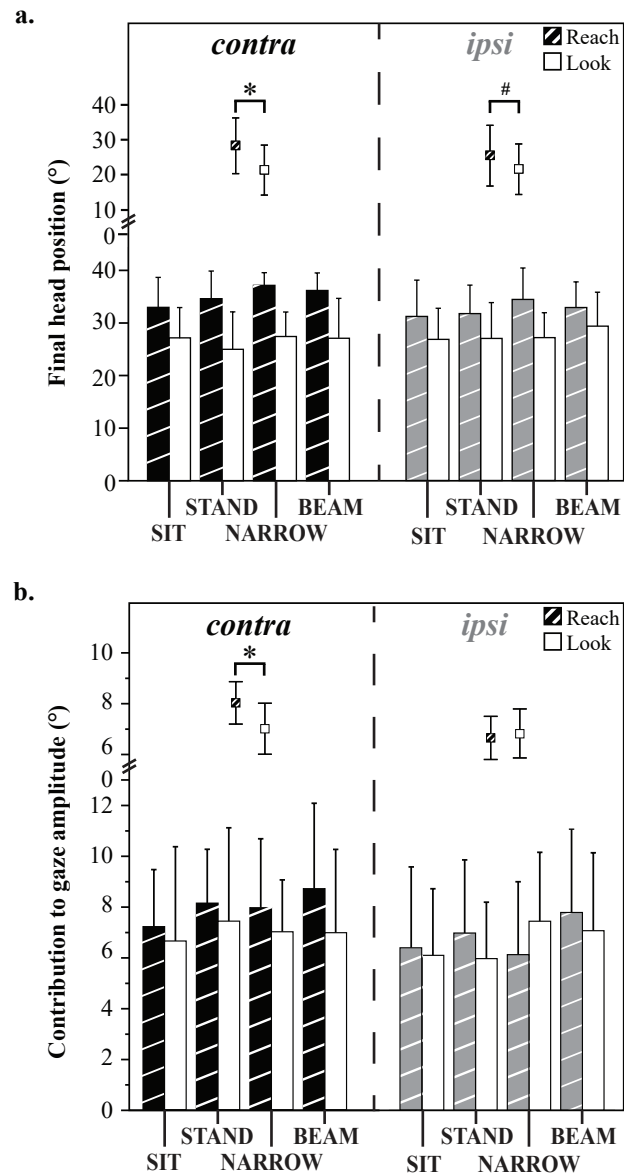**Figure 5**
Stamenkovic et al., 2018

Figure 6
Stamenkovic et al., 2018
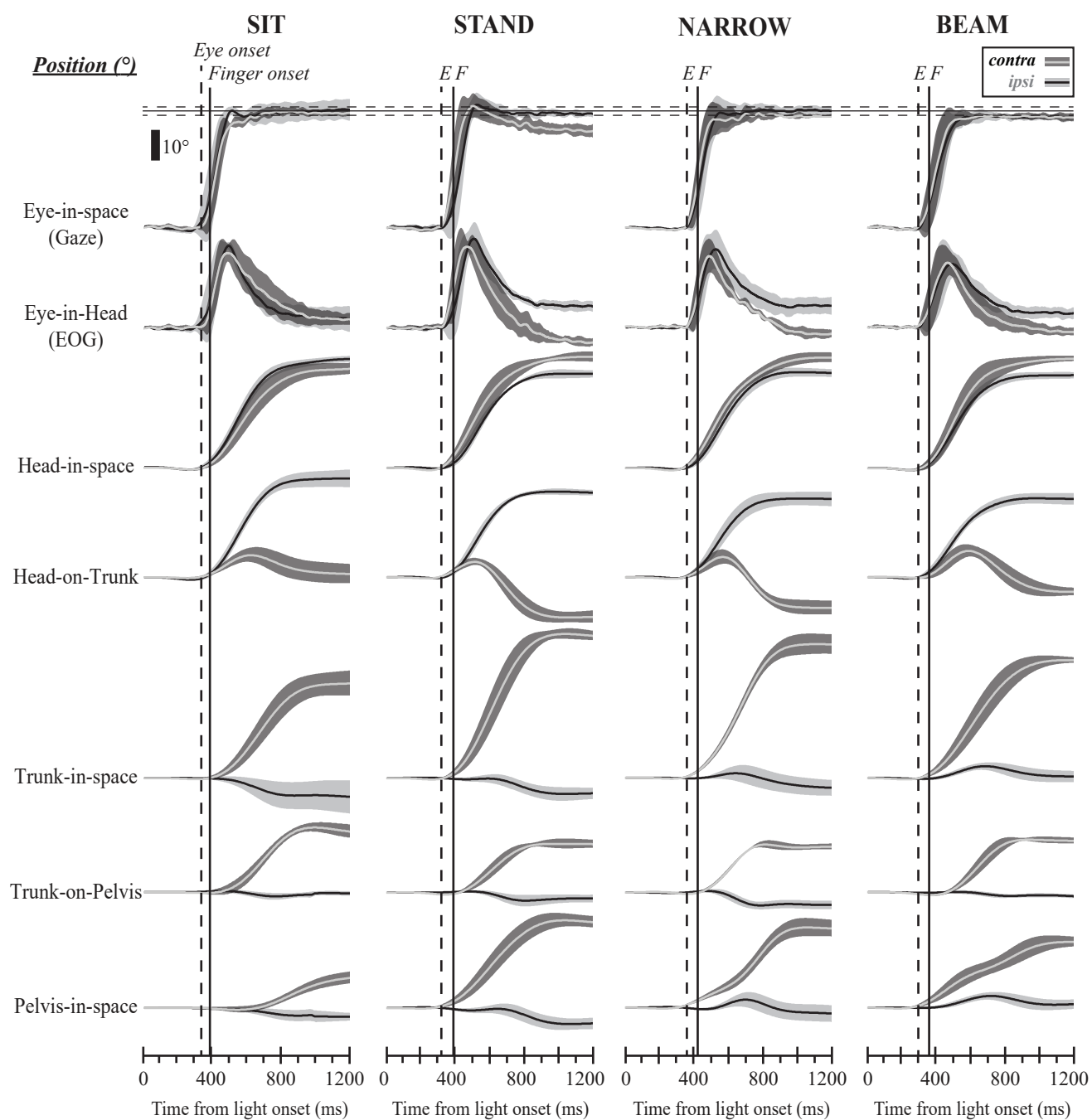
Figure 7
Stamenkovic et al., 2018
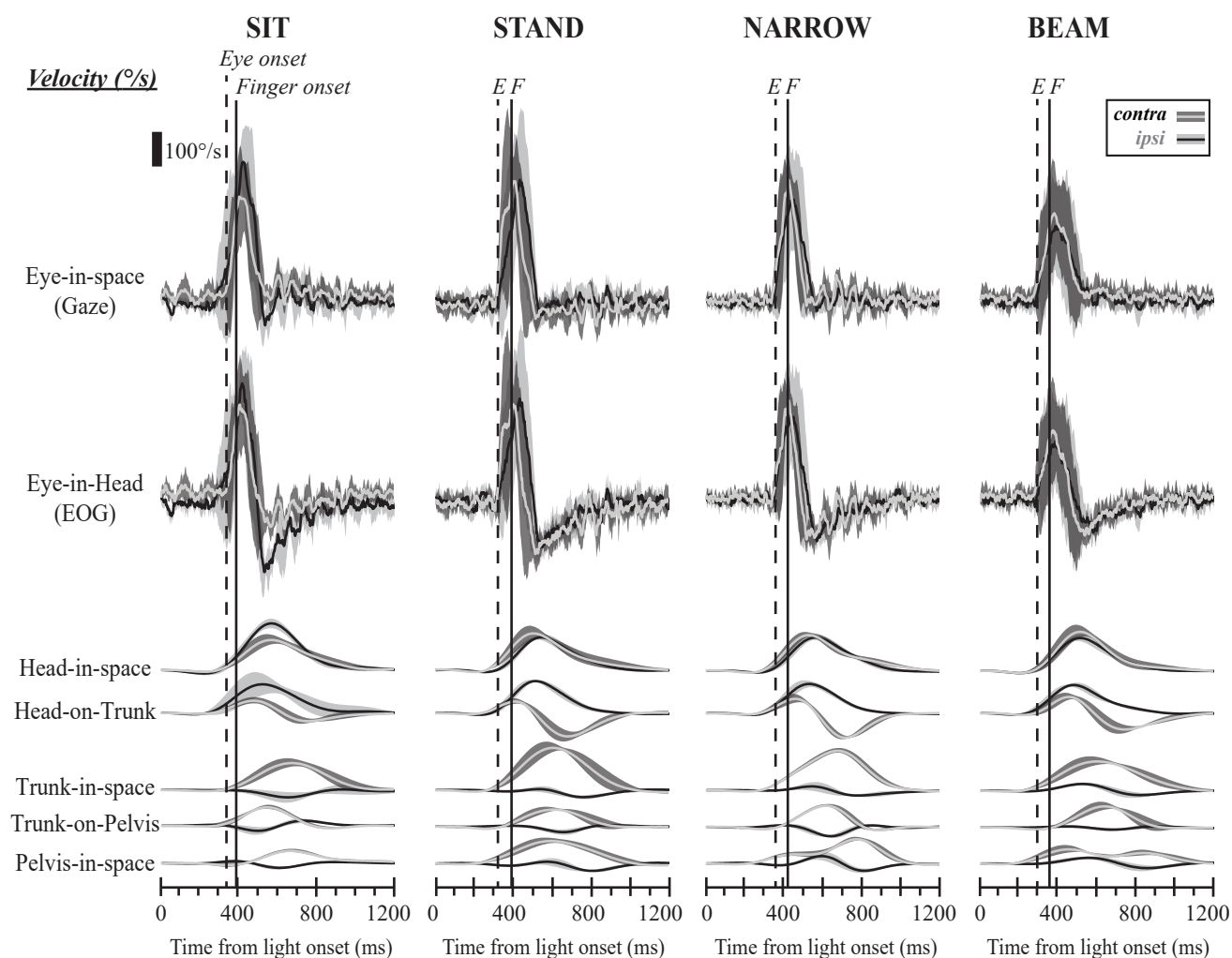
Figure 8
Stamenkovic et al., 2018

a.

ipsilateral

Onset from light stimulus (ms)

Eye Head Finger (SIT) Eye Head Finger (STAND) Eye Head Finger (NARROW) Eye Head Finger (BEAM)

b.

contralateral

Onset from light stimulus (ms)

Eye Head Finger (SIT) Eye Head Finger (STAND) Eye Head Finger (NARROW) Eye Head Finger (BEAM)
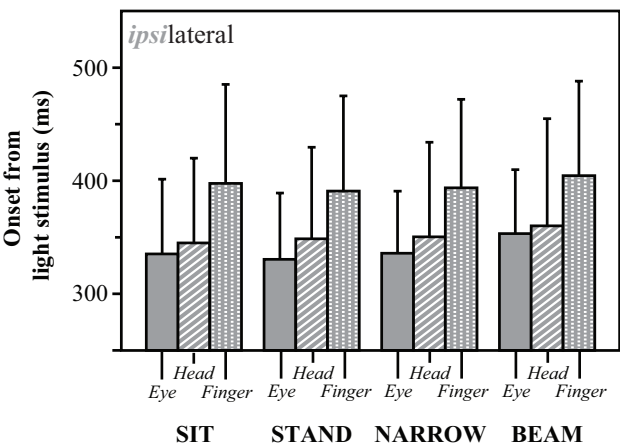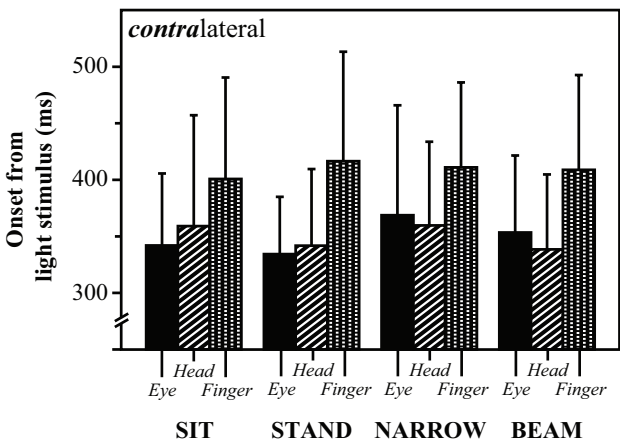
Figure 9
Stamenkovic et al., 2018

contralateral

a.
SIT: y = 1.03x - 47.69; r² = 0.802
STAND: y = 0.85x + 12.71; r² = 0.871
NARROW: y = 0.66x + 75.61; r² = 0.747
BEAM: y = 0.49x + 132.47; r² = 0.561

ipsilateral

b.
SIT: y = 0.86x + 17.95; r² = 0.914
STAND: y = 0.83x + 15.62; r² = 0.932
NARROW: y = 0.9x + 4.6; r² = 0.807
BEAM: y = 0.88x + 2.76; r² = 0.810

c.
SIT: y = 1.15x - 10.37; r² = 0.759
STAND: y = 1.02x + 37.85; r² = 0.781
NARROW: y = 0.84x + 106.48; r² = 0.491
BEAM: y = 0.84x + 111.63; r² = 0.473

d.
SIT: y = 0.98x + 54.51; r² = 0.814
STAND: y = 0.83x + 100.35; r² = 0.819
NARROW: y = 1.03x + 39.14; r² = 0.714
BEAM: y = 1.21x - 31.03; r² = 0.732

e.
SIT: y = 1.09x + 50.01; r² = 0.936
STAND: y = 1.19x + 27.70; r² = 0.929
NARROW: y = 1.3x + 0.62; r² = 0.857
BEAM: y = 1.49x - 43.69; r² = 0.860

f.
SIT: y = 1.14x + 33.01; r² = 0.912
STAND: y = 1.03x + 64.86; r² = 0.902
NARROW: y = 1.12x + 40.44; r² = 0.921
BEAM: y = 1.33x - 17.30; r² = 0.873

Head latency (ms)

Eye latency (ms)

Finger latency (ms)

Figure 10
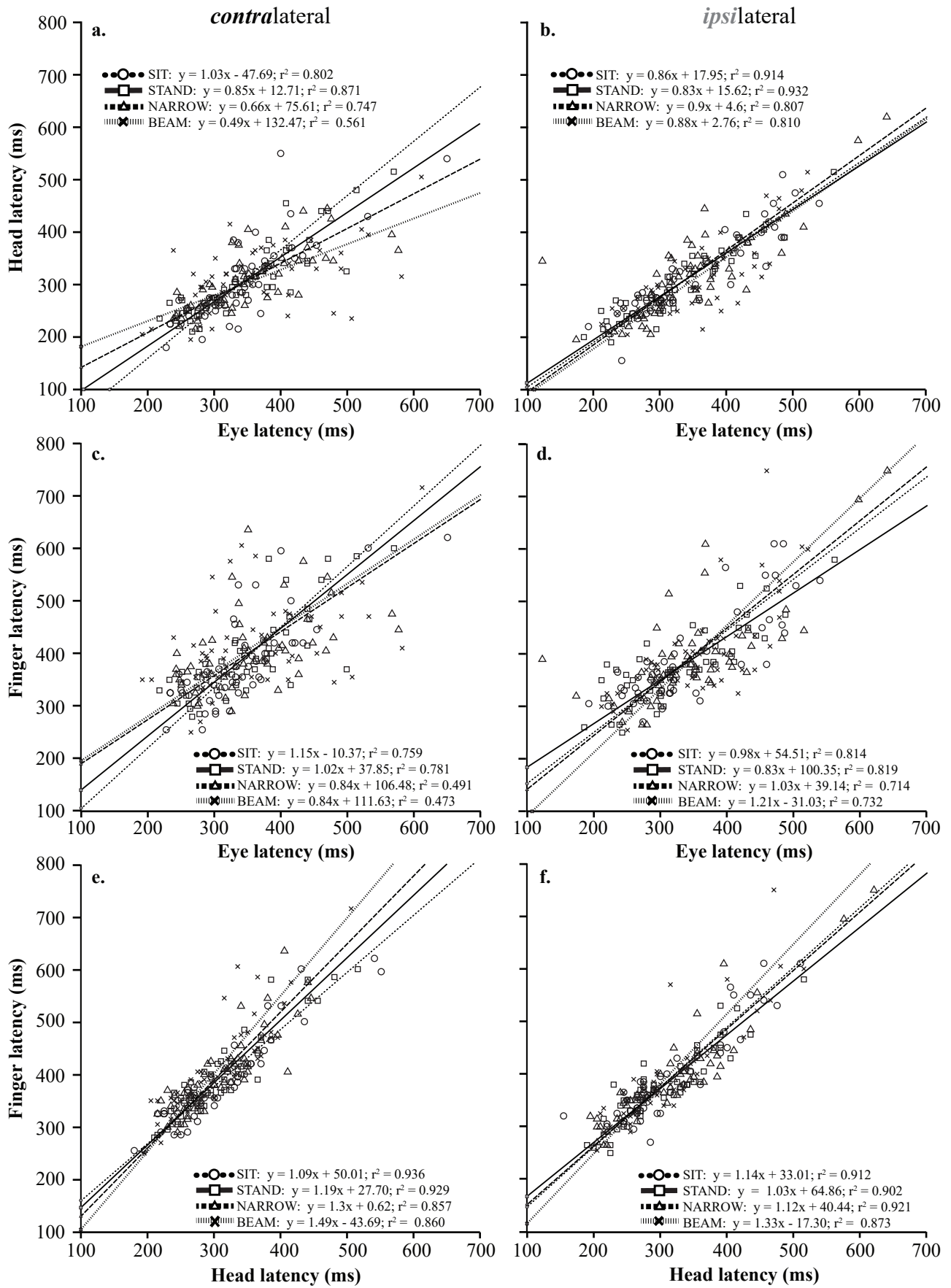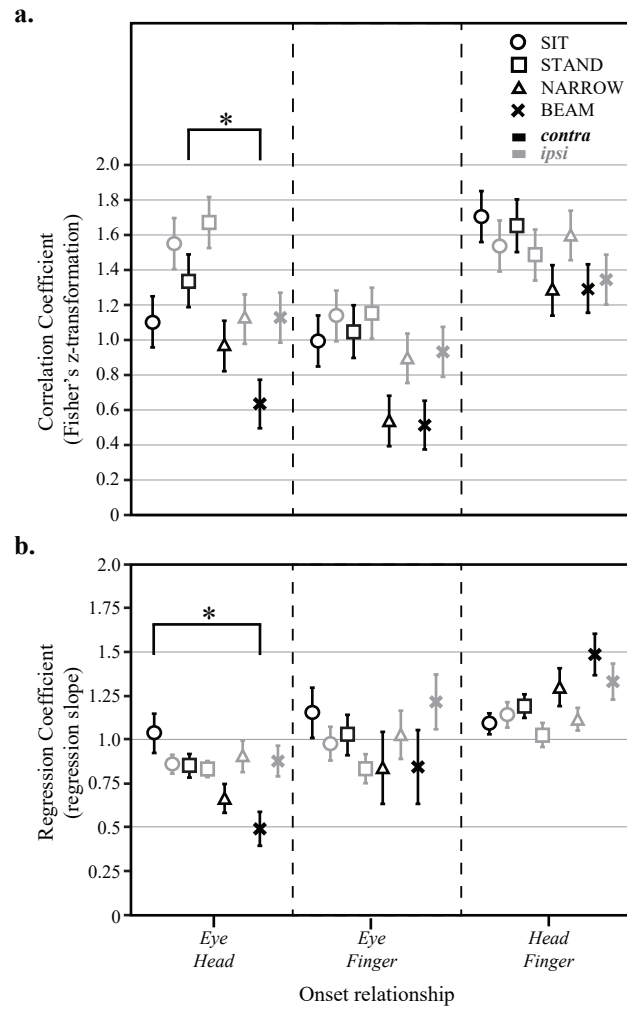# Stamenkovic et al., 2018

Figure 11
Stamenkovic et al., 2018