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AGE-RELATED EFFECTS OF INCREASING POSTURAL CHALLENGE ON EYE MOVEMENT ONSET LATENCIES TO VISUAL TARGETS

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Abstract

When a single light cue is given in the visual field, our eyes orient towards it with an average latency of 200 ms. If a second cue is presented at or around the time of the response to the first, a secondary eye movement occurs that represents a re-orientation to the new target. While studies have shown that eye movement latencies to 'single-step' targets may or may not be lengthened with age, secondary eye-movements (during 'double-step' displacements) are significantly delayed with increasing age. The aim of this study was to investigate if the postural challenge posed simply by standing (as opposed to sitting) results in significantly longer eye movement latencies in older adults compared to the young. Ten young (<35 years) and 10 older healthy adults (>65 years) participated in the study. They were required to fixate upon a central target and move their eyes in response to 2 types of stimuli: 1) a single-step perturbation of target position either 15º to the right or left, and 2) a double-step target displacement incorporating an initial target jump to the right or left by 15º, followed after 200 ms, by a shift of target position to the opposite side (e.g., +15º then -15º). All target displacement conditions were executed in sit and stand positions with the participant at the same distance from the targets. Eye movements were recorded using electro-oculography. Older adults did not show significantly longer eye movement latencies than the younger adults for single-step target displacements, and postural configuration (stand compared to sit) had no effect upon latencies for either group. We categorised double-step trials into those during which the second light changed after or before the onset of the eye shift to the first light. For the former category, young participants showed faster secondary eye shifts to the second light in the standing position, while the older adults did not. For the latter category of double-step trial, young participants showed no significant difference between sit and stand secondary eye movement latencies, but older adults were significantly longer standing compared to sitting. The older adults were significantly longer than the younger adults across both postural conditions, regardless of when the second light change occurred during the eye shift to the first light. We suggest that older adults require greater time and perhaps attentional processes to execute eye movements to unexpected changes of target position when faced with the need to maintain standing balance.

Keywords: Balance, Ageing, Gaze, Electro-oculography, Target perturbations.

INTRODUCTION

We direct our eyes around a scene that often contains more information than can be captured in a single glance using saccades to bring objects of interest into our central visual awareness. These saccadic eye movements are physiologically hardwired to the extent that when a bright light is presented in the visual field, human gaze almost automatically orients towards it. The initial eye shift is a reflexive one that occurs with an average latency of approximately 200 ms (Pelisson et al. 2010; Hu and Walker 2011). However, if a second light cue is presented at or around the time of response to the first, a secondary eye movement occurs resulting from an inhibition of the initial response and a re-orientation of the eye towards the new target (Gaymard et al. 1998; McPeek et al. 2000). The CNS controls this secondary eye shift based on an error signal created between the ‘reflexive’ saccade and a visual representation of the new target position (Tian et al. 2013).

Various studies have suggested that older adults display longer initial eye-movement latencies towards visual targets (Abel et al. 1983; Carter et al. 1983; Huaman and Sharpe 1993; Munoz et al. 1998; Owsley 2011). However, others have suggested the contrary; that older adults preserve the ability to produce rapid saccades with latencies similar to the young (Warabi et al. 1984; Hotson and Steinke 1988). Results have also shown that the older adults display significant delays in secondary eye-movements, when a second target is presented during the response to the first (Creasey and Rapoport 1985; Bock et al. 2013). The majority of the data comparing initial and secondary eye movements in older adults with young participants has however, been obtained during experiments conducted in the seated position. It remains to be determined whether similar eye movement behaviour is displayed when standing compared to sitting. These two biomechanically different situations vary in their emphasis on the complex interactions between visual, vestibular and proprioceptive control with regard to eye-movements and/or postural stability.

Much of our knowledge about the relationship between vision and balance has been obtained largely by comparing eyes open and closed conditions, and observing the effects upon body sway (Uchida et al. 1979; Hytonen et al. 1993; Fujita et al. 2005; Rougier and Garin 2006;

Guerraz and Bronstein 2008; Uchiyama and Demura 2008). While it has been shown that older adults sway more in response to unexpected eye-movements (Speers et al. 2002; van Wegen et al. 2002; Monzani et al. 2005), the relationship between postural configuration and eye-movement behaviour is not well understood. Reed-Jones et al. (2014) have reported similar eye-movement latencies to light cues in sitting and standing positions in older adults compared with the young. Interestingly, while not using an older adult population, a number of studies have reported longer eye-movement latencies in young participants during whole body movements executed in the standing position, suggesting that the CNS requires additional time to process eye movements in these situations (Hollands et al. 2004; Anastasopoulos et al. 2009; Di Cesare et al. 2013). If postural constraints increase eye-movement latencies to target displacements in older adults over and above those of their younger counterparts, it may be predicted that they need to devote more attentional resources to the dual task of standing and fixating targets, as postural constraints increase. As a first step towards understanding this, we intended simply to compare the sitting and standing positions in terms of older adults' ability to execute eye-movements towards targets, and how their performance compares to a young control group.

The purpose of this study was therefore twofold: 1) to investigate if the standing position evokes quantitatively different eye movements compared to the sitting position, and 2) to investigate if older adults demonstrate quantitatively different eye-movement latencies to visual targets compared to the younger adults. We hypothesised that, in contrast to the young, older adults would display significant delays in the onset of initial and secondary eye movements in the standing position.

MATERIAL AND METHODS

Participants

Ten healthy 18-35 year olds (mean age: 25.4 ±4.3 years; mean height: 166.2 ±5.6 cm; mean weight: 70.1 ±10.1 Kg) and 10 healthy older adults (mean age: 70.4 ±3.5 years; mean height: 169.3 ±6 cm; mean weight: 71.1 ±7.2 Kg) persons participated voluntarily in this study. All declared that they had normal or corrected-to-normal vision (no participant had visual field defects, glaucoma or conditions that could impact their mid-peripheral visual field), and no recorded history of neurological, vestibular or orthopaedic impairment. No participant wore bifocal glasses. The Human Research Ethics Board of the University of Wollongong (HE13/438), approved this study. All procedures were conducted according to the Declaration of Helsinki.

Experimental set-up

For all experiments, participants were placed behind three targets; a central target and two others each placed 15º to the right (+15º) or to the left (-15º) of the central one (see Fig. 1). Targets were red LEDs (model number: RL5-R1-360, SuperBright LEDs Inc., St. Louis, Missouri, USA) mounted upon adjustable plastic dowels contained in a semicircular support. Targets were set to shoulder (acromion process) height for each participant, in each postural configuration (sitting or standing, see below). The distance between the initial (central) target and each participants' sternum corresponded to 130% of the length of their arm, measured from the acromion process to the right index finger tip (with the arm outstretched). As we have previously used this distance to study postural adjustments during arm movements in sitting vs. standing positions in young participants (Hua et al. 2013), we sought to evaluate any possible differences in eye movement behavior using the same distance.

FIGURE 1 ABOUT HERE

A custom-built direct current electro-oculography (EOG) system was used to measure horizontal eye position. Two Ag/AgCl surface electrodes were placed on the outer canthi of each eye with respect to the eyes and on the forehead between both eyes (the ground electrode) to obtain binocular recordings of eye movements (see Fig. 1a). Electro-oculographic signals were sampled at 1000 Hz. Digital signals recorded from target illumination and extinction were captured by the LabView version 12 software (National Instruments, North Ryde, Australia) and synchronised with the EOG signal through a Vicon MX A/D controller (Vicon, Oxford, U.K).

Experimental procedures

The experiment was divided in two parts: a seated session of data collection (sit) and a standing (stand) one. In each group (young and older adults) conditions were counter-balanced: the first 5 participants from each group initially executed trials in the sit condition, while the second 5 executed the stand condition first. In the sit condition, participants sat on an adjustable seat, so that their knees were flexed at 90º and their heels were firmly on the floor. In both conditions, the medio-lateral distance between the feet corresponded approximately to their shoulder width. Tape was used to ensure that foot position was maintained between trials. Target height and distance was also kept constant between the two postural conditions (see above).

Presentation of visual target stimuli consisted of single-step (SS) and double-step (DS) paradigms. In the single step paradigm (SS), there was a random period of 1-0.5 sec after the trial was started during which participants fixated the initial, central target, either a right (+15º) or a left (-15º) light illuminated (L1), in an attempt to reduce the predictability of the target onset time. The participants were instructed to shift their eyes and look at the target. The L1 target remained illuminated for 1 sec (see Fig. 1b). Double step (DS) trials began as those for SS; the initial target was extinguished and L1 (+15º or -15º) illuminated. However, after 200 ms, L1 extinguished and the contralateral L2 (-15º or +15º respectively) illuminated. This therefore required a second corrective eye-movement from the position following the initial SS eye shift to the next illuminated target (L2, see Fig. 1b). Thus, a total of 4 experimental conditions resulted: SS (+15º), SS (-15º), DS (+15º then -15º), and DS (-15º then +15º). In addition, a number of control trials were presented during which only the initial target was illuminated (not either of the others), in an attempt to reduce prediction of an upcoming perturbation. At least 10 trials were collected in each experimental condition and a further 30 trials during which L1 or L2 did not illuminate. Thus, we aimed to collect at least a total of 150 trials from each participant. Sit and stand conditions were performed on the same day during the same session. Each session lasted approximately 40 minutes and rest breaks were given between each 30-40 trials to reduce fatigue.

Data analysis

Target light and EOG signals were exported from the data collection system and combined into a single file for analysis using Matlab (The Mathworks, Natick, MA). Electro-oculographic signals were low-pass filtered at 35 Hz using an 8th order Bessel filter (zero delay). Eye movement direction is represented by a left-handed coordinate system around the vertical axis. Rightward eye movements are represented by positive voltages and vice versa (negative voltages) for leftward eye shifts. For each trial, the onset latency of SS or DS eye movements was quantified with respect to the onsets of L1 and L2, respectively. Eye movement onsets for SS perturbations (measure *a* in Fig. 1a) were determined as the point at which the EOG signal deflected positively or negatively (+15º and -15º targets, respectively) above the threshold of the mean signal +2SD for 500 ms after the onset of L1. The onset of the second eye-movement after L2 (measure *b* in Fig. 1a) was identified using an interactive program. Two other measures (*c* and *d* in Fig. 1b) were taken. The time between the onset of the first eye shift and L2 onset (*c* in Fig. 1b) and the inter-eye shift interval (IESI, the difference between the onsets of the first and second eye shifts, *d* in Fig. 1b). Data processing was performed blindly (trial names did not identify participants as young or older adults, or as being sit or stand trials). All eye movement onset latencies (SS and DS) were verified by a second experimenter. Inter-experimenter reliability was assessed using Krippendorff's alpha coefficient (Krippendorf 1970). Coefficients were typically >0.8, suggesting a high inter-experimenter reliability (Krippendorf 2004).

Statistical analysis

Differences in onset latencies for each type of eye movement (SS and DS) were analysed using 2 x 2 analyses of variance (ANOVAs) that compared the mean differences between groups, using pooled data and split between two within-subject factors. The first repeated factor was *posture* (sit vs. stand), and the second was *age* (young vs. older adults). We searched for interactions between these variables and used *post hoc* Tukey HSD tests to examine differences between levels in each factor. Tukey HSD tests may be performed in the absence of a significant interaction effect (especially when variable densities are different) or even without a preliminary analysis of variance even when assumptions of normality and homogeneity of variance are questionable (Zar, 1999, p.209). Linear regression analyses examined the relationships between the first and second eye movements in the DS condition for each group. All left and right eye movements or combinations (DS conditions) were pooled. Differences are reported if significant at $p<0.05$ or $p<0.01$.

RESULTS

Average (+/- 1SD) EOG signals to SS (to the right, +15º) and DS (initially to the +15º, then the left, -15º target, see inset) perturbations in sit and stand conditions are illustrated in Figs. 2a to d, for one typical young (Figs. 2a and c) and an older adult (Figs. 2b and d) participant. Eye movements to SS target perturbations showed clear increases in voltage approximately 200 ms after the onset of L1 in both postures for both young and older adult participants (dashed rectangles indicate variability of the onset times of the eye movements). Eye movements to DS perturbations were characterised by a plateau after the illumination of L2 and a reversal of the EOG signal towards the newly illuminated target. Generally, the reversal in the EOG signal towards the second target (for a DS perturbation) was longer in latency than the initial eye movement to a SS target perturbation (both postures, and young and older participants).

For the DS target perturbations, we divided the trials into two categories: those in which the first eye-movement towards L1 occurred either before or after the onset of this light (200ms). The breakdown of the number of trials for young and older adults in both postures is shown in Figs. 3a-d.

FIGURES 2 and 3 ABOUT HERE

Mean SS EOG onset latencies are represented graphically in Fig. 4 (far left column). Posture did not significantly affect the onset latencies of SS eye movements in the young or the older adults. Moreover, in each posture, the older adults did not show significantly longer SS eye-movement latencies than the young (*sit*: 198.9 ±5 ms, young vs. 228.3 ±9.9 ms, older adults and *stand*: 199.9 ±5.3 ms, young vs. 218.8 ±9.7 ms, older adults). There was also no significant interaction between the factors posture and age ($F_{1,702}$)=0.89, p>0.05).

FIGURE 4 ABOUT HERE

Figure 4 (middle columns) shows clearly that when eye movements to the initial L1 target were produced before the illumination of the second (L2) target for DS perturbations (all shift1<200ms trials in Figs. 2a-d), eye-movement onset latencies to L2 were comparable (in ms) to those produced for SS perturbation. There was a non-significant interaction between posture and age ($F_{(1,261)}=0.37$, $p>0.05$). Tukey *post hoc* tests revealed however that the onsets of these secondary eye-movements occurred significantly earlier for the young participants compared to the older adults, regardless of posture (sit: $p<0.05$; stand: $p<0.05$). For younger participants, there was also significant effect of posture on the onsets of these secondary eye movements – they started sooner when standing than sitting (sit: 213 ±8.2 ms vs. stand: 178.6 ±6.5 ms, $p<0.05$), a trend that was noticeable (but not significant), in the older adults.

When eye movements to the initial L1 target occurred after the illumination of the second (L2) target during DS perturbations (all shift1>200ms trials in Figs. 3a-d), onset latencies to L2 were far longer in both the young and the older adults, than those produced for SS perturbations (see Fig. 4 right columns). There was a significant interaction effect between posture and age ($F_{(1,479)}=2.47$, $p<0.05$) in this condition. *Post hoc* analysis revealed that secondary eye-movement latencies occurred significantly later for the older adults compared to the young (sit: $p<0.01$; stand: $p<0.01$). While no significant differences were found between the two postures for the young participants (sit: 295 ±9.3 ms vs. stand: 292.2 ±8.3 ms), the standing position was found to significantly delay the onsets of eye movements to L2 for the older adults (sit: 357.3 ±13.3 ms vs. stand: 389.7 ±12.5 ms; $p<0.01$).

FIGURE 4 ABOUT HERE

We explored if, in each population, the delay of the subsequent eye movement to L2 could be predicted by the onset latencies in each posture, only in the DS condition. Figure 5 shows linear regressions of the initial and secondary eye movement onset latencies for young (Fig. 5a and c) and older adults (Fig. 5b and d) participants and for the two trial categories of DS (L2) latency. The absolute values from light onset (L1 and L2, respectively) have been graphed. When onset latencies to L1 occurred before the onset of L2 (shift1<200ms, Figs. 5a and b), neither the young nor the elderly participants displayed significant relationships between initial and secondary eye movements, suggesting that these two eye-movements occurred independently of one another. However, when onset latencies to L1 occurred after the onset of L2 (shift1>200ms, Figs. 5c and

d) regardless of postural configuration, relationships between initial and secondary eye movements were all significant (young, sit: r^2=0.55, p<0.01; young, stand: r^2=0.53, p<0.01; older adults, sit: r^2=0.5, p<0.01; older adults, stand: r^2=0.31, p<0.01), suggesting that the secondary eye shift to L2 was related to the time taken for the eye to move to L1. For these significant regressions, the linear equations clearly show that, while onsets of the secondary eye movement could be predicted from the onsets of the initial shift with a delay of only 17.6 ms (sit) and 37.4 ms (stand) in the young participants, those of the older adults showed greater values in sit conditions (59.4 ms) and most importantly, values of secondary (DS) eye movements could be predicted to be delayed by some 171.4 ms in the standing condition. Therefore, coupled with delays in absolute onset latency, these linear regressions predicted that standing slows DS eye movements in the older adults, when two eye movements (to L1 and L2) must be executed concurrently, but hardly so in the young. Finally, we also attempted to investigate if parallel processing occurred with respect to the onsets of the first and second eye shifts. Theoretically, if parallel processing occurred, in either population the inter-eye shift interval (IESI, the difference between onset to L1 and L2) should show a negative correlation with the delay between the onset of the first eye shift and L2 onset, for those trials in which the first eye shift >200ms. Unfortunately, neither the sit or stand trials displayed this relationship in the young (Fig. 5e), nor in the older adults during sitting (see Fig. 5f), suggesting that parallel processing (rather than sequential) occurred. However, some evidence of a decrease in the IESI with an increase in the time between the first eye shift and L2 onset did occur for the older adults while standing, albeit rather a low r^2 value (0.1, see Fig. 5f).

FIGURE 5 ABOUT HERE

DISCUSSION

This study aimed to investigate if, compared to the sitting position, standing had an effect upon: 1) initial, reflexive eye movements to a simple one-step change in visual target position (SS target displacements), and/or 2) eye movements produced to a second visual stimulus (DS target displacements) occurring theoretically during or towards the end of the initial one. Our results (summarised in Fig. 6) showed that, for SS target displacements, standing compared to sitting did not lengthen the time taken to produce a response in either the young or in the older adults, nor were the latter significantly slower at producing the initial response than the young. However, for the DS target displacements (right side of the schema in Fig. 6) the effect of posture depended upon when the initial eye movement to L1 was completed in relation to the illumination of L2 (200ms after L1); if the first eye movement had been completed, essentially there were two successive eye shifts. Interestingly, in this situation standing compared to sitting reduced the latency of the eye shift to the second target in the young but not significantly so in the older adults. However, if the first eye movement had *not* been completed before the illumination of L2, two concurrent eye shifts had to be controlled. Here, the young were not significantly affected by standing in terms of the time needed to produce the secondary eye movement, but standing did significantly slow the response in the older adult participants. In comparison to the young, the older adults consistently displayed slower eye movements when reacting to L2 during DS perturbations regardless of when the perturbation occurred in relation to the production of the first eye movement to L1.

FIGURE 6 ABOUT HERE

Younger and older adult participants performed similarly in terms of their SS eye movements regardless of posture. This would therefore partly corroborate the results of Spooner et al. (1980) who reported that SS eye-movements occur sooner than 250 ms when in the sitting position. Other studies have however, reported latencies longer than 250 ms in older adults compared to the young (Wheeless et al. 1966; Sharpe and Sylvester 1978) when sitting. Due to the previous findings that older persons have longer eye-movement latencies to visual targets (Abel et al. 1983; Carter et al. 1983; Huaman and Sharpe 1993; Scialfa and Joffe 1997; Munoz et al. 1998;

Klein et al. 2000; Yang et al. 2006; Owsley 2011) we initially hypothesised that standing would further delay these eye-movements. However, this hypothesis was not supported by our results. Our older adults seemed therefore to have preserved retinal reflexes and the activation of their extra-ocular muscles to fixate targets (Warabi et al. 1984; Hotson and Steinke 1988; Moschner and Baloh 1994; Bono et al. 1996; Rougier and Garin 2006; Reed-Jones et al. 2014), regardless of the neural requirements to stand and any possible decay in the processing of visual information with age. Indeed, it is likely that the respective 27 ms and 19 ms (sit and stand) average differences in latency between our young and older adult participants to SS target displacements reflected such an age-related decay.

One possibility that must be considered is that the older adults perhaps displayed differences in their balance (e.g., increased postural sway) but conserved their ability to produce reflexive eye movements, as a result of dual processing demands posed by the visual stimulus and maintaining balance. Although we have not quantified changes in sway between sitting and standing for obvious reasons related to the base of support being entirely different, we could have done so for SS (and DS) target displacements between the young and older participants only in the standing position. However, it would have been difficult to parse out the possible effects on sway of producing eye movements to targets from sway induced by any movement of the head. To do so would have required an analysis of trials with equivalent head rotations (if they existed) left or right in all participants. Nevertheless, the hypothesis that balance would be degraded while the control of eye movements is maintained as unlikely in view of the findings that *decreases* in postural sway have been recorded during the execution of gaze shifts (Uchida et al. 1979). Indeed, stability has been reported to actually improve in these situations (Rhodes et al. 2004; Legrand et al. 2013).

Clear eye movement latency differences were found between young and elderly using in our study. We used an adapted version of the double step paradigm (Becker and Jurgens 1979) with concurrent processing of two sequentially illuminated targets (at a 200 ms inter-stimulus interval) to observe the largest amount of primary and secondary eye movement (as in McPeek et al. 2000). As shown in Fig. 4 and explained schematically in Fig. 6, if the first eye movement to L1 had been completed before the illumination of L2, then latencies of the second eye-movement were comparable to those recorded for the SS target displacements. However, the onset latency of the secondary eye-movement was actually reduced in the young when they were standing compared to when they were sitting. This finding may point to a greater 'priming effect' of visual cues during quiet stance (compared to sitting). Interestingly, despite slight decreases in onset latency of the second eye shift, the older adults did not show the same decrease in latency as the young for standing as opposed to sitting. By contrast, if the first eye movement to L1 had been completed *after* the illumination of L2 then absolute latencies of the secondary eye-movement in the young and the older adults were delayed by between 22% (young, stand) and 44% (older adults, sit and stand) of the time taken to initiate a response to SS targets. Using a different task, Young and Hollands (2012) also showed that older adults are significantly delayed in initiating gaze and steps to a target that jumps during the swing phase, a protocol that requires online corrections of foot placement. In a DS paradigm such as the one adopted in this study, the secondary eye-movement to the second target displacement requires the computation of a retinal error signal resulting from the extinction of the first light and the illumination of the second, as well as a prediction of the position of the second light target to finely tune final eye position (Duhamel et al. 1992; Gredeback and Kochukhova 2010; Ibbotson and Krekelberg 2011; Wong and Shelhamer 2012). Our linear regressions (Fig. 5) showed that, for trials in which the eye shift to L1 occurred after the onset of L2, older adults were delayed to a greater extent than the young, especially during standing (predicted to be around 171 ms). We also explored the possibility that parallel processing occurred whereby the greater the difference in time between the first eye shift and L2 onset, the shorter the IESI. Unfortunately, our data did not support the existence of parallel processing whereby the latency between eye shifts shortened if the first eye shift was longer, except a weak (but nevertheless significant) correlation for the older adults during standing (Fig. 5f). This may in itself be interesting, as it might suggest that under greater postural constraints, because of the delay in the second eye shift, older adults are constrained to shorten the IESI and process both eye shifts in a parallel manner.

Under normal circumstances of postural equilibrium, it is well known that older adults are highly visually dependent (Lord et al. 2006), as they demonstrate lower joint proprioception, reduced plantar sole sensitivity and decreased muscular force. This might explain why the elderly group displayed similar latencies of SS eye movements between the two postures and latencies were no different to those of the young. However, in view of the known, general cortical degeneration (Creasey and Rapoport, 1985), slowed reaction times on dual task paradigms in the elderly (Rubichi et al. 1999), slowed online correction of arm movements to visual targets (Sarlegna, 2006) and the significant interaction between target distance and age on horizontal saccade generation reported with age (Yang et al. 2006), it is likely that when faced with tasks requiring a reprogramming of eye position through prediction and planning, older adults display deficits in the integration of postural equilibrium and eye movement control. This is significant considering that rapid sub-cortical and cortical loops participate in the processing of visual and visuomotor corrections (Gaveau et al. 2014) and postural equilibrium (Jacobs and Horak 2007). As this study did not examine elements of postural equilibrium between young and older adults in the standing position, it remains to be shown if the latter displayed significant deficits in balance in the DS target displacement condition.

In conclusion, we have shown that older adults preserve their ability to produce single-step (reflexively driven) eye movements when standing compared to sitting and are not slower than the young. However, when eye movements require a concurrent correction to an initial shift through the detection of the change in target position, standing significantly slows the response in the older adults, a trend not observed in the younger adults. We therefore conclude that ageing diminishes the ability to integrate the control of eye movements and standing balance, or that ageing reduces attentional resources available for visual and motor tasks, such that standing affects the ability to attend to changing visual targets. As vestibular and proprioceptive function generally declines at a faster rate than vision with age (Maylor and Wing, 1996), older adults become more reliant on vision to maintain balance. Therefore, the standing position may impose greater demands on visual processing for older than for younger adults. Thus, we may assume that there would be greater competition between the allocations of neural resources to process vision during the control of eye movements while standing in older adults.

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FIGURE LEGENDS

Figure 1. a. Experimental set-up. Participants either sat or stood behind 3 targets consisting of red light-emitting diodes (LEDs); a central one and two others arranged at 15º to either side of it. Two types of target shift were presented: 1) single-step, and 2) double-step. See description of procedures in Materials and Methods. b. Schema depicting the timeline of single-step and double step target displacements and changes in voltage of each target LED. For single and double step perturbations a total of 4 measures were taken (illustrated on the electro-oculography, EOG traces) and explained in the data analysis section of the Methods.

Figure 2. Mean (+/-1SD) traces of the electro-oculographic signal obtained during single (a) and double-step (b) target displacements in both a young (upper row) and an older adult (lower row) participant. Sit and stand traces are represented in black and dashed traces, respectively. Times of onset latency of eye movement shifts to single- and double-step target displacements are shown as dashed boxes for sit and stand conditions, respectively.

Figure 3. Frequency histograms showing numbers of double-step trials used in the analysis for the young participants, sit (a) and stand (b) conditions and the older adult participants, sit (c) and stand (d) conditions. In each plot, numbers of trials (*n*) are shown for eye onset latencies to the initial light (L1) that occurred before (shift1<200ms), or after (shift1>200ms) the onset of the second light (L2 onset).

Figure 4. Bar graphs depicting latencies of eye movement shifts to single-step (left columns, SS) and double-step (right columns, DS) target displacements. Young and older adult participants are shown as open and black filled bars, respectively. * = significantly different at $p<0.05$..

Figure 5. Linear regressions plotted between the onset latencies of initial versus secondary (DS) gaze shifts for young (a, c) and older adult (b, d) participants. For each participant group plots represent regressions in either of the two DS trial categories: initial eye shift<200ms or >200ms in latency. Panels (e) and (f) represent linear regressions between the time delay between the first eye shift and L2 onset (measure *c* in Fig. 1b) and inter-eye shift interval (measure *d* in Fig. 1b).

Figure 6. Model summarising the effects of single- and double-step visual target perturbations.

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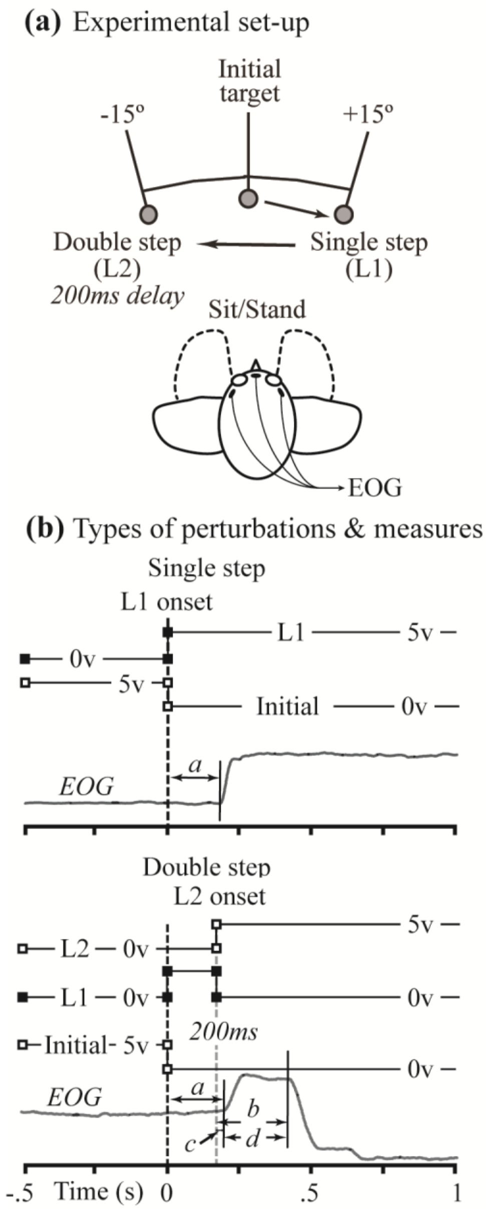
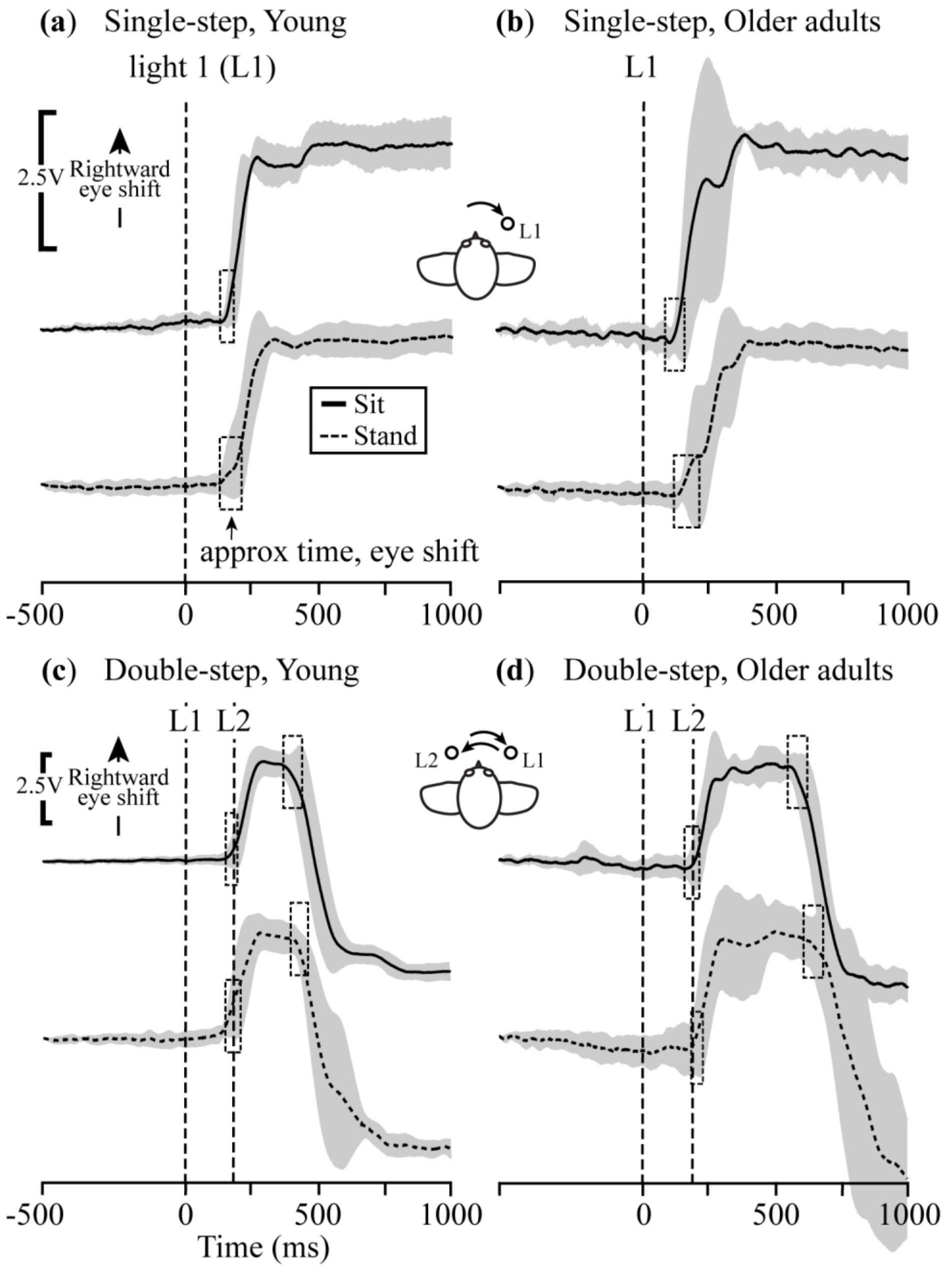
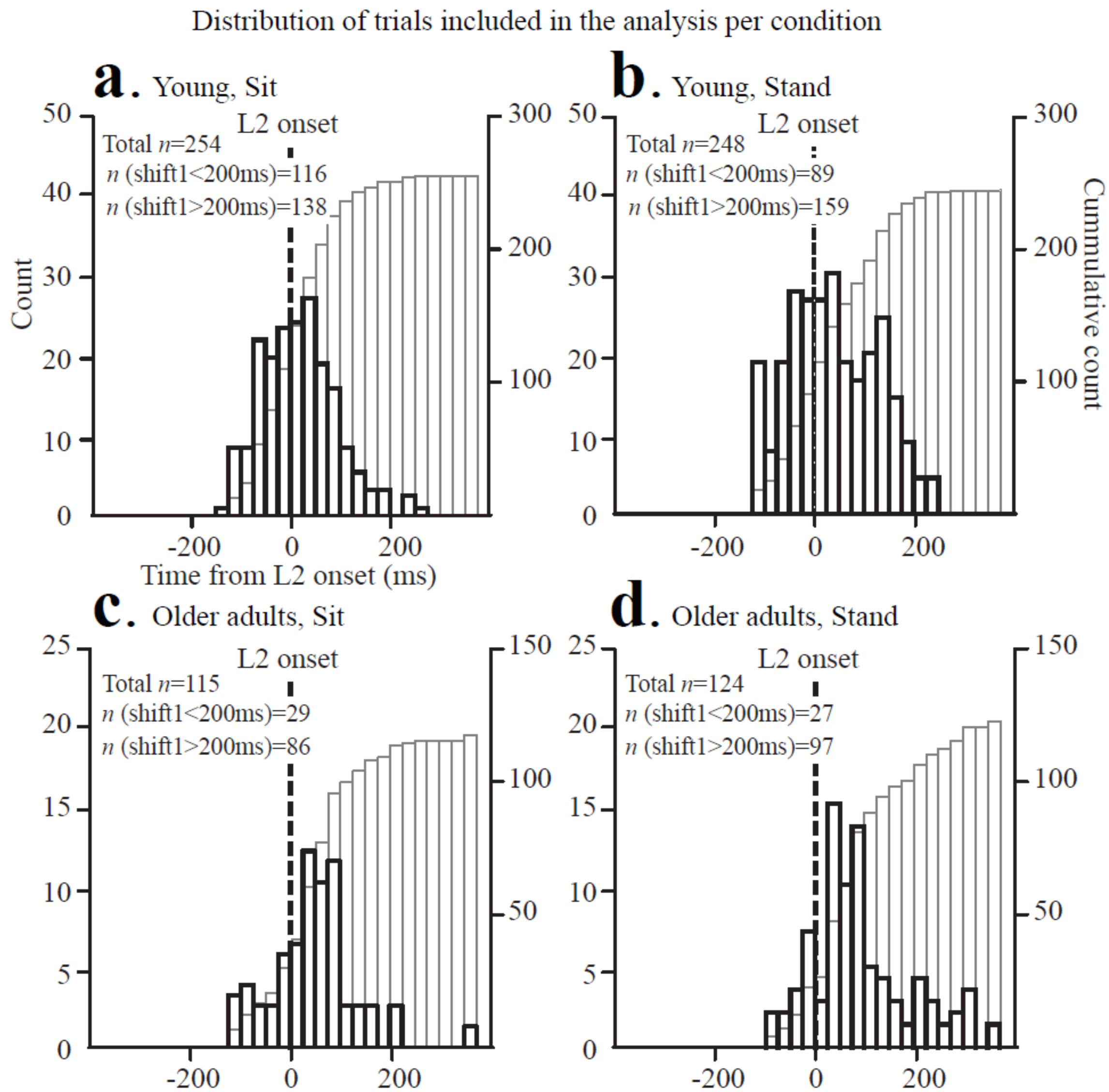
Jimenez et al. Figure 1

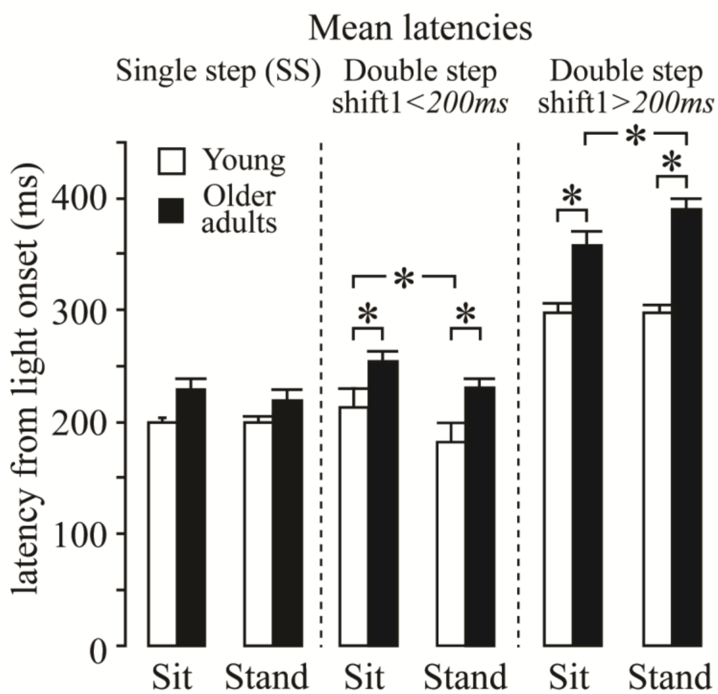


Jimenez et al. Figure 2

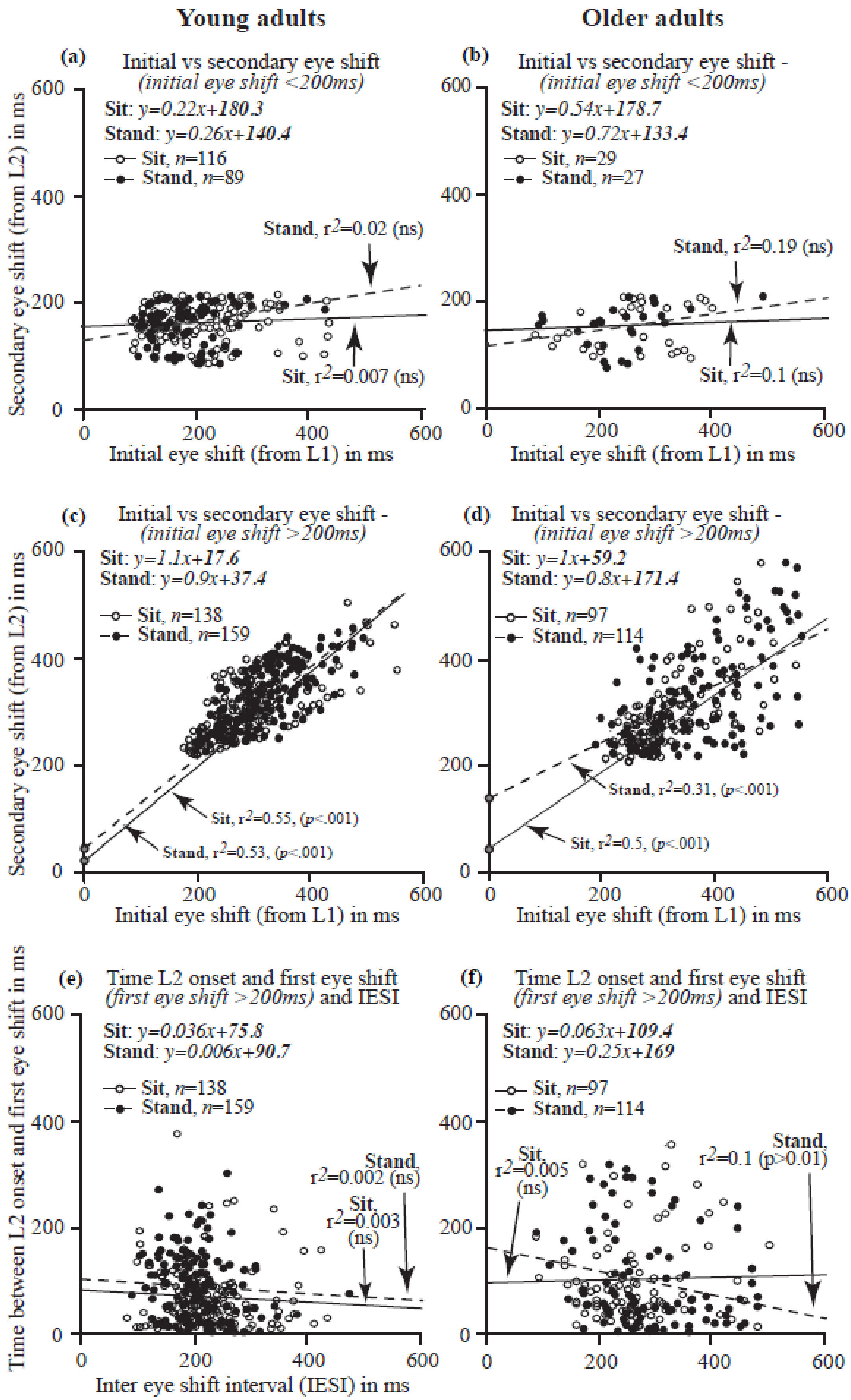



Distribution of trials included in the analysis per condition
a. Young, Sit
L2 onset
Total n=254
n (shift1<200ms)=116
n (shift1>200ms)=138
Count
Cummulative count
Time from L2 onset (ms)
b. Young, Stand
L2 onset
Total n=248
n (shift1<200ms)=89
n (shift1>200ms)=159
c. Older adults, Sit
L2 onset
Total n=115
n (shift1<200ms)=29
n (shift1>200ms)=86
d. Older adults, Stand
L2 onset
Total n=124
n (shift1<200ms)=27
n (shift1>200ms)=97

Jimenez et al. Figure 4



Jimenez et al. Figure :



Jimenez et al. Figure 6