‘The effects of constraining vision and eye movements on whole-body coordination during standing turns’

Rebecca K. Robins[a]

Mark A. Hollands[a]

[a] Research Institute for Sport and Exercise Sciences, Liverpool John Moores University, Liverpool, UK

M.A. Hollands (✉)

Tom Reilly Building

Byrom Street

Liverpool

L3 3AF

UK

Phone: +44 0150 9046 254

Email: M.A.Hollands@ljmu.ac.k

Abstract

Turning the body towards a new direction is normally achieved via a top-down synergy whereby gaze (eye direction in space) leads the upper body segments, which in turn lead the feet. These anticipatory eye movements are observable even in darkness and constraining initial eye movements modifies the stereotyped top-down reorientation sequence. Our aim was to elucidate the relative contributions of vision and eye movements to whole-body coordination during large standing turns by observing the effects of separately removing visual information or suppressing eye movements throughout the turn. We predicted that constraining eye movements would modify the steering synergy, whereas removing vision would have little effect. We found that preventing eye movements modified both timing and spatial characteristics of axial segments and feet rotation. When gaze was fixed, gait initiation, but not axial segment rotation, was delayed in comparison to both full vision and no vision turns. When eye movements were prevented, the predictable relationship between the extent head rotation led the body and peak head angular velocity was abolished suggesting that anticipatory head movements normally subserve gaze behaviour. Additionally, stepping frequency significantly reduced during the gaze fixation condition but not during the no vision condition, suggesting that oculomotor control is linked to stepping behaviour.

Keywords

Eye movements, Gaze, Turning, Vestibulo-ocular reflex, Segment reorientation

Introduction

During large whole-body turns, reorientation is normally achieved via the steering synergy, which is characterised by an initial saccade towards the turn direction followed by reorientation of the head, axial body segments and then the stepping movements of the feet. Following the initial saccade, there is an observable nystagmus pattern characterised by alternating slow counter rotation of the eye (slow phases) back towards the centre of the orbit, and anti-compensatory eye movements (fast phase) that move the eyes in advance of the turning head and body. Since the early 1960s, it has been known that fast anti-compensatory saccadic eye movements drive the eyes in advance of the head (Melvill Jones, 1964) during active and passive head turns and that during sinusoidal head rotation the resulting eye response is modulated by a slow waveform, phase advanced with respect to head position (Mishkin and Melvill Jones, 1966). These observations led to the suggestion that it is advantageous for the eyes to lead the head during rotation in order to expedite fixation of an intended "point of visual interest" (Mishkin and Melvill Jones, 1966). The primary drive for these eye movements is likely to be vestibular in origin (Anastasopoulos et al. 2009). However, it has also been shown that similar eye movements are observable even in the absence of vestibular input (Cohen, Matsuo, & Raphan, 1977) and that vision (via the optokinetic reflex) and neck proprioception (cervicocular reflex observed in vestibular patients) can contribute to the generation and maintenance of eye nystagmus (Bronstein and Hood 1986). Therefore, multiple mechanisms are in place to ensure that the eyes lead head and body rotations during turning. Intuitively, one might assume that these anticipatory eye movements serve to provide visual information describing the relative location of the individual with respect to the environment in order to aid in the coordination of the head, body and feet rotation. However, previous studies analysing walking turns suggest that differences in eye, body and stepping characteristics elicited by removing vision are

relatively small (Grasso et al. 1998; Authié et al. 2015). Eye movement characteristics were largely similar with and without vision and therefore the question remains as to whether, and how, anticipatory eye movements influence stepping and whole-body coordination during locomotor turns.

What is clear from the literature is that anticipatory eye movements that normally precede head and body rotations play an important role in *triggering* the typical top-down reorientation sequence. In a series of experiments, Reed-Jones and colleagues (2009a) showed that steering responses could be evoked via rotation of the visual scene. While stepping-in-place, participants viewed a 1st person perspective video simulating the visual experience of walking towards and around a corner. The authors showed that significant eye and axial segment rotations were triggered with relative inter segment timing that was characteristic of real world voluntary turning. Subsequently, participants performed the same visually elicited steering protocol, but with a fixed gaze condition that prevented participants from making any eye movements. The fixed gaze condition effectively abolished the anticipatory steering responses (Reed-Jones et al. 2009b). Translating this paradigm to real-world steering, participants were asked to walk towards a wall and make a 90° turn under free gaze and fixed gaze conditions (Ambati et al. 2013). During the fixed gaze condition, participants were required to fixate on a target on the wall until the transition stride of the turn, which effectively suppressed the initiating saccade. When the fixation target reached the limit of the visual field, participants began to use normal turning nystagmus. The authors found that fixed gaze during turn initiation caused a disruption in the sequence of body segment reorientation and that turns were initiated in an *en bloc* fashion i.e. head and body turned together. Although these studies showed that anticipatory eye movements play an important role in initiating the turning sequence they did not explore the role of subsequent

eye movements throughout the duration of the turn and did not dissociate the effects of disrupting vision from preventing eye movements.

The aim of the current study was to elucidate the relative contributions of vision and eye movements to whole-body coordination during standing turns by observing the effects of separately removing vision and preventing eye movements on coordination of the eyes, head, body and feet. We predicted that the constrained eye movement condition would modify motor coordination, whereas vision removal would have relatively little effect on eye and body kinematics.

Methods

Participants

Seventeen healthy young adults (9 male, 8 female, mean age 24.92 ± 3.00 *SD*) volunteered and informed consent was obtained from all individual participants included in the study. Participants were excluded if they reported neurological, musculoskeletal or cognitive impairments or if they were taking medication for anxiety and/or dizziness or used an assistive walking device. All participants had normal or corrected to normal visual acuity (20/20 or better). The experimental protocol was approved by the Liverpool John Moores Research Ethics Committee. All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Protocol

Participants stood facing a projector screen (2.74 x 3.66 m Cinefold Projection Sheet, Draper, Inc., Spiceland., Indiana, USA) approximately four metres away, on which an animated clock demonstrating the required turn direction and amplitude for the subsequent trial was shown followed by a short time interval and an audio signal that cued the participant to begin turning. Participants were told to imitate the direction and amplitude of the animated clock arm as accurately as possible, look straight ahead at the completion of the turn and return to the starting position upon instruction. Prior to the experimental session, a familiarisation phase was performed to limit turn speed variability within and between the participants. The familiarisation phase began with the participant viewing the turn demonstration videos used in the experimental trials, followed by two audio signals (i.e. a beep) separated by a time interval (1.5s for 90° turns and 3s for 180° turns). The participant was instructed to begin turning on the first signal and finish turning on the second signal (i.e. complete rotation towards the new direction) on the second signal. When asked to "turn around" to point in a new direction all participants invariably ended up with head, body and feet aligned with the new travel direction. None of the subjects questioned the instructions or seemed confused about how to align their body segments. A minimum of two practice trials were performed for each direction and amplitude combination; practice trials were continued until both the investigator and participant were satisfied with the participant's performance.

The trials were arranged in three blocks: full vision (FV), no vision (NV) and gaze fixation (GF) conditions. Other experimental conditions included turn direction (left or right) and turn amplitude (90° or 180°). The FV condition was performed free from any eyewear (with the exception of corrective lenses) or headgear and allowed the participant full visual information at all times. The NV condition was performed using PLATO visual occlusion spectacles (Translucent Technologies, Toronto, Canada). Fabric was used to surround the frames in

order to remove any peripheral vision, which permitted the participant to perform the turns with eyes open, but without any visual information about environmental features. The GF condition was performed using a device (Fig. 1a) which allowed free movement of the head from the neck with a fixed point in the line of sight approximately 35 cm in front of the participant. Participants were instructed to maintain their gaze on this point (Fig. 1b) throughout the course of each GF trial. All laboratory lights remained lit throughout the session. Counter-balancing measures were taken to account for the potentially confounding effect of block order. Trial order within each block was fully randomised for each participant. Five trials were recorded for each condition for a total of 60 trials.

Data collection

Participants were outfitted with 39 spherical reflective markers (14 mm diameter) placed according to the Plug-in-Gait (PiG) setup (Vicon, Oxford, UK). These markers were tracked using a Bonita motion analysis system (Vicon, Oxford, UK) at a sampling frequency of 200 Hz. A BlueGain wireless electro-oculography (EOG) system (Cambridge Research System Ltd.) was used to record horizontal eye movements. Surface electrodes were placed on the outer canthi of each eye and a reference electrode was placed on the forehead. EOG signals were sampled at a frequency of 1000 Hz. Raw eye rotation data were converted from mV to degrees by using a linear regression of the eye versus head rotation using the VOR, as the degree of rotation of the eye is in approximate unity with the degree of rotation of the head (Reed-Jones et al. 2009a, b). The two datasets were synchronised using a LabVIEW programme that simultaneously marked the time point within the EOG data acquisition software and illuminated an IRED within the capture volume that was identified by Vicon. The two datasets were temporally lined up post-hoc during analysis.

Data analysis

Angular displacement profiles for the head, thorax, pelvis and left and right feet in the global reference frame were determined from the PiG model in Vicon Nexus; analysis was limited to rotations within the yaw plane (i.e. rotations around the vertical axis). The MATLAB (R2014a) programming environment was used to obtain all measures from the kinematic datasets. All kinematic data were passed through a dual low-pass 4th order Butterworth filter using a cut-off frequency of 6 Hz. Displacement profiles were differentiated to yield angular velocity and acceleration profiles for each segment. Turn onset latencies were calculated with respect to the audio signal. Onset latencies for the axial segments (head, thorax and pelvis) were defined as the earliest time point preceding segment displacement of 5° that was >0° and >0°s^{-1}. The end of rotation was determined as the first zero crossing in the velocity profile following the end of the segment rotation. The time-course of the turn trials varied in duration and therefore, time-normalised profiles were created for the axial segments using the onset and offset latencies from the axial segments (i.e. the head, thorax, and pelvis). The earliest onset latency (typically the head yaw onset latency) and the final axial offset latency were chosen for the normalisation procedure. Normalisation was performed using a customised MATLAB function, which increased each time series to a length of 2000 data points (i.e. longer than all individual time series) and interpolated the missing data points. Normalisation was performed in this way so that the segments could be compared to each other over the whole course of all axial segment rotation. Using the normalised axial segment profiles, angular separation profiles were obtained from subtracting one profile from another, resulting in head-thorax, head-pelvis and thorax-pelvis profiles. Turn speed was defined as peak head yaw velocity during the turn. Peak head velocity was chosen since it was clearly definable and showed a consistent bell-shaped profile across participants and trials. Measures of turning speed relying on identification of the timing of termination of turning proved

problematic due to variability in the time it took participants to stand still once they had turned to the new location. The head was chosen since it consistently leads the other segments when turning and contains both the visual and vestibular apparatus that are primarily responsible for driving turn-related eye movements.

Analysis was performed on all individual steps that occurred during each trial. Initially, the maximum velocity was determined for both feet for each trial. Steps were counted by determining the number of peaks that reached 15% of the maximum velocity for that foot. Step onset latencies and end times were determined with respect to individual peak step velocity. Step onsets were determined as the first time point $\geq 30°s^{-1}$ preceding peak step velocity and step end time was determined as the first frame $<30°s^{-1}$ following peak step velocity. Individual step size, placement amplitude, step velocity and step acceleration were determined from step onset to step end.

Prior to analysing, EOG data for each trial were visually inspected simultaneously with head onset latency and end times. Lower and upper limits for further analysis were manually determined to eliminate saccades and fixations which occurred prior to and following the turn. All data were then passed through a low-pass 4^{th} order Butterworth filter using a cut-off frequency of 30 Hz. Eye rotation velocity and acceleration profiles were created by differentiating displacement profiles. All EOG profiles were processed so that the turn direction was aligned positively along the y-axis, i.e. all fast phases were shown as increasing and slow phases were shown as decreasing. Potential fast phases were determined using time intervals beginning with negative-to-positive zero crossings and ending with positive-to-negative zero crossings in the velocity profile. Potential fast phases were deemed to be actual fast phases if the velocity was $\geq 30°s^{-1}$ and the amplitude was $\geq 1.5°$. The time of the positive

zero crossing was determined to be the fast phase onset and the time of the negative zero crossing was determined to be the fast phase end. Eye-in-orbit positions at fast phase onset and end were determined and all individual fast phase amplitudes, velocities and accelerations were obtained from fast phase onset to fast phase end. Trials performed within the GF block were visually inspected for protocol adherence using eye displacement profiles and were excluded if any fast phases or saccades that exceeded fast phase amplitude criteria (≥1.5°) were elicited.

All data were reviewed and visually inspected for protocol adherence. Trials were excluded if: 1) the participant was unable to perform the designated trial condition correctly, 2) any segment was not modelled throughout the course of the whole trial, 3) filtering procedures were insufficient in reducing noise or 4) if specific measures were unable to be obtained using the limits determined by the customised script.

Statistical analysis

The statistical package SPSS (22.0) was used for all statistical procedures. A 2 x 2 x 3 repeated measures ANOVA was performed on all kinematic dependent variables with direction (left or right), amplitude (90° or 180°) and visual condition (FV, NV or GF) as repeated measures factors. As GF trials elicited no fast phases, a 2 x 2 x 2 RM ANOVA was performed on all EOG dependent variables, which included only FV and NV data. No effects of direction were found; therefore, the presented results are from a 2 x 3 and 2 x 2 RM ANOVA design for the kinematic and EOG data, respectively. RM ANCOVA was subsequently performed on significant results to control for turn speed using peak head velocity as a time-varying covariate. Pearson's Product moment correlation was used to determine the strength of the relationships between the dependent variables. Frequency

distribution analysis was performed on all fast phase characteristics and Kolmogorov-Smirnov Z was run to determine differences between the distributions from each experimental condition. All mean values are presented with standard deviations unless otherwise stated. Statistical significance was set at $P<.05$ and a Bonferroni's correction was used for multiple comparisons.

Results

Segment onset latencies

The order of segment reorientation was consistent between all visual conditions and began with the axial segments, followed by the rotation of the eyes and then the onset of the leading and trailing feet (Fig. 2). However, the exact order of onset of the axial segments was inconsistent between experimental conditions. There was a main effect of turn amplitude on the rotation onset latencies for the head ($F_{(1, 16)} = 6.30$, $P<.05$), thorax ($F_{(1, 16)} = 4.83$, $P<.05$), pelvis ($F_{(1,16)} = 6.24$, $P<.05$), leading foot ($F_{(1, 16)} = 10.91$, $P<.01$) and trailing foot ($F_{(1, 16)} = 20.52$, $P<.001$) which showed that onset latencies during 180° turns were earlier than 90° turns for all visual conditions. There was no main effect of turn amplitude on the onset latency of the eye. Pearson's product moment correlation analysis revealed significant correlations between the onset latencies of all segments for all visual conditions ($P<.001$).

There was a significant main effect of visual condition on the onset latencies of the leading step ($F_{(2, 32)} = 22.17$, $P<.001$) and the trailing step ($F_{(2, 32)} = 19.49$, $P<.001$); pairwise comparisons revealed that the onset latencies of both the leading and trailing feet in the GF condition were significantly later ($P<.001$) than the onset latencies in the FV and NV conditions. The onset latency of the leading step was approximately 120 ms later and the onset latency of the trailing step was 200-300 ms later in the GF condition compared to the

FV and NV conditions (Table 1). RM ANCOVA with turn speed as a covariate was performed on the leading and trailing step onset latencies, however, the effects of GF were preserved demonstrating that differences in turn speed between the visual conditions cannot explain the delay in step onset.

Intersegmental relationships

RM ANOVA was performed on peak angular separation and a main effect of turn amplitude was found on the peak head-thorax separation ($F_{(1, 16)} = 32.48$, $P<.001$) and peak head-pelvis separation ($F_{(1, 16)} = 18.93$, $P<.01$), but not on the peak thorax-pelvis separation, which showed that segmental separation increased with increased turn amplitude (Table 2). Main effects of visual condition were found on the peak head-thorax separation ($F_{(1.149, 18.390)} = 6.31$, $P<.01$) and peak head-pelvis separation ($F_{(1.206, 19.292)} = 6.17$, $P<.01$), which showed that removal of vision reduced segmental separation and suppression of anticipatory eye movements via fixation further reduced segmental separation, however, the differences between NV and GF were not significantly different. No interactions were found between turn amplitude and visual condition. RM ANCOVA was performed to determine if the differences between the conditions in peak head-thorax and peak head-pelvis were due to turn speed and found that the effects of GF were lost, demonstrating that differences in turn speed between the visual conditions could explain the effect of the visual conditions on peak segment separation.

Pearson correlation analysis between peak head yaw velocity and peak head-pelvis separation revealed a significant but weak relationship ($R^2 = .13$, $P <.001$). As turn speed was found to vary significantly, separate correlations were performed for each visual condition. Peak head yaw velocity accounted for roughly a third of the variability in peak head-pelvis separation in

FV (R^2 = .34, *P<.001*) and this relationship reduced to around a fifth in the NV condition (R^2 = .20, *P*<.001), however, the relationship disappeared in the GF condition (R^2 = .01, *P<.001*) (Fig. 3).

Stepping characteristics

RM ANOVA was performed on the leading step size and the trailing step size. An interaction between turn amplitude and visual condition was found on the leading step size ($F_{(2, 32)}$ = 6.78, *P*<.01). Post hoc analysis revealed that the size of leading steps were significantly larger during 180° turns in the FV (*P*<.05) and GF (*P*<.001) conditions, but did not differ between amplitudes in the NV condition (Table 3). A main effect of turn amplitude ($F_{(1, 16)}$ = 17.67, *P*<.01) and a main effect of visual condition ($F_{(2, 32)}$ = 4.10, *P*<.05) were found on the trailing step size. Trailing step size was significantly larger during 180° turns in all visual conditions. Trailing step size did not differ between visual conditions during 90° turns, but was significantly smaller in the NV condition than FV (*P*<.05) during 180° turns; trailing step size did not differ significantly between NV and GF during 180° turns.

Step duration was calculated for all steps as the interval between step onset and step placement time. RM ANOVA was performed on the leading step duration and the trailing step duration. A main effect of visual condition was found on the leading step duration ($F_{(2, 32)}$ = 3.40, *P*<.05), which showed that leading steps to 180° were significantly longer during GF than NV (*P*<.05). A main effect of turn amplitude ($F_{(1, 16)}$ = 6.22, *P*<.05) and a main effect of visual condition ($F_{(2, 32)}$ = 4.65, *P*<.05) were found on the trailing step duration. Post hoc analysis found that trailing steps were significantly longer in the 180° condition during FV only (*P*<.01) and trailing steps to 180° were significantly longer during GF than NV (*P*<.05).

Step frequency was calculated for each turn as the number of steps taken divided by stepping duration (i.e. the interval between the onset of the leading step to the placement of the last step). RM ANOVA was performed on the step frequency and found a main effect of turn amplitude ($F_{(1, 16)} = 43.79$, $P<.001$) and a main effect of visual condition ($F_{(2, 32)} = 7.39$, $P<.01$); the increase in turn amplitude from 90° to 180° caused a decrease in step frequency and the increased constraints on vision (i.e. first vision removal, then fixation) also caused a scaled reduction in step frequency (Fig. 4). A significant interaction between turn amplitude and visual condition was found on step frequency ($F_{(2, 32)} = 5.27$, $P<.05$). Pairwise comparisons showed that there were no significant differences in step frequency between the FV and NV conditions in either the 90° or 180° trials. However, the FV and NV step frequencies were significantly higher than GF step frequency for both turn amplitudes (Fig. 4).

RM ANCOVA was performed on the significant step variables to determine if the main effects of visual condition could be explained by changes in turn speed. The effects of visual conditions were preserved for all step variables demonstrating that changes in turn speed could not explain the effects caused by the visual conditions.

Fast phase characteristics

Raw data traces of the in the FV condition (a) compared to the NV condition (b) are shown in (Fig. 5).

Main sequence analysis was performed by plotting peak fast phase velocity as a function of fast phase amplitude (Figure 6) for the FV and NV conditions. Only fast phases with an amplitude <30° were included in this analysis as there were very few data points above this

threshold in the NV condition and we wished to avoid the influence of differences in the range of data points on the correlation results. A power function was used to fit the data according to that performed by Kaminiarz et al. (2009); curve estimation procedures also found a power function to be the most appropriate fit for the datasets. Significant relationships were found for both FV and NV, however, the FV condition had a stronger correlation (R^2 = .56, P <.001) than the NV condition (R^2 = .33, P <.001). A fisher transformation was used to compare correlation coefficients between the conditions, which founds significant differences between the FV and NV conditions. As indicated by the lower power function variable the main sequence curve was somewhat flattened in the NV condition compared to the FV condition.

Frequency distribution analysis was performed on all fast phases elicited during the experiment. Analysis of the eye-in-orbit position at fast phase onset found the eye was most frequently between -5° to +5° from the centre orbit in both FV and NV conditions. However, fast phases elicited in the NV condition were generally closer to the centre, with only 2% of fast phases elicited from greater than +15° compared with 15% of fast phases in the FV condition. Furthermore, fast phases in both FV and NV conditions were elicited from negative eccentric positions (i.e. eye pointed away from turn direction) approximately 40% of the time and from positive eccentric positions 60% of the time. Eye-in-orbit position at fast phase end was more centrally located in the NV condition, with approximately 79% of eye-in-orbit positions at 15° or less away from centre orbit compared to only 44% in the FV condition. In both FV and NV conditions only 5% of fast phases ended at a negative eccentric orbital position.

Frequency distribution analysis on fast phase amplitudes found a positively skewed distribution for both FV and NV fast phases, which showed that approximately 66% of fast phases elicited in FV and approximately 87% of fast phases in NV were 15° or smaller (Fig. 6a). Analysis of fast phase velocity found a normal distribution for both FV and NV conditions, however the mean velocity for fast phases in the NV was slower, between 200-250°s^{-1} than in the NV condition, while the mean fast phase velocity was around 300°s^{-1} (Fig. 6b). Kolmogorov-Smirnov Z tests found no significant differences between any of the fast phase characteristic distributions.

Discussion

This is the first study of the effects of separately removing vision and preventing eye movements on coordination of the eyes, head, body and feet during standing turns. We predicted that constraining eye movements would result in altered turn coordination (i.e. modify the typical top-down synergy), whereas removing vision would have a relatively small effect on eye and body movement characteristics. In line with our prediction, we found that although removing visual input resulted in subtle changes to anti-compensatory eye movement characteristics (which were generally smaller and slower), eye, head, body and feet coordination was effectively preserved. We found that preventing eye movements modified both timing and spatial characteristics of axial segments and feet rotation. When gaze was fixed, gait initiation, but not axial segment rotation, was delayed in comparison to both FV and NV turns. During GF, the predictable relationship between the extent of head anticipation and peak head velocity (see Figure 3) was abolished. Additionally, stepping frequency significantly reduced during GF, but not during the NV condition, suggesting that oculomotor and stepping motor control processes do not normally operate independently.

Gaze fixation delays step initiation and decreases stepping frequency

In both the FV and NV conditions, participants consistently began reorientation with the axial segments in an *en bloc* manner, followed eye rotation, rather than adopting the gaze-initiated steering strategy commonly reported (Anastasopoulos et al. 2009; Degani et al. 2010; Grasso et al. 1998; Hollands et al. 2001, 2004; Reed-Jones, Reed-Jones, et al. 2009; Reed-Jones, Hollands, et al. 2009). One possible explanation is that previous studies have used visual cues presented in the peripheral visual field that likely evoked an initial reflexive saccade or visual search behavior, as the goal of these tasks is frequently to align gaze with a target. Our protocol was dependent on spatial memory rather than 'targeted' turn locations, such as those used in previous studies that likely evoked an initial reflexive saccade or visual search behavior, and therefore it is unsurprising that the characteristic initial eye movement differed.

As predicted, onset latencies in the FV and NV conditions were remarkably similar, however, in the GF condition, there was a significant delay in the onset of stepping in both the leading and trailing feet, which suggests that eye movement, but not visual input, has a direct influence on the initiation of gait during standing turns. Additionally, step frequency was reduced in the GF condition but not during the NV condition. These findings support the hypothesis that oculomotor control and stepping behaviour are intrinsically linked. This has been previously demonstrated in precision stepping tasks where saccades made to step targets are followed by stepping movements with a tightly coupled temporal delay, which is present in ambient lighting, no lighting and during temporary visual denial of the step target (Hollands et al. 1995; Hollands and Marple-Horvat, 2001).

Previous research on turns during walking have shown that both head-on-trunk fixation (Hollands, Sorensen and Patla, 2001) and gaze fixation (Ambati et al. 2013) alters axial

segment coordination at turn initiation. When the head was immobilised (by fixing it to the trunk), yaw rotation of the trunk began *earlier* than during normal turning. Presumably, early trunk yaw compensated for the loss of head-on-trunk movement and aligned the head in the appropriate direction for further rotation, as the timing of the displacement of the feet did not differ significantly between head-free and head-fixed turns. Reed-Jones et al. (2009b), investigated steering responses (i.e. axial rotation with similar temporal and spatial characteristics to actual steering) while stepping-in-place during both free-gaze and fixed-gaze conditions. The group found the typical anticipatory steering behaviour in the free-gaze condition, but significant delays in the steering response in the fixed-gaze condition; additionally, during fixed-gaze, the top-down sequence of reorientation was abolished and steering occurred *en bloc*. During real world steering, fixed-gaze prevented anticipatory steering behaviour, caused the same delays in body segment reorientation seen during visually elicited steering, and led to *en bloc* reorientation (Ambati et al. 2013).

Visual constraints alter intersegmental coordination

While all turns in the current study began in an *en bloc* manner, the course of rotation throughout the FV and NV turns were clearly organised in a top-down manner, where the eyes anticipated the head and the head anticipated the other axial segments, which is the same strategy employed during complex curve walking (Bernardin et al. 2012). We chose to use a slow turn speed to limit variations in turning speed because a) our pilot data showed that inter-subject variations in turn speed were smaller during slower turns than faster turns and b) a slower speed ensured stability of the head-mounted device. In the current study, we found an association between peak segmental separations and turn speed, and that the visual condition influenced this relationship. During the FV condition, peak head velocity accounted for approximately 34% of the variability of peak head-peak separation; this relationship

reduced to around 20% in the NV condition. When eye movements were prevented, the variability in peak head-pelvis separation due to peak head velocity was less than 1%. The results of the RM ANCOVA on peak head-thorax and peak head-pelvis separation suggest that differences in turn speed between the visual conditions may account for the reduced segment separation in the NV and GF conditions. It is clear from our results and many previous studies (Grasso et al. 1998; Bernardin et al. 2011; Authié et al. 2015) that gaze anticipates the other body segments during the majority of rotation and that anticipation occurs whether or not visual information is available, but removal of vision causes a reduction in turn speed that alters anticipation characteristics. Our results demonstrate that preventing anticipatory eye movements reduces turn speed more and causes a greater alteration in intersegmental coordination than vision removal alone, suggesting that eye movements are intrinsic to the control of intersegmental coordination. However, a significant limitation of this study was the restrictive turn speed that we choose to attempt to elucidate findings related to visual conditions only and not those that could be attribute to differences in turning speed. Future studies could implement a similar protocol using a head-mounted virtual reality device, such as the Vive, which allows greater mobility than our device.

Visual influence on eye movement characteristics

Our results show that main sequence characteristics and frequency distribution of fast phase amplitudes are substantially similar in the absence of vision but the fast phase amplitudes are generally smaller i.e. less anticipatory in nature as evident in the slightly flattened power curve in the NV main sequence displayed in figure 6. Nevertheless, these results demonstrate the predominant contribution of vestibular input to driving eye movements during the locomotor turning paradigm we used.

Comparisons of fast phase characteristics between the FV and NV conditions found that fast anti-compensatory eye movements in FV were generally larger, faster and more likely to begin and end at eccentric positions within the orbit than NV fast phases. These differences presumably reflect the additive contribution of optokinetic and/or voluntary saccadic drive to vestibular nystagmus when vision is available (see Barnes, 1993 for review). Eye movements due to optokinetic input only are generally small in amplitude (3-4°) and have a similar frequency (2-3 Hz) to that observed in this experiment (Abadi, 2002). However, *if* optokinetic and vestibular input are added linearly, as suggested by Robinson (1977), we would expect that fast phases during FV would be approximately 3-4° higher than fast phases from NV trials. However, it is clear from the amplitude distribution (Fig. 6) that fast phase amplitudes do not simply increase linearly when vision is available, but that there is a greater range of amplitudes than fast phases elicited without visual input. A gaze anchoring mechanism is a more likely explanation for the differences between spatial characteristics in FV and NV. Gaze anchoring on salient environmental features via saccadic eye movements are likely similar to the alternating saccade and fixation strategy employed during manual reaching tasks (Neggers and Bekkering, 2001; Rand, 2014), precision stepping (Hollands et al. 1995; Hollands and Marple-Horvat, 2001) and obstacle crossing (Patla, 1997). Gaze anchoring could presumably be used to provide the head with intermittent stabilised reference point during rotation. However, analysis of the visual scene during turning would be necessary to confirm this hypothesis, which is not possible using EOG.

Conclusion

Eye and body coordination during large whole-body turns is preserved in the absence of visual input, however, inhibiting eye movement during turning causes significant modifications to stepping characteristics including the initial onset of gait and stepping

frequency throughout the turn. Preventing eye movements also alters the intersegmental coordination of the axial segments by effectively removing the relationship between turn speed and the positional relationships between the head and pelvis. These findings support previous suggestions that eye movement control is intrinsic to the turning synergy and that turning behaviour is controlled by a phylogenetically old mechanism that serves to realign gaze, i.e. turns are controlled via whole-body gaze shifts.

Conflict of Interest

The authors declare that they have no conflict of interest.

References

Abadi RV (2002) Mechanisms underlying nystagmus. J R Soc Med, 95:231-234

Ambati VNP, Murray NG, Saucedo F, Powell DW, Reed-Jones RJ (2013) Constraining eye movements when redirecting walking trajectories alters turning control in healthy young adults. Exp Brain Res, 226:549-556

Anastasopoulos D, Ziavra N, Hollands MA, Bronstein A (2009) Gaze displacement and inter-segmental coordination during large whole body voluntary rotations. J Neurol, 260:2057-2065

Authié CN, Hilt PM, N'Guyen S, Berthoz A, Bennequin, D (2015) Differences in gaze anticipation for locomotion with and without vision. Front Hum Neurosci, 9, Article 312

Barnes GR (1993) Visual-vestibular interaction in the control of head and eye movement: the role of visual feedback and predictive mechanisms. Prog Neurobiol, 41:435-472

Bernardin D, Kadone H, Bennequin D, Sugar T, Zaoui M, Berthoz A (2012) Gaze anticipation during human locomotion. Exp Brain Res, 223(1):65-78

Bronstein AM, Hood JD (1986) The cervico-ocular reflex in normal subjects and patients with absent vestibular function. Brain Res, 373 (1-2):399-408

Cohen B, Matsuo V, Raphan T (1977) Quantitative analysis of the velocity characteristics of optokinetic nystagmus and optokinetic after-nystagmus. J Physiol, 270:321-344.

Degani AM, Danna-Dos-Santos A, Robert T, Latash ML (2010) Kinematic synergies during saccades involving whole-body rotation: A study based on the uncontrolled manifold hypothesis. Hum Movement Sci, 29(2):243-258

Grasso R, Prévost P, Ivanenko YP, Berthoz A (1998) Eye-head coordination for the steering of locomotion in human: An anticipatory synergy. Neurosci Lett, 253:115-118

Hollands MA, Marple-Horvat DE (2001) Coordination of eye and leg movements during visually guided stepping. J Motor Behav, 33(2):205-216

Hollands MA, Marple-Horvat DE, Henkes S, Rowan AK (1995) Human eye movements during visually guided stepping. J Motor Behav, 27(2):155-163

Hollands MA, Sorensen KL, Patla AE (2001) Effects of head immobilization on the coordination and control of head and body reorientation and translation during steering. Exp Brain Res, 140(2):223-233

Hollands MA, Ziavra NV, Bronstein AM (2004) A new paradigm to investigate the roles of head and eye movements in the coordination of whole-body movements. Exp Brain Res, 154(2):261-266

Kaminiarz A, Königs K, Bremmer F (2009) The main sequence of human optokinetic afternystagmus. J Neurophysiol, 101(6):2889-2897

Melvill Jones, G (1964) Predominance of anticompensatory oculomotor response during rapid head rotation. Aerosp Med, 35:965–968

Mishkin S, Melvill Jones G (1966) Predominant direction of gaze during slow head rotation. Aviat Space Environ Med, 37:897–900

Neggers SFW, Bekkering H (2001) Gaze anchoring to a pointing target is present during the entire pointing movement and is driven by a non-visual signal. J Neurophysiol, 86(2):961-970

Patla AE (1997) Understanding the roles of vision in the control of human locomotion. Gait Posture, 5:54-69

Rand MK (2014) Segment interdependency and gaze anchoring during manual two-segment sequences Exp Brain Res, 232:2753-2765

Reed-Jones RJ, Hollands MA, Reed-Jones JG, Vallis LA (2009a) Visually evoked whole-body turning responses during stepping in place in a virtual environment. Gait Posture, 30:317-321

Reed-Jones RJ, Reed-Jones JG, Vallis LA, Hollands MA (2009b) The effects of constraining eye movements on visually evoked steering responses during walking in a virtual environment. Exp Brain Res, 197:357-367

Robinson, DA (1977) Linear addition of optokinetic and vestibular signals in the vestibular nucleus. Exp Brain Res, 30:447-450

Figure Legends

Fig. 1 a) The fixation device allowed free head-on-trunk movement that permitted uninterrupted gaze fixation. b) A small dot was placed in the centre of the panel as the gaze fixation point; participants were required to fixate on this point from the completion of the turn demonstration video to the end of the trial.

Fig. 2 Bar graph showing the mean onset latencies of all segments with amplitude conditions collapsed. The initiation of reorientation of the head, thorax and pelvis was *en bloc* in all experimental conditions and axial segment rotation began before the initial eye rotation or the initiation of stepping by the feet. The initial rotation of the eyes were similar both with visual input (FV) and when visual input was removed (NV). The onset latency of the leading foot was approximately at the same time as the eye onset in both FV and NV conditions, but there was a delay in leading foot onset in the GF condition. The onset of the trailing foot was delayed in the GF condition compared to the FV or NV conditions. Error bars represent 95% confidence intervals and asterisks represent statistically significant differences between the visual conditions. Onset latencies were calculated with respect to the audio signal that cued the participant to begin turning. FV = full vision; NV = no vision; GF = gaze fixation.

Fig. 3 a) Peak head velocity accounted for approximately a third of the variability in peak head-pelvis separation during FV turns. b) During NV turns, peak head velocity accounted for around a fifth of the variability in peak head-pelvis separation. c) The relationship between peak head velocity and peak head-pelvis angular separation effectively disappears when eye movements were suppressed in GF. FV = full vision; NV = no vision; GF = gaze fixation.

Fig. 4 There was an interaction between turn amplitude and visual condition that showed that differences in stepping frequency between FV and NV were non-significant in both turn amplitudes, but GF caused a significant reduction in stepping frequency. Error bars represent 95% confidence intervals and asterisks represent statistically significant differences between visual conditions. FV = full vision; NV = no vision; GF = gaze fixation.

Fig. 5 The figure shows representative displacement traces for a) one FV trial to 180° and b) one NV trial to 180°. In the FV turn, the nystagmus (eye trace) is prominent and shows the typical saw-tooth pattern. While the nystagmus is still evident during the NV condition, the amplitude of each eye movement is significantly reduced in comparison to the FV turn. It is also necessary to indicate that the turns in each condition were performed at similar velocities, as evident by the slopes of the head, thorax, and pelvis segments, as was required by our protocol; this demonstrates that the differences in eye movement characteristics displayed by our participants were due to the different visual conditions. Furthermore, both traces show a clearly that gaze leads the other body segments throughout the majority of the turn. All participants in the study were found to display similar behaviour. FV = full vision; NV = no vision.

Fig. 6 Main sequence plots for fast phases in FV and NV. a) A strong relationship between fast phase amplitude and fast phase velocity in the FV condition that fit the main sequence relationship found in previous studies (Pelisson, Prablanc, and Urquizar, 1988). b) The relationship between fast phase amplitude and fast phase velocity was significantly weaker when visual input was removed. The number of data samples was 1839 and 2100 for the FV and NV conditions, respectively. FV = full vision; NV = no vision.

Fig. 7 Cumulative frequency distributions for FV and NV conditions. The distribution of fast phase amplitudes was positively skewed in both conditions and the vast majority of fast phases were 15° or smaller in amplitude. K-S Z found no statistically significant differences between FV and NV cumulative distributions of fast phase amplitude. FV = full vision; NV = no vision.

Table 1

Mean (± standard deviation) onset latencies (s) for all segments for all experimental conditions. FV = full vision; NV = no vision; GF = gaze fixation.

Table 2

Mean (± standard deviation) for all peak segment velocity and all peak segment separations for all experimental conditions. Turn onset – turn end describes the time from initial segment onset, usually the head, to the time in which the final body segment, typically the pelvis, ceased movement. All peak segment velocities and peak segment separations were calculated from within this interval. FV = full vision; NV = no vision; GF = gaze fixation.

Table 3

Mean (± standard deviation) for all stepping variables for all experimental conditions. FV = full vision; NV = no vision; GF = gaze fixation.

Table 1

		FV	NV	GF
Head	90°	.80 ± .39	.84 ± .39	.90 ± .47
	180°	.77 ± .38	.77 ± .37	.82 ± .41
Thorax	90°	.81 ± .37	.83 ± .37	.88 ± .45
	180°	.81 ± .37	.78 ± .37	.79 ± .38
Pelvis	90°	.83 ± .37	.84 ± .38	.89 ± .46
	180°	.80 ± .38	.79 ± .38	.82 ± .40
Eye	90°	1.26 ± .50	1.29 ± .54	*n/a*
	180°	1.25 ± .43	1.20 ± .50	*n/a*
Leading Foot	90°	1.25 ± .30	1.31 ± .29	1.48 ± .34
	180°	1.23 ± .33	1.3 ± .28	1.41 ± .27
Trailing Foot	90°	1.97 ± .42	2.05 ± .40	2.33 ± .51
	180°	1.90 ± .44	1.96 ± .34	2.22 ± .40

Table 2

		FV	NV	GF
Peak Head Velocity (°s^{-1})	90°	92.54 ± 29.29	72.32 ± 20.55	64.93 ± 16.48
	180°	105.43 ± 31.09	92.26 ± 29.18	79.49 ± 19.47
Peak Thorax Velocity (°s^{-1})	90°	78.15 ± 19.40	66.97 ± 17.88	61.45 ± 14.17
	180°	93.30 ± 23.59	82.04 ± 21.64	74.05 ± 17.43
Peak Pelvis Velocity (°s^{-1})	90°	84.69 ± 23.44	71.99 ± 18.51	67.14 ± 15.86
	180°	100.10 ± 25.58	88.58 ± 21.64	80.66 ± 19.95
Peak Head-Thorax Separation (°)	90°	7.83 ± 9.08	4.65 ± 4.23	4.34 ± 3.61
	180°	10.68 ± 7.95	6.86 ± 4.38	5.77 ± 4.34
Peak Head-Pelvis Separation (°)	90°	9.81 ± 9.86	6.12 ± 4.78	6.26 ± 4.35
	180°	12.38 ± 9.19	7.93 ± 5.21	7.29 ± 5.41
Peak Thorax-Pelvis Separation (°)	90°	3.88 ± 1.22	3.09 ± 0.99	3.41 ± 1.26
	180°	3.90 ± 1.45	3.25 ± 0.83	3.35 ± 1.41
Turn Onset – Turn End (s)	90°	2.79 ± .73	3.10 ± .78	3.35 ± .77
	180°	4.03 ± 1.02	4.60 ± 1.07	5.00 ± 1.15

Table 3

		FV	NV	GF
Leading Foot Step Size (°)	90°	54.30 ± 18.74	51.85 ± 18.67	51.64 ± 16.65
	180°	57.79 ± 19.24	51.35 ± 15.79	57.68 ± 17.64
Trailing Foot Step Size (°)	90°	72.94 ± 19.49	70.53 ± 17.08	73.21 ± 14.75
	180°	90.39 ± 28.67	82.60 ± 24.05	88.29 ± 26.11
Leading Foot Step Duration (s)	90°	.55 ± .19	.55 ± .21	.61 ± .28
	180°	.55 ± .23	.52 ± .15	.57 ± .19
Trailing Foot Step Duration (s)	90°	.65 ± .23	.66 ± .25	.72 ± .30
	180°	.66 ± .20	.63 ± .15	.68 ± .22
Step Frequency (Hz)	90°	1.54 ± .41	1.48 ± .32	1.38 ± .34
	180°	1.49 ± .37	1.46 ± .28	1.29 ± .29

Figure 1

Click here to download Figure Fig1.eps

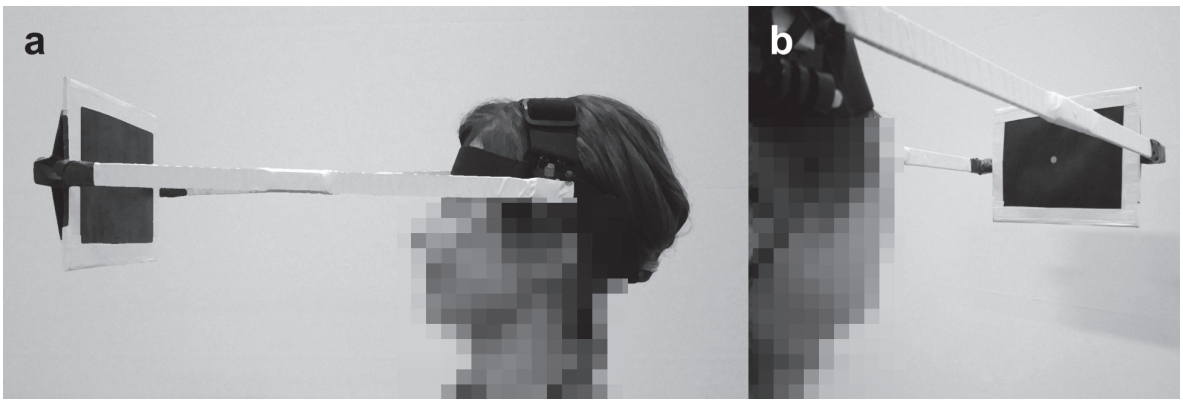

Figure 2

Click here to download Figure Fig2.eps

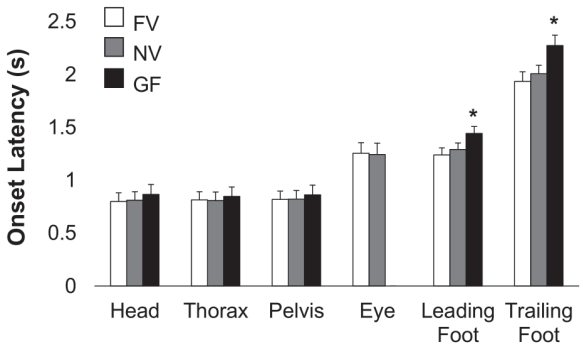

Figure 4

Click here to download Figure Fig4.eps

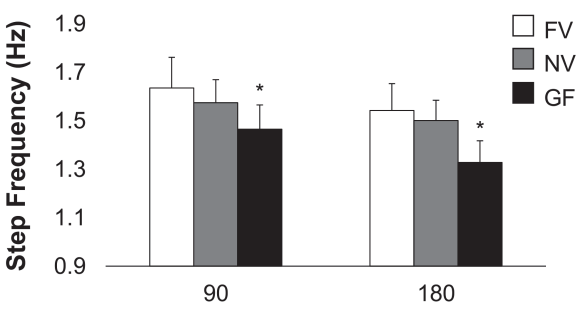

Figure 3

Click here to download Figure Fig3.eps

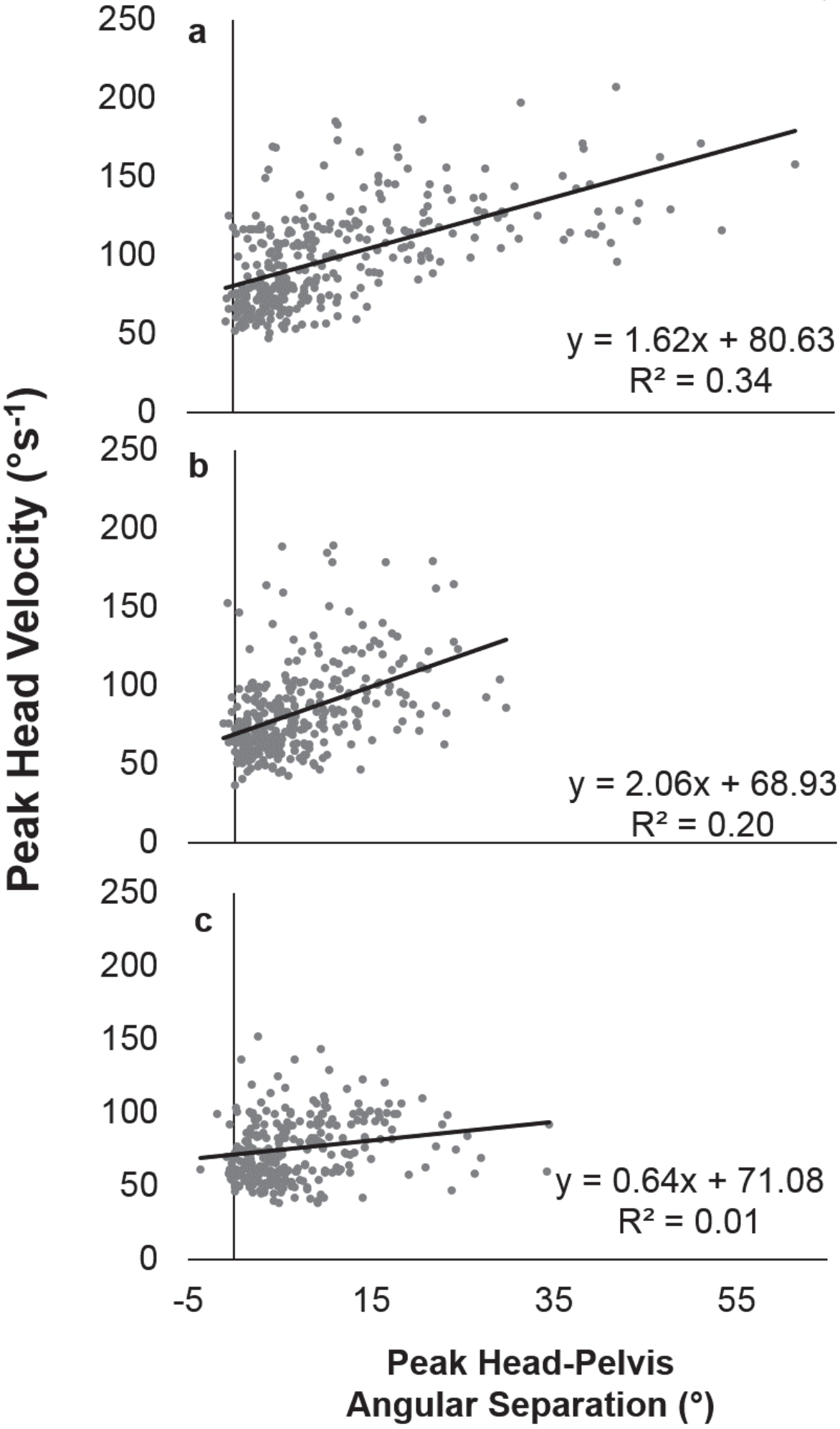

Figure 5

Click here to download Figure Fig5.eps

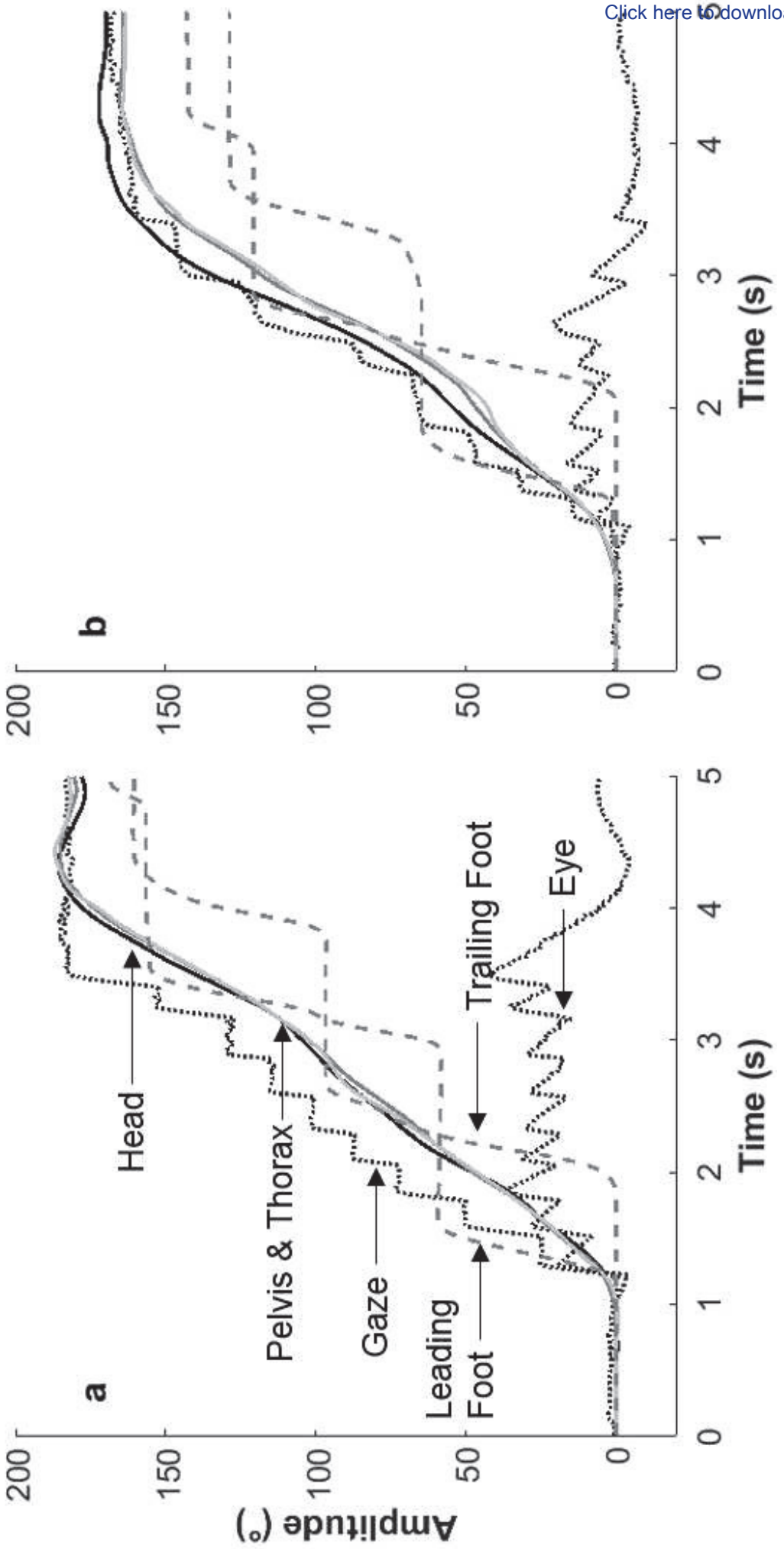

Figure 6

Click here to download Figure Fig6.eps

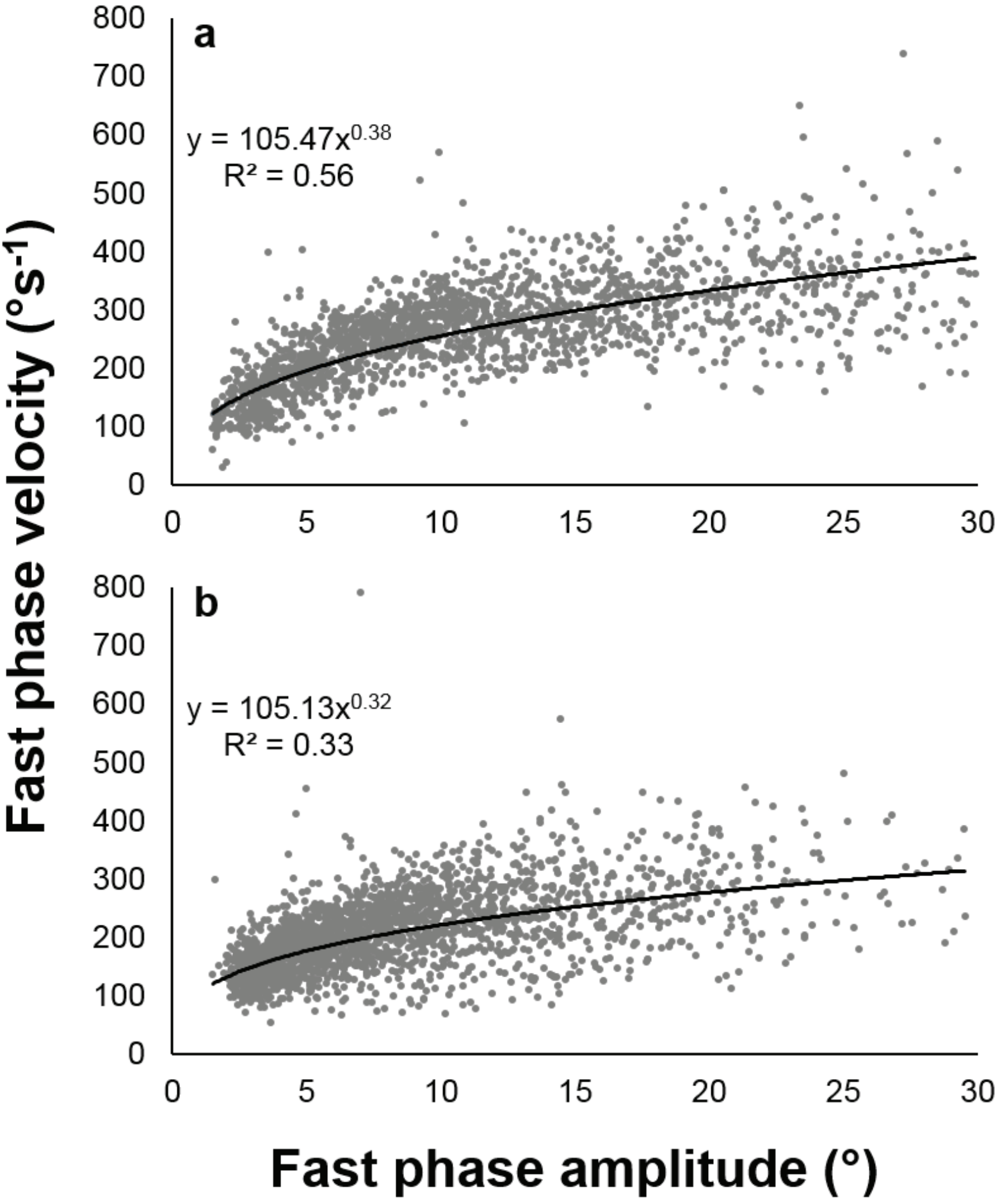

Figure 7

Click here to download Figure Fig7.eps