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Visual field motion during a body pull affects compensatory standing and stepping responses

St George R.J.[1,2], Di Giulio I.[1,3], Day B.L.[1]

[1]Department of Clinical and Movement Neurosciences, UCL Queen Square Institute of Neurology, London, UK.

[2]Sensorimotor Neuroscience and Ageing Research Group, School of Psychological Sciences, University of Tasmania, Australia.

[3] Centre for Human & Applied Physiological Sciences, King's College London, London SE1 1UL, United Kingdom.

Corresponding author: Rebecca J. St George

    Email: Rebecca.StGeorge@utas.edu.au

    Postal address: Private Bag 30, Psychology Department, University of Tasmania, Hobart, 7001.

Key points summary

- It is unclear whether the visual input that accompanies a perturbation of a standing person can affect whether a recovery step is taken.
- Visual motion speeds were manipulated during unexpected forward and backward shoulder pulls.
- Visual motion that appeared slower than actual body motion reduced the initial in-place resistance to the perturbation.
- Due to the modulation of the in-place response, less pull force was needed to trigger a step when visual velocity appeared slower than normal.
- The visuomotor postural response occurred earlier and was larger when the full-field visual input was paired with a mechanical perturbation.

Abstract

The aim of this study was to determine how visual motion evoked by an upper body perturbation during standing affects compensatory postural responses. This was investigated by rotating the visual field forwards or backwards about the ankle, time-locked to a forwards or backwards shoulder pull. Kinematic, kinetic and electromyographic responses were recorded to a range of pull forces over 160 trials in 12 healthy adults (mean = 31 years, S.D. =5.8). Stepping threshold forces and in-place postural responses were compared between conditions.

When the visual field moved in the same direction as the pull, so that the apparent velocity of the body was reduced (SLOW condition), the pull-force required to induce a step was less than when the visual field either rotated in the opposite direction (FAST) or was unaltered (NATURAL). For in-place responses, the body was displaced further in the direction of the pull in the SLOW condition. This was due to a reduction in the resistive force from lower leg muscles 130ms after the visual motion onset. In trials with no pull, the visual motion induced postural responses that were later (290ms) and had smaller amplitudes compared to when visual motion is paired with an unexpected perturbation of the body.

The results suggest that the apparent speed of the visual environment during a perturbation does influence whether a compensatory step is taken, not via a direct effect on the decision to step but by modulating the initial in-place response.

Introduction

When a standing person is pushed, a postural response is triggered to counter the perturbing force in order to maintain stability. Generally, there will be an initial *in-place* response — where the feet do not move and the perturbing force is resisted. In some cases, a *stepping* response will follow — where the base of support is adjusted. A critical role of somatosensory, proprioceptive and vestibular input in shaping the postural response has been established (Do et al., 1990; Allum et al., 1994; Inglis et al., 1994; Bloem et al., 2000). However, it is unclear whether visual information is used in the postural response to recover from a perturbation that threatens stability. As dependence on vision increases with age and sensorimotor impairment (Bugnariu & Fung, 2007; Slaboda et al., 2011) it is important to understand how visual input contributes to compensatory postural responses.

A mechanical perturbation to the body that moves the head in space inevitably produces relative visual motion. This may induce optic flow of the visual scene on the retina, evoke compensatory eye movement to keep the image stabilised, or a combination of the two. Thus, the direction and speed of the visual motion provides information about head motion, from which body motion in space can be inferred. Prior literature suggests that the level of visual involvement in postural responses depends on the size and frequency of the perturbation. For example, in quiet standing when there are no external perturbations, the body leans in the direction of full-field visual motion with ground reactive force latencies of 190-300ms (Bronstein & Buckwell, 1997; Guerraz et al., 2001; Day et al., 2016). When the

standing surface tilts about the ankle joint at low perturbation frequencies, manipulating

visual motion has been found to modulate the in-place postural response (Diener et al.,

1986; Slaboda et al., 2011; Slaboda & Keshner, 2012). However, for higher frequency

transitory tilts of the standing surface, visual input has not been found to have any effect on

the in-place response (Vidal et al., 1982; Diener et al., 1986). These findings suggest that

postural responses to higher perturbing forces are driven by mechanisms largely dependent

on non-visual sensory inputs.

However, the role of visual input in larger perturbations may not be so

straightforward. Perturbing upright stance with a tilt of the floor about the ankle joint is

unusual to encounter in daily life and is a perturbation that directly triggers lower-limb

proprioceptive reflexes. Although there are brief vertical accelerations of the head soon

after tilts of the floor, their high frequency nature makes them more a vestibular stimulus

than a visual one (Carpenter et al., 1999). In contrast, a push at the shoulder is not an

uncommon experience and may evoke earlier and greater head motion (thus more visual

motion). Furthermore, no prior study in humans has manipulated visual input during

perturbations that are strong enough to threaten in-place stability requiring a stepping

response. As there is some evidence in primates that visuomotor responses can be hastened

in situations where stability is threatened (Vidal et al., 1979; Lacour et al., 1981), visual input

may be more involved in the postural response when perturbations are strong enough to

trigger a stepping response. This study aimed to determine whether full-field visual motion

associated with a perturbation to the upper body could alter the trigger for a stepping

response. We investigated this by manipulating the apparent velocity of the visual scene

during unexpected shoulder pulls at forces high enough to evoke a step.

Although a stepping response tends to occur at higher perturbation forces, previous work has shown that the pull force per se does not trigger this transition from in-place to stepping response. Rather it is the position and velocity of the body's centre of mass (CoM) during the initial phase of the perturbation that predicts whether, or not, a step is subsequently taken (Pai et al., 1998; Pai et al., 2000; Hof et al., 2005; Hasson et al., 2008). This early trigger is reflected in the finding that step preparation (as indicated by a lateral weight shift) is often initiated well before the vertical projection of the body's CoM is at the limits of the base of support (McIlroy & Maki, 1993). Thus, the decision to step is based on a predicted future state of the CoM formed from the current state of the CoM. However, the brain does not have direct knowledge of the body's CoM position or velocity; it must generate an estimate from the sensory signals evoked by the perturbation and the body's subsequent behaviour. Somatosensory, proprioceptive, vestibular signals as well as vision all contribute to the internal representation of body motion (DeAngelis & Angelaki, 2012; Britton & Arshad, 2019).

Here we hypothesised that the visual motion evoked during an upper-body perturbing force would inform the brain's estimate of body motion and would impact the postural response. Thus, visual motion that is artificially made slower than actual body motion would reduce the estimate of body velocity, whereas visual motion that is made faster would do the opposite. The effects of such visually-based body velocity estimates on the in-place and stepping responses will depend on whether visual input is used by these compensatory mechanisms and how they interact. Consider the outcome if the in-place mechanism uses visual input to shape its response. If, for example, the apparent body velocity were artificially reduced, one would expect less initial in-place resistance. This, in

turn, would lead to greater body motion and so an increased likelihood of a step being required. Alternatively, if artificially reduced visual motion does not influence the initial in-place response, but nonetheless is incorporated into body velocity estimates that informs the decision to step, then a decreased likelihood of a step being triggered would be expected. Opposite effects would be expected if the apparent body velocity was increased by artificially increasing visual motion during a perturbation.

Methods

Ethical Approval

Twelve healthy volunteers (7 female) with an average age of 31 years (S.D. = 5.8) gave written informed consent to participate in this study. All participants had normal or corrected-to-normal vision and did not suffer from any known neurological or orthopaedic problems. All experimental protocols were approved by the UCL Research Ethics Committee (#5454/001) and conformed to the Declaration of Helsinki (except for registration in a database).

Equipment

Participants stood at a comfortable foot-width, with each foot on a separate force plate, at a distance of 60cm from a screen to their right that was suspended from floor to ceiling (Figure 1A). Four inextensible strings were connected to the body harness worn by subjects at the front and back of each shoulder. These cables were attached to two rotatory servomotors (Kollmorgen, Radford, VA, USA) that were operated in torque feedback mode. One motor was in front, and one motor was behind the participant. To ensure a smooth

resistance, even at low torques, the motors were outfitted with anti-cogging features. The subject performed the experiment in a harness that was attached to an overhead wire that allowed unrestricted movement of a few steps forward or backward, yet prevented impact with the ground.

A projector (InFocus SP8600, 24 fps, 1920x1080 resolution) was positioned 6.6 metres from the large (2.43 x 2.2m) rear projection screen. A visual pattern was projected onto this screen which filled subjects' field of view when their head was rotated 90 degrees to the right. The laboratory was otherwise in darkness. The projected visual pattern consisted of coloured dots (18 mm diameter) randomly positioned with a density of 300 dots/m^2.

Wireless surface electromyography (EMG, Delsys, Inc., Boston, MA, USA) were recorded bilaterally from the tibialis anterior (TA) and medial gastrocnemius (GAS) muscles. The 3-D positions of infrared emitting diode markers were recorded from the 7th cervical vertebra; and bilaterally from: the metatarsal heads, heels, malleoli, femoral epicondyles, acromions, posterior skull, posterior superior iliac spine and the wrists. Kinematic data were sampled at 200Hz. The EMG, ground reaction 3-D forces (Kistler, Winterthur, Germany), output from force transducers in serial connection to the puller motors, analogue output from the motors, and the visual motion start and stop events were recorded synchronously at 1000Hz with a CODA motion-capture system (Charnwood Dynamics, Rothley, UK).

A central computer communicated with the computer giving commands to the motors, the computer presenting the visual stimulus and the computer collecting the data. To approximate the visual motion that occurs when a standing person is pulled at the shoulder, the visual scene was rotated about an axis coincident with the subject's ankle

joint. Furthermore, the onset of visual scene motion was triggered to occur at a time when the head would naturally start moving from a mechanical pull. Pilot testing of pulls that were strong enough to evoke a step revealed the peak angular velocity of the head was of the order of 12.0 deg/s (S.D. =2.3), and the onset time of head motion was 132.4ms (S.D. = 34.1ms) after the central control computer 'go' command. Measurements with a photodiode showed there was a mean time delay of 30.8ms (S.D. = 8.9ms) from the computer 'go' command to the actual movement of the visual scene (for more information see (Day et al., 2016). Therefore, in order to present the moving visual stimulus in the earliest phase of head motion (approximately 1 S.D. faster than the mean onset), a 70ms delay was imposed between the computer 'go' command to the pulling motors and the 'go' command to start visual motion. The angular velocity of the projected visual scene reached a peak of 12 deg/s and was applied over the same time scale as the pull force, 1.5 seconds total including 0.5 second on and off ramp profiles (Figure 1B). The visual scene was controlled by software written in Matlab R2012B (The Mathworks, Inc., Natick, MA, USA) using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007).

[Figure 1 about here]

Procedure

Subjects were told to remain standing to the best of their ability during the trials and only to step if required. Subjects were asked to rotate their head to the right just before trial onset and to keep their head in this orientation for the trial duration (6 seconds) so that the screen filled their field of view (FOV). Perturbations were applied precisely 2 seconds after the experimenter pressed the trial start command. When comparing the head yaw position within the first 500ms of the pull there tended to be a small backward deviation of the head

for forward pull conditions (1.3°, 95% CI [0.80,1.80]) and a forward rotation of the head for backward pulls (4.2°, 95% CI [2.7, 6.1]). Even with these changes in head yaw, the FOV (assuming 120° of arc) remained inside the bounds of the projection screen (average FOV limit= 0.26m, 95% CI [0.21, 0.31] and FOV limit= 0.18m, 95% CI [0.08, 0.28] inside the bounds of the screen for forward and backward pulls respectively). Subjects were encouraged to rotate and stretch their neck at the end of each trial to prevent neck strain or adaptation. To keep subjects alert and minimise fatigue, sit-down rest breaks were every 20 trials.

Phase 1 of the procedure estimated force thresholds for stepping by testing subjects over a 20N pull force window at 2N even-integer increments for each of the 3 randomly presented visual field conditions; visual field forward, visual field backward and visual field stationary (NATURAL) and 2 randomly presented pull directions; pull forward and pull backward. The 20N window was initially estimated based on subject height and weight. If the initial estimate was incorrect and the subject was able to resist stepping at the highest pull force, or stepped at the lowest pull force, the window was shifted higher or lower respectively by 10N, and Phase 1 testing began again. Based on Phase 1 stepping data (60-80 trials) a stepping threshold was estimated.

In Phase 2 there were more pulls spanning the stepping threshold estimate randomized with pulls that required an in-place response. The threshold honing pulls were selected over a 7N window, spanning the stepping threshold estimate from Phase 1 at 2N odd-integer increments for the three visual conditions. When combined with Phase 1 data, subjects were tested at 1N force increments over the critical threshold window for each of the three visual conditions in the two pull directions. In-place trials were achieved by pulling

subjects with a force set at two-thirds of their Phase 1 stepping threshold estimate in the

NATURAL condition. These in-place pulls were repeated 7 times for each of 9 conditions:

visual field (forward, backward, NATURAL) x pull direction (forward, backward, none). The

number of Phase 2 trials was the sum of threshold pulls (4 pull forces x3 visual conditions x2

pull directions) plus in-place pulls (7 repeated pull forces x 3 visual conditions x3 pull

conditions) giving 87 trials. The average number of total trials across Phase 1 and Phase 2

was 160.

Data Analysis

Stepping trials

A step was identified when there was a reduction of vertical force to less than 5N on one of

the force plates coupled with an anterior/posterior displacement of the foot in the direction

of the pull. Force thresholds for stepping were found in each condition by plotting a data

point for each trial pull force on the abscissa versus step (stance=0, step=1) on the ordinate

axis (Figure 1C). A sigmoidal curve was fitted to the data. The value at 50% of the amplitude

was taken as the step threshold.

Trials in which the relative visual motion was slower than in the NATURAL condition

were categorised as the SLOW condition. This occurred when the pull direction and the

visual field motion were in the same direction i.e. pull forward and visual field forward, or

pull backward and visual field backward. Trials were assigned to the FAST condition when

the relative visual motion was faster than the NATURAL condition due to the pull direction

and the visual field motion occurring in opposite directions, i.e. a pull forward and visual

field backwards, or a pull backwards and visual field forwards. Significant effects of the

visual field motion on the step threshold were tested with a repeated measures ANOVA

with visual motion (SLOW/NATURAL/FAST) and pull direction (forward/backward) as the fixed factors. Contrast tests investigated between-level effects.

In-place trials

Ankle, knee and hip flexion/extension joint angles and change in head angle with respect to the ankle were calculated from the kinematic data using Visual3D software (C-Motion, Inc). To investigate kinematic differences between visual conditions, the area under the curve (AUC) of head, hip, knee and ankle angle in the AP direction over a 2.5 second window after the pull onset was determined for each participant. Differences in kinematic traces in angles were calculated to determine the latency when a change in visual condition caused a change in a kinematic variable. The latency was defined as the time when the difference trace deviated more than three standard deviations of the pre-pull baseline fluctuations. Area under the curve of AP horizontal shear forces (F_y) in a window 130-270ms after the visual field motion were calculated. This window corresponded to the first significant divergence between visual conditions.

EMG signals were zero offset by subtraction of the mean over the two-second baseline period, rectified and low-pass filtered at 50Hz with a zero phase, 4th order Butterworth filter. EMG traces were normalized for each participant by dividing by the area under the mean agonist EMG response during the period of peak perturbing force in the NATURAL condition. Thus, activity in the TA muscles in each trial was divided by the area under the mean TA trace from 2.5-3 seconds obtained during NATURAL backward pulls, whereas the GAS data were normalized in each trial by dividing by the area under the mean GAS trace from 2.5-3 seconds obtained in the NATURAL pull forward condition.

Within-subject changes in the EMG response to the different visual field conditions were determined from the integrated area under the normalised rectified traces. As the centre of pressure (CoP) traces diverged between visual conditions 130ms after the onset of visual motion, we selected the EMG window 60 to 120ms after onset of the visual field motion to allow time for the electromechanical coupling delay. This window corresponded to the earliest time of supraspinal influence in the legs (Corden et al., 2000).

Parameters calculated from the in-place trials were the dependent variables in repeated measures ANOVAs, with pull direction (forwards/backwards) and visual motion (NATURAL/ SLOW/FAST) as factors. Contrast tests analysed differences between levels within the factors. During quiet standing with no pull a repeated-measures ANOVA investigated differences in postural variables between visual motion conditions.

In all trials, lateral weight shifts that were indicative of step preparation were identified when there was a lateral shear force (Fx) after the pull of over 5N that lasted more than 50ms occurring concurrently with diverging vertical forces (Fz) under the two feet. The latency and peak of lateral Fx, of the first lateral shift and the lateral shift prior to the step were recorded. The percentage of trials with lateral weight shifts, latency, CoP position, CoP velocity and Fx magnitude at lateral weight shift onset and peak were compared between visual conditions with repeated measures ANOVAs. All data were processed in Matlab (R2018a, MathWorks, Inc., MA, USA) and statistical analysis was performed with SPSS (IBM SPSS version 20).

Results

Stepping Thresholds

Mean stepping threshold force was significantly higher for forward pulls (75.9N, S.D.=22.0) than backward pulls (49.1N, S.D.=8.8, p<0.001). The applied visual field motion during the pull had a significant main effect on stepping threshold (p<0.001). Figure 2 shows the relative changes in group and individual step thresholds between visual conditions. During forward pulls, the stepping threshold was on average 2.4N (SD=2.7) lower in the visual field forward (SLOW) compared to NATURAL condition, and 1.1N (SD=2.1) higher in the visual field backward (FAST) compared to NATURAL condition. Whereas, for backward pulls, the stepping threshold was 1.6N lower (SD=2.5) in the visual field backward (SLOW) compared to NATURAL condition, and 0.6N (SD=1.2) higher in the visual field forward (FAST) condition compared to NATURAL. Contrast tests showed that when the visual field was moving in the same direction as the pull (SLOW) the stepping threshold was significantly reduced compared to the NATURAL condition (p=0.002). When the visual field was moving in the opposite direction to the pull (FAST) the threshold was slightly elevated but was not significantly different to the NATURAL condition (p=0.146). There was not a significant visual motion by pull direction interaction (p=0.363).

[Figure 2 about here]

In-place postural responses

When participants were pulled at two-thirds of their NATURAL stepping threshold, there were significant main effects of pull direction (p=0.008) and visual motion (p=0.015) on displacement of body segments (Figure 3). There was no pull direction x visual motion

interaction (p=0.580).   Contrast tests showed significantly greater joint angle displacements for the SLOW compared to the NATURAL condition at the ankle (p=0.007), knee (p=0.005), hip (p=0.003) and head (p=0.006). Thus, for forward pulls, with a forward visual field, the head moved further forward and there was greater hip and ankle flexion and greater knee extension compared to NATURAL visual motion. Whereas, for backward pulls with a backward visual field the head moved further backwards and there was greater hip and ankle extension and greater knee flexion compared to NATURAL vision. These displacements were not significantly different for the FAST compared to the NATURAL condition at the ankle (p=0.468), knee (p=0.394), hip (p=0.342), or head (p=0.370). Of all of the body kinematics recorded, the ankle angle was the first joint to show a divergence between NATURAL and SLOW visual conditions; for forward pulls this occurred at 297ms (95% CI[225,362), and for backward pulls at 283ms (95% CI[208, 338]) after onset of visual motion. When there was no pull, visual field motion still had a significant effect on displacements of body segments (p=0.025). Although contrast tests showed only displacements at the head and hips for the backward visual field motion were significant (p=0.018 and p=0.038 respectively) all other contrasts were not significant (p>0.154, for all comparisons).

[Figure 3 about here]

When there was no pull, differences in antero-posterior horizontal ground reaction forces (Fy) between visual conditions were apparent and occured 290ms (95% CI [272,311]) after the onset of the visual motion (Figure 4A). During the pull, Fy forces acted on the body initially in the opposite direction to that of the pull in order to remain standing. There was no effect of visual motion direction on the Fy onset latency (p=0.75), but the size of the Fy

force did differ between visual field conditions 130ms, 95% CI[119,143] after visual motion

onset (Figure 4). There was a signficant main effect of relative visual motion on AUC of F_y

traces in the time window 130-270ms after visual field motion in the pull conditions

(p=0.002) but not in the no pull conditions (p=0.55). For the FAST condition, F_y force over

this window was not different to the NATURAL condition (p=0.506) (white trace in Fig 4B,

black trace in Fig 4C). However, for the SLOW condition the initial F_y reacting to the pull was

less than for the NATURAL condition (p=0.016) (black trace in Fig 4B, white trace in Fig 4C).

There was no significant pull direction by visual field direction interaction (p=0.431).

[Figure 4 about here]

The initial onset latency of the EMG agonist muscle in response to a pull was not affected by

the visual motion (p=0.274). However, in the window 60 to 120ms after visual motion onset

there was a significant interaction between the visual field motion and the direction of the

pull in the GAS (p=0.032) and TA muscles (p=0.006) response (Figure 5). The agonist

muscles resisting the pull (TA for backward pulls and GAS for forward pulls) were reduced in

the SLOW visual field condition compared to their activity in the NATURAL visual field

condition (p=0.001). Furthermore, the antagonist muscle activity (GAS for backward pulls

and TA for forward pulls) was increased in the SLOW condition compared to the NATURAL

condition (p=0.005). For the FAST condition, there was no systematic effect of the visual

motion on EMG activity for agonist (p=0.397) or antagonist muscles (p=0.217).

[Figure 5 about here]

Incidence and latency of step preparation

A lateral weight shift, as evidence of step preparation, was observed in 52% of trials and there was no difference in incidence between visual conditions (p=0.393). The latency of the lateral shift occurred earlier for backward pulls (360ms, 95%CI [311,401]) compared to forward pulls (486ms, 95% CI [436,536], p=0.026). There were no significant effects of visual field condition on the size (*p*=0.668) or latency (*p*=0.055) of the lateral weight shift, or the position of CoP at the start of the shift (*p*=0.819).

Discussion

This is the first study to demonstrate that the motion of the full-field visual environment during a perturbation can influence whether or not a step is taken. These findings challenge earlier studies in which triggered postural reactions were thought to be stereotyped (Nashner et al., 1979; Vidal et al., 1982; Diener et al., 1986) and visual motion was thought to only affect the propensity to step through exposure *before* the perturbation (Hoshiyama et al., 1993). Here we demonstrate that the in-place response and the likelihood of stepping may be affected by visual feedback generated *during* the perturbation.

We had postulated that changing the relative velocity of the visual motion would modulate the perceived body motion and the observed effects on the postural response would reveal underlying mechanisms of the visuo-postural system. The results showed that the full-field visual motion had an influence on the in-place response. The in-place muscle activation response was influenced by vision within the first 60-120ms of visual motion (130-190ms after the pull onset). In-place resistance to the pull was initially reduced for the

SLOW condition, when visual field motion indicated that the body was moving slower than it actually was. Activation of agonist muscles in the lower leg that normally worked to resist the pull were reduced, while antagonist activation increased (Figure 5). This reciprocal muscle behaviour reduced the forces opposing the pull and so the body was displaced further than normal. This increased displacement would then have been detected by proprioceptors, vestibular receptors and cutaneous receptors and this feedback triggered a step to avoid falling. This heightened veridical feedback appeared to dominate the decision to trigger a step and avoid falling.

When the visual field motion indicated that the body was travelling faster than it actually was (FAST), there were no effects on the in-place postural response. Although the visual input was distorted, the feedback from non-visual sources would have been unaffected. If visual information carried any significant weight in the decision to take a step, increased visual motion indicating greater body velocity should have biased the step response towards a lower than normal threshold. Given this did not happen (in fact the threshold was slightly higher than normal) suggests that the visual channel carries very little, if any, weight for the decision to step. Alternatively, the result may reflect the non-linear relationship between visual field speed and postural control (Day et al., 2016), as vision contributes most to standing stabilization in the low frequency range (Fitzpatrick & McCloskey, 1994). Therefore, an increase in visual velocity may have less influence on posture than a decrease in visual velocity. This non-linearity may have contributed to the reduced modulation of the in-place and stepping response for the FAST condition.

Faster visuomotor responses

Visual field motion alone evoked postural sway in the same direction as the visual motion with a mean ground reaction force (GRF) latency of 290ms. This latency is in the range of previously reported responses to visual stimuli obtained in quietly standing individuals (Bronstein & Buckwell, 1997; Guerraz et al., 2001; Day et al., 2016). However, when the same visual motion was presented in conjunction with the pull, GRF responses to the visual stimuli were hastened to 130ms. This faster response corresponded to a lower leg EMG activation window 60-120ms after visual motion onset. Expediting the response by 160ms suggests either different neural pathways are engaged or visual input is gated-in during co-incident visual and mechanical perturbations.

When the body is perturbed by an external force the automatic short latency reflex (SLR) acting through spinal circuity attempts to counter the perturbation, with lower leg muscle activation in the range of 80-120ms (Nashner & Cordo, 1981). The long latency reflex (LLR) refers to the epoch following the SLR but before outright voluntary control and it reflects the temporal overlap of multiple neural contributors including ongoing input from the spinal cord as well as supraspinal contributions (Kurtzer, 2014). LLR responses can be modified according to the task and global limb dynamics indicating access to an internal body schema (Jacobs & Horak, 2007). In the current study, the latency of the visual influence on the postural response (from 130ms after the pull) spans the LLR timescale in the lower leg (Friedemann et al., 1987; Corden et al., 2000). Thus, visual input during upper body perturbations modulates the neural pathways involved during the LLR time period.

Larger visuomotor responses

The visually-evoked postural response was not only earlier but also larger when paired with the pull compared to no pull, which demonstrates that it has variable gain depending on the

context. A prior study by Soechting and Berthoz (1979) also showed variable gain in the postural response to visual motion (Soechting & Berthoz, 1979). They showed that when horizontal motion of the visual surround was in conflict with translation of the standing surface, the body leaned twice as far in the direction of image velocity during a perturbation than when the visual stimulus was in isolation. However, unlike our study, the Soechting and Berthoz study found that the postural response to visual motion occurred at approximately the same latency in both stationary and perturbed conditions. The response found in their study may not have been faster because the surface translation was well below stepping threshold and was not a threat to stability. In our study, there was a heightened threat as people were forced to step on some trials to avoid falling. Furthermore, by translating the standing surface the prior study evoked a lean of the body in the opposite direction to body translation so the relative dynamics of the horizontal visual translation may have been more complex. An advantage of shoulder-pulls versus platform translation or waist pulls to study the fast visuomotor response is that there are fewer degrees of freedom for head motion, so the effect of the perturbation and visual motion can be more precisely controlled.

Neural Pathways

This is not the first study to demonstrate the existence of fast acting visuomotor pathways to the lower leg that respond according to the relative speed of visual motion (Nashner & Berthoz, 1978; Lacour et al., 1981; Reynolds & Day, 2005). A series of experiments that exposed vertically falling monkeys to variable visual motion and variable falling speeds showed that the velocity of the visual surround could modify EMG activity of the lower legs 60ms after onset of the fall in a directionally specific way (Vidal et al., 1979; Lacour et al., 1981).

Our findings could also use similar mechanisms to the phenomenon of rapid leg adjustments during a step to visual target jumps being made even faster when combined with a startling auditory input (Reynolds & Day, 2007). Reticulospinal pathways may be involved in accelerating the visuomotor response during unexpected or 'startling' perturbations. The superior colliculus receives input directly from the ocular nerve (Bisti et al., 1974), and has fast output pathways for controlling limb movement (Courjon et al., 2004). It can also integrate multimodal sensory input from visual, vestibular and somatosensory inputs (Wallace et al., 1993) so may be involved in body schema representation. The reticular formation receives input from the colliculus (Harting, 1977) and is activated by vestibular stimulation (Peterson & Abzug, 1975). Startle reflexes are mediated by the RF through reticulo-spinal pathways and their EMG responses in lower leg muscles during standing are within the time scale seen in our study (Brown et al., 1991). A classical startle reflex is unlikely to explain the results in the current study because our responses show a specific agonist/antagonist activation pattern dependant on the relative visual velocity, indicating access to an internal model rather than a generalized co-contraction. Also startling stimuli can accelerate planned motor responses (Campbell et al., 2013), but in the current study, conditions were randomized so a planned response was unlikely. Vestibulospinal pathways may also mediate the response, as visual-vestibular interactions have been shown in the vestibular nuclei of the brainstem (Waespe & Henn, 1977), and photic stimuli can activate the vestibular nuclei with latencies of only 28ms (Azzena et al., 1978).

The motor cortex may be involved in modulating the size of the visuomotor response as postural LLR scaling is known to be abolished during the TMS-induced silent period (Kimura et al., 2006). Corticospinal pathways are influenced by the basal ganglia so it is not

surprising that people with Parkinson's Disease are less able to modulate the size of the LLR reflex according to context (Bloem et al., 1995) and have impaired stepping to external perturbations (Di Giulio et al., 2016).

When is the decision to step made?

It is an enduring notion that stepping responses occur only when the initial in-place reactions fail to restore equilibrium: the ankle, hip, step sequence of responses (Horak & Nashner, 1986). However, our data suggest that the decision to step is more complex. If we assume that the lateral displacement of the centre of pressure toward the stepping foot prior to unloading and lifting the foot is when the decision to step occurred (McIlroy & Maki, 1993), then likelihood of a step appeared to fluctuate moment-to-moment in parallel with the in-place response. These preparatory adjustments were often observed in our data even when there was no subsequent step, or multiple times before a step was finally taken. Therefore, steps were planned *during* active in-place resistance and often these plans were abandoned when in-place resistance was sufficient to maintain stability. This observed behaviour supports a compensatory postural response model proposed by McIlroy and Maki (McIlroy & Maki, 1993) that has parallel, rather than sequential control of the two types of reactions. The cerebellum is likely involved in this parallel processing of the decision to step as it predicts future states of the body based on current sensory information and ongoing motor commands. The cerebellum also has prominent connections to both the primary motor cortex (Middleton & Strick, 1998) and also provides input to the RF and modulates its action (Asanuma et al., 1983).

Implications

This study has shown that the relative velocity of visual motion experienced during a destabilizing upper body perturbation affects the postural recovery response in young healthy participants. Because visual dependency is greater in elderly people (Slaboda et al., 2011) and in some clinical populations such as cerebral palsy (Slaboda et al., 2013) and stroke patients (Marigold & Eng, 2006; Manor et al., 2010) the visual effects on compensatory postural responses revealed in the current study may be even larger in groups at higher fall risk. Understanding how this visuomotor response is affected by age and movements disorders will be a fruitful line of enquiry for future studies and will improve our understanding of the pathophysiology of postural instability and falls.

Being pushed or pulled unexpectedly can take place in a static visual environment where the visual motion input accurately reports the perception of body motion. However unexpected pulls may also occur in environments that are more visually active, potentially with visual motion ambiguities such as standing on public transport or being jostled in a moving crowd of people. In such cases, visual input may be an inaccurate source of body motion and result in inappropriate postural responses.

Conclusion

This study has revealed the early and specific influence of visual motion on balance mechanisms that respond to external perturbations. The visually-evoked postural response was shown to be amplified and expedited to the legs during destabilising perturbations. In situations where a person trips, slips or is pushed unexpectedly, the fast visuo-motor response identified in this study will play a role in the balance strategy to prevent falling.

Additional Information

Competing interests

All authors declare that they have no competing interests in this work.

Author contributions

All experiments were performed at the Whole-body Sensorimotor Laboratory, Sobell Department of Motor Neuroscience and Movement Disorders, UCL Institute of Neurology.

R.J.St.G. and B.L.D. conceived and designed the experiments. R.J.St.G and I.D.G. acquired the data. R.J.St.G and B.L.D. contributed to data analysis and interpretation. R.J.St.G drafted the manuscript. All authors critically revised the manuscript.

All authors approved the final version of the manuscript. All authors agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved. All persons designated as authors qualify for authorship, and all those who qualify for authorship are listed.

Authors' Translational Perspective

When we are pushed or pulled unexpectedly a fast and effective reaction by the postural muscles is required to avoid falling over. This study has shown that the relative speed of the full-field visual motion experienced during a destabilizing upper body perturbation is used by the nervous system to control the postural response. The effect of visual field motion on muscle activity in the legs is earlier and larger when visual field motion occurs together with

an external pull. The reliance on visual information for balance increases in older people and in people with certain neurological disorders. This study may therefore open a window into understanding better the pathophysiology of postural instability and falls in high risk groups.

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Figure Legends

Figure 1. Experimental setup and protocol

A. The experimental setup showing that the projected visual scene rotated about the ankle joint. **B.** Each trial was a combination of one type of pull (forward, back or none) and one type of projected visual image motion (forward, back or none). The graph showing head velocity is representative data of a participant who remained standing when pulled at their stepping threshold. **C.** Example data showing how the stepping threshold (Th) was determined. All stance (0) and step (1) events for each condition were plotted against the peak pull force. The step threshold was the force corresponding to the 0.5 value of the fitted curve.
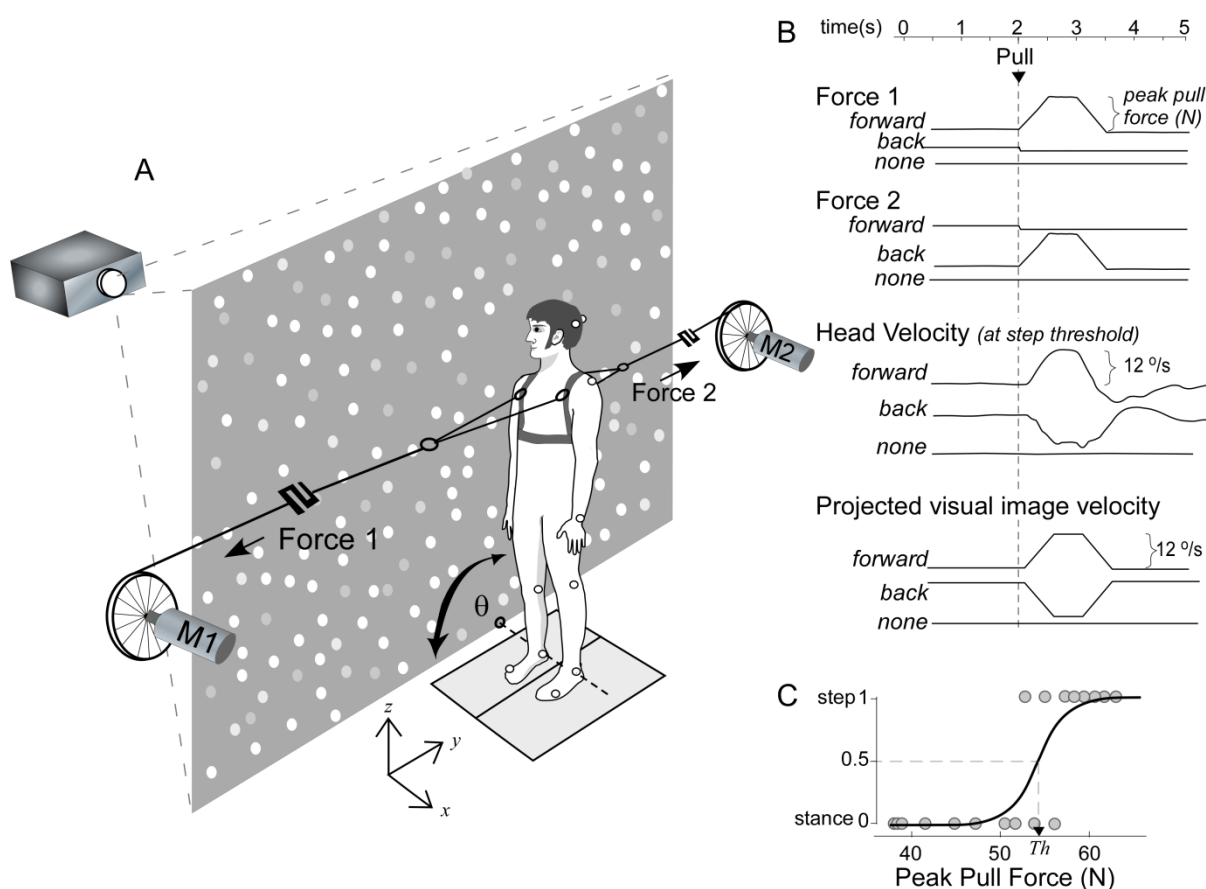
Figure 2. Stepping thresholds

The upper panel shows the fitted threshold curves to the combined data points of all subjects for the three visual field conditions for forward pulls (**A**) and backward pulls (**B**). The combined data set was created by subtraction of each person's threshold force in the NATURAL visual condition from all pull forces received by that participant for both the forward and backward pull directions. The lower panel shows individual participants' step threshold changes for forward pulls (**C**), and backward pulls (**D**). The black lines and circles show the group means, grey data points and lines show individual participants' step threshold changes.
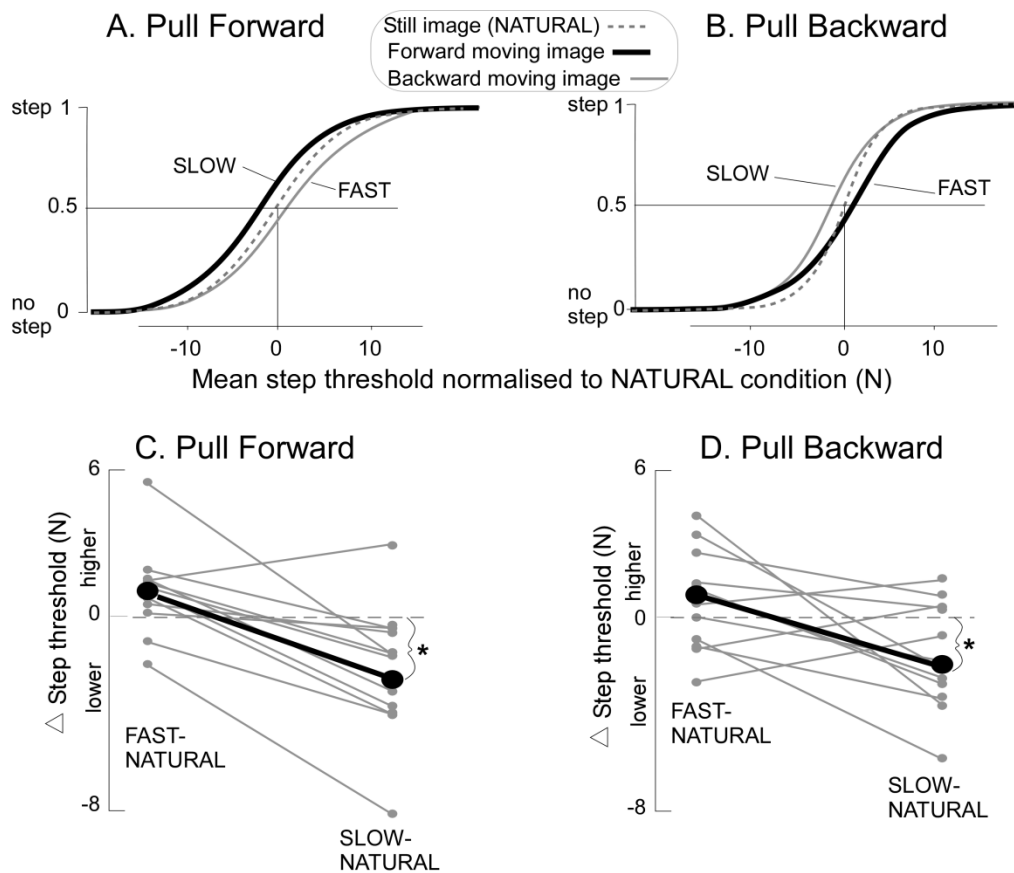
Figure 3. Kinematic changes of the head, hip, knee and ankle for in-place responses.

The mean timeseries of each of the three visual field conditions are shown: NATURAL (dotted lines), visual field motion forwards (black lines) and visual field motion backwards (grey lines) during standing with no pull (left column), pull forward (central column) and pull backward (right column). Onset timing of the pull force and the projected visual motion are indicated by the vertical lines. Individual data points show the corresponding area under the curve of angular body changes for the 2.5 second window following pull onset. For the no pull conditions, the data points on the left show backward visual motion ('*back*'), data points in the middle show no visual motion and data points on the right show forward visual motion ('*forward*'). For the pull conditions, angular changes to pulls with slower relative visual motion are shown on the left ('*slow*'), natural visual motion are in the middle and angular changes to faster relative visual motion are shown on the right ('*fast*').
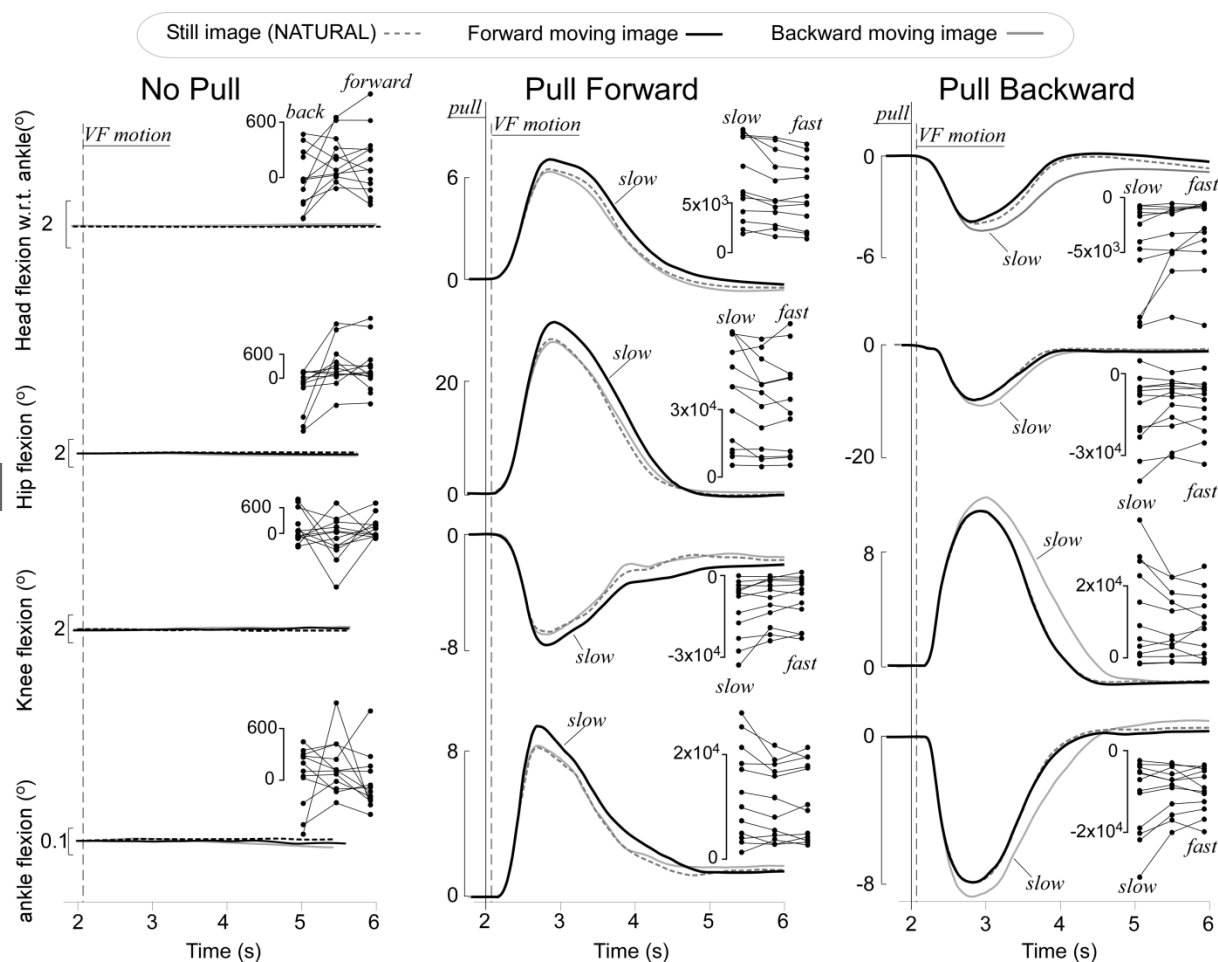
Figure 4. Ground reactive force differences with in-place responses

Mean Fy difference traces between the visual field moving conditions and the visual field stationary (NATURAL) condition. The black line with grey shading is the mean difference in Fy between the visual field rotating backwards and NATURAL conditions. The white line with black shading is the mean difference in Fy between the visual field rotating forward and NATURAL conditions. **A.** No external perturbation. **B.** Backward pulls, where the grey shading represents the SLOW condition. **C.** Forward pulls, where the black shading represents the SLOW condition. The shaded regions show the 95% confidence interval. The area under curve (AUC) of the Fy timeseries was calculated 130ms after visual motion onset, over a 140ms time window. The AUC of the Fy resistive forces for each of the visual conditions are shown to the right of the corresponding timeseries. The size of the resistive force against the direction of the pull force are shown in **B** and **D**.
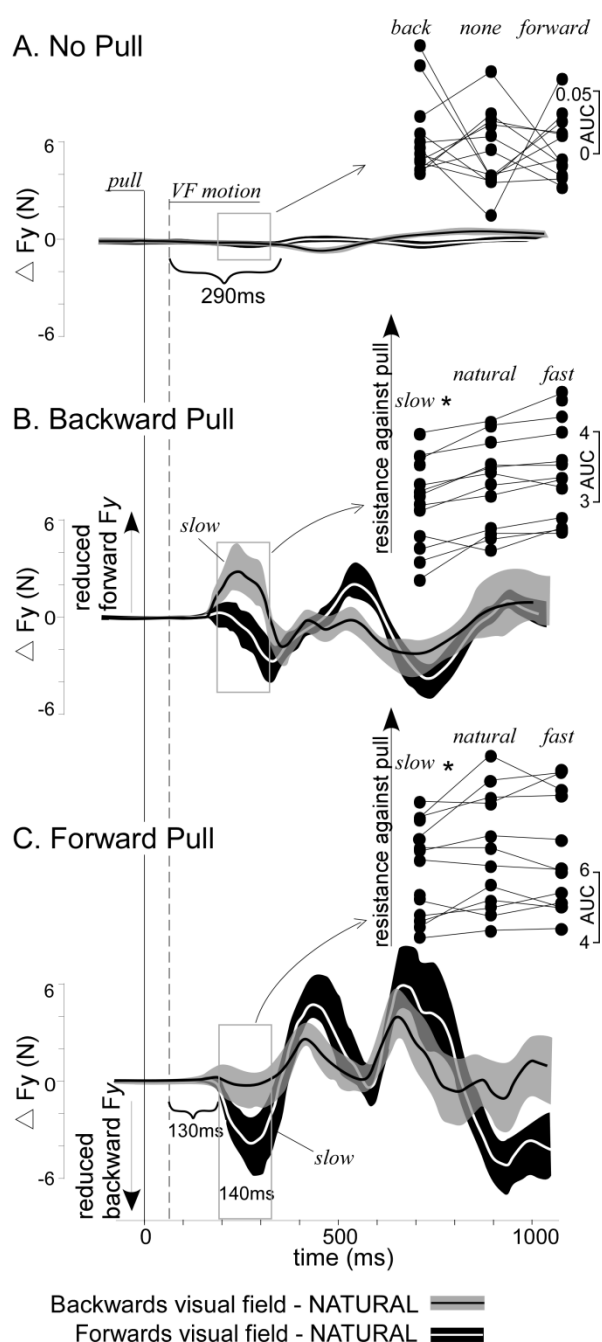
Figure 5. EMG responses of the ankle extensors (GAS) and flexors (TA).

The panel on the left shows a single participant's EMG mean responses in the TA and GAS muscles during backward and forward pulls for the three visual field motion conditions. The rectangle shows the 60ms window, 60ms after the onset of the visual field motion in which AUC of EMG traces was calculated. The panel on the right shows the group mean of AUC differences between visual field moving and NATURAL conditions (large diamonds). The error bars show the standard deviations. Circular data points show the mean of individual participants.
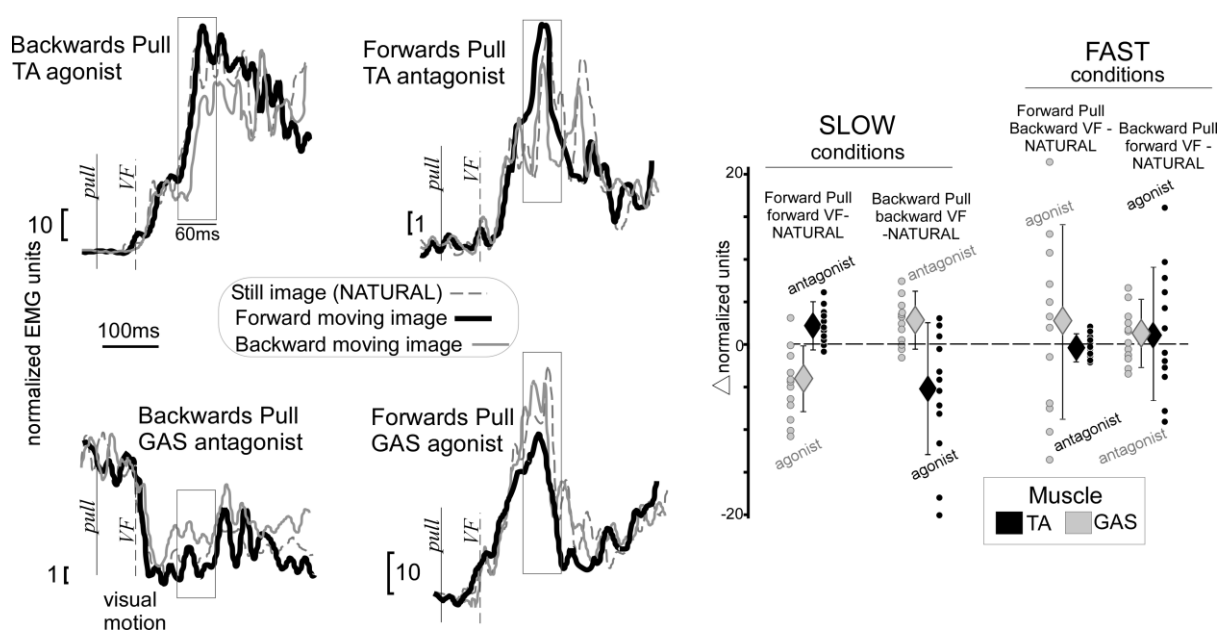
Author Profile (100 words)

Dr St George is an NHMRC Early Career Fellow working in the School of Psychology at UTAS in Hobart. After completing her PhD at NeuRA with Dr Richard Fitzpatrick in Sydney she worked at OHSU in Portland with Prof. Fay Horak and the UCL Institute of Neurology in London with Prof. Brian Day. Her research focuses on understanding the sensorimotor and neurocognitive contributions to balance and postural control.