Exp Brain Res
DOI 10.1007/s00221-012-3132-6

RESEARCH ARTICLE

Postural reorientation does not cause the locomotor after-effect following rotary locomotion

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Received: 5 October 2011 / Accepted: 16 May 2012

Abstract After a period of stepping on a rotating platform, blindfolded subjects demonstrate a tendency to unconsciously turn when stepping in place, an after-effect known as podokinetic after-rotation (PKAR). Recent studies have also reported a change in postural orientation following the adaptive period and have suggested that this is causally related to PKAR. Here, we assess changes in trunk orientation following platform adaptation and determine their relationship to PKAR. Specifically, we determine whether a reorganized standing posture causes PKAR. Ten subjects stepped on a platform rotating at 60°/s for 10 min, with a cadence of 100 steps/min. Following adaptation, a significant PKAR response was seen, with a mean yaw rotation velocity of 6.0 ± 2.2°/s. In addition to this dynamic after-effect, there was a significant twist of the trunk with respect to the feet when standing still (6.9° ± 4.5°; mean ± SD), confirming the presence of a postural reorientation after-effect. However, the magnitudes of the two after-effects did not correlate ($r = 0.06$, $p = 0.87$). Furthermore, in a second experiment, a prolonged passive twist of the trunk was used to induce postural reorientation. However, in this case, PKAR was not induced. These results demonstrate that PKAR is not an automatic consequence of reorganized standing posture.

Keywords Adaptation · After-effect · Body orientation · Locomotion · Posture

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Introduction

Following a period of stepping in place on a rotating platform, individuals unconsciously turn in circles when asked to step in place on a stationary surface without vision (Gordon et al. 1995; Weber et al. 1998). This locomotor after-effect is known as 'podokinetic after-rotation' (PKAR). Throughout the adaptive period, during contact with the platform, the feet are rotated beneath the trunk, in the direction of platform rotation. Subsequent to the adaptive period, when stepping in place without vision on a stationary surface, the relative rotation between the feet and trunk is preserved. That is to say, the trunk rotates above the stationary stance foot, in a direction opposite to platform rotation (Earhart et al. 2001). It was initially proposed that PKAR occurs because motor output for rotary locomotion is recalibrated to the perception of zero rotation from other sensory channels during the adaptive period (Gordon et al. 1995). But other authors have suggested that sensory conflict during the adaptive period is not a prerequisite for PKAR, as the after-effect is also demonstrated following a period of rotary locomotion with naturally occurring perceptions of rotation from other sensory channels (Juergens et al. 1999). However, the exact mechanism underlying PKAR remains unknown.

An adaptive period of rotary locomotion also results in a reorganized standing posture, consisting of a fixed rotation of the trunk over the feet in the same direction as PKAR (Hollands et al. 2007; Scott et al. 2011). Both Hollands et al. and Scott et al. have suggested that PKAR is causally related to this postural reorientation. However, the exact relationship between the two after-effects remains unclear. Specifically, we are interested in the possibility that postural reorientation causes PKAR.

Published online: 04 June 2012

Postural after-effects that alter the relative orientation of body segments have previously been shown following static adaptive periods. For example, a prolonged static head turn with eyes closed leads to a perceived gradual return of the head to the forward facing position (Gurfinkel et al. 1989). If the head is then realigned with the body, it is perceived as oriented in the opposite direction to the original turn or tilt (Guerraz et al. 2006; Mars et al. 1998). It is therefore evident that a prolonged change in body segment orientation can modify their subsequent perceived relative orientation. Hence, prolonged body twist would likely induce a reorganized standing posture. Previous studies suggest that changes in head posture can cause blindfolded subjects to turn while stepping (Jahn et al. 2006; Toussaint et al. 2008), but is this true for unperceived changes in body posture? It is unclear whether this would automatically cause PKAR.

Here, we determine whether the postural reorientation after-effect causes PKAR. We ask the following questions:

1. Is there a correlation between PKAR and postural reorientation magnitude?
2. Does postural reorientation, induced by a period of static body re-alignment, automatically cause PKAR?

Methods

Ten subjects (5 male) aged 20–30 years (mean ± SD: 23 ± 3 years) participated in a series of experiments. All gave informed consent and had no known neurological disorder. The experiments were approved by the local ethical review committee at the University of Birmingham and performed in accordance with the Declaration of Helsinki. The magnitude of postural reorientation and PKAR after-effects was measured following adaptive periods of rotary locomotion and static trunk-on-feet twist in Experiments 1 and 2, respectively. Two experiments were conducted to ensure after-effects induced by the first adaptive period did not interfere with those induced by the second. For example, it has been demonstrated that PKAR is still present up to 8 h following a period of rotary locomotion (Weber et al. 1998). For an illustration of the experimental protocol, see Fig. 1.

Experiment 1: Rotary locomotion

Baseline measures of postural orientation and stepping rotation were established prior to the adaptive period. The orientations of recording sensors placed on the body were measured during a 1-min period of blindfolded standing. Subjects were instructed to stand facing directly forwards with all body segments aligned, feet together and arms folded. The positions of all subjects' feet were marked on the floor so they could be returned to the same position post-adaptation by the experimenter. Subjects then performed a 1-min period of blindfolded stepping in place whilst attempting to maintain a constant head and trunk orientation, in order to identify any pre-existing rotation bias. In an otherwise quiet laboratory, subjects stepped with a cadence of 100 steps/min, guided by a digital metronome attached to the upper arm (Seiko DM-11, Minato, Tokyo, Japan). Following the stepping trial, and prior to removing the blindfold, subjects were randomly rotated in both directions by the experimenter to ensure they were unaware of any tendency to turn when stepping. Mean rotation across all subjects was not significantly different to zero during the baseline period (-0.14 ± 0.94°/s, $t(9) = 0.45$, $p = 0.66$; negative values indicate leftward rotation).

Following baseline trials, the blindfold was removed in order to perform the adaptive period of rotary locomotion. Subjects stepped in place for 10 min in the centre of a circular platform, 75 cm in diameter, rotating at 60°/s using a DC shunt motor (Parvalux SD12C, Bournemouth, Dorset, UK) and reversing controller (RS Components 425-5254,

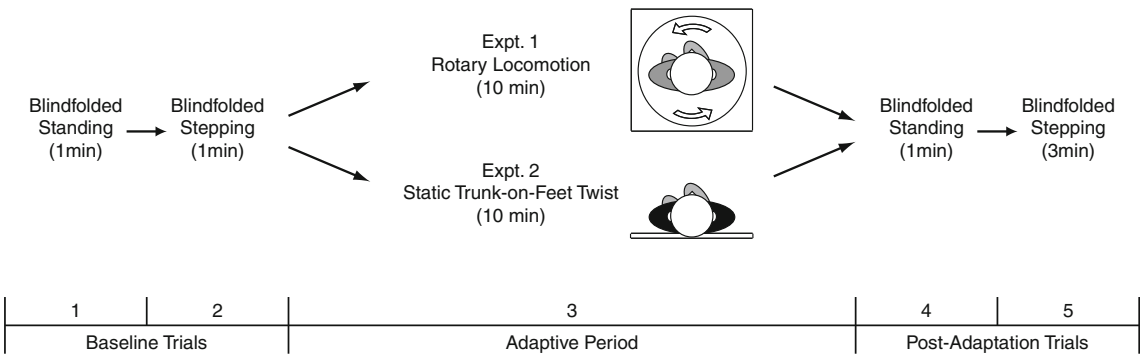

Fig. 1 Schematic of experimental protocol. Experiment 1 involved a 10-min adaptive period of rotary locomotion on a rotating platform. Experiment 2 involved a 10 min static trunk-on-feet twist. Both adaptive periods were preceded and succeeded by blindfolded standing and stepping

Corby, Northants, UK). Half the subjects experienced clockwise platform rotation and half anti-clockwise. As for the baseline period, step cadence was 100 steps/min, as prescribed by the metronome. Subjects were instructed to fixate on a target positioned straight ahead and were reminded of this after 5 min. A hand rail was available in case of a loss of balance.

Subjects were blindfolded immediately upon completion of the adaptive period. They were then required to complete post-adaptation trials of standing and stepping to determine the magnitude of any postural reorientation and PKAR, respectively. Firstly, postural orientation was assessed during 1 min of quiet stance without vision. The experimenter guided the blindfolded subject to stand with their feet in exactly the same position as during the baseline trials. Trunk orientation with respect to the feet was measured. To assess PKAR, subjects then performed a 3 min stepping in place trial, during which trunk rotation was measured. All instructions were identical to those given during the baseline period.

Experiment 2: Static trunk-on-feet twist

Experiment 2 was performed to investigate postural reorientation and PKAR after-effects induced by a prolonged static twist. Experiments 1 and 2 were performed at least 7 days apart, a more than sufficient period for residual effects of rotary locomotion to disappear (Weber et al. 1998). In Experiment 2, subjects first repeated the baseline trials as described for Experiment 1. During baseline stepping trials, mean rotation across all subjects was not significantly different to zero ($-0.07 \pm 0.43°$/s, $t(9) = 0.53$, $p = 0.61$).

Following baseline trials, subjects performed an adaptive period comprising a static trunk-on-feet twist. Standing subjects were strapped by way of a climbing harness (Black Diamond Bod Harness, Salt Lake City, UT, USA) to a fixed metal bar horizontally mounted at pelvis height. They were then required to align their feet with markings on the laboratory floor to achieve a trunk-on-feet twist of 30° about a vertical axis; half were rotated clockwise and the remainder anti-clockwise. Subjects were instructed to keep their head and trunk aligned and to keep the legs straight at the knee joint. This ensured that the static rotation occurred mainly at the hip joint. In addition, subjects were instructed to face a target positioned straight ahead to keep visual feedback the same as during the rotary stepping task. The static twist was maintained for 10 min and subjects were reminded of the instructions after 5 min.

After the adaptive period, subjects performed post-adaptation trials of standing and stepping as in Experiment 1, to investigate after-effects.

Data acquisition and analysis

Euler angles of sensors placed on the trunk (C7) and the dorsal surface of each foot were recorded at 30 Hz using an electromagnetic 3D motion tracking system (Polhemus Fastrak, Colchester, VT, USA). Yaw (i.e., rotation about the vertical axis) of each sensor was calculated by multiplying the recorded Euler angles by a rotational matrix according to the Tait-Bryan sequence (Reynolds 2011). Yaw data were low-pass filtered (0.2 Hz, 4th order, zero-phase butterworth) to remove step-by-step oscillations in angular signals, thus providing mean orientation of segments. For standing trials and adaptive periods, trunk yaw relative to the feet was calculated. For stepping trials, trunk yaw velocity was derived by differentiation. Changes in trunk-on-feet orientation and trunk yaw velocity during the adaptive and post-adaptation periods were calculated relative to baseline.

Postural orientation was calculated as the average trunk yaw with respect to the feet during the 1 min post-adaptation trial of blindfolded standing. PKAR was calculated as the average trunk yaw velocity from 30 s until the end of the 3 min post-adaptation trial of blindfolded stepping. In both experiments, measures of postural reorientation and PKAR were approximately equal and opposite between clockwise and anti-clockwise rotations. Therefore, data following clockwise platform rotation and anti-clockwise static trunk-on-feet twist were inverted in Experiments 1 and 2, respectively. As a result, positive values represent trunk-on-feet twist in the same direction as during the adaptive period, in both experiments.

To assess statistical significance of the postural reorientation and PKAR, they were compared to baseline using paired-sample t tests in SPSS 16.0 (SPSS Inc, Chicago, IL, USA). The following relationships were evaluated using Pearson correlation coefficients: (1) the relationship between postural reorientation and PKAR after-effect magnitudes (i.e., average trunk-on-feet twist over 1 min standing and average PKAR between 30 s–3 min, respectively), (2) the relationship of trunk-on-feet twist during the adaptive period with the subsequent postural reorientation after-effect magnitude, (3) the relationship between postural reorientation magnitudes following rotary locomotion and static body twist adaptive periods. Figures illustrate mean ± SE, whereas mean ± SD is reported in the text.

Results

Experiment 1: After-effects following rotary locomotion

During the adaptive period of rotary locomotion, use of the hand rail was only required for the first few seconds; after

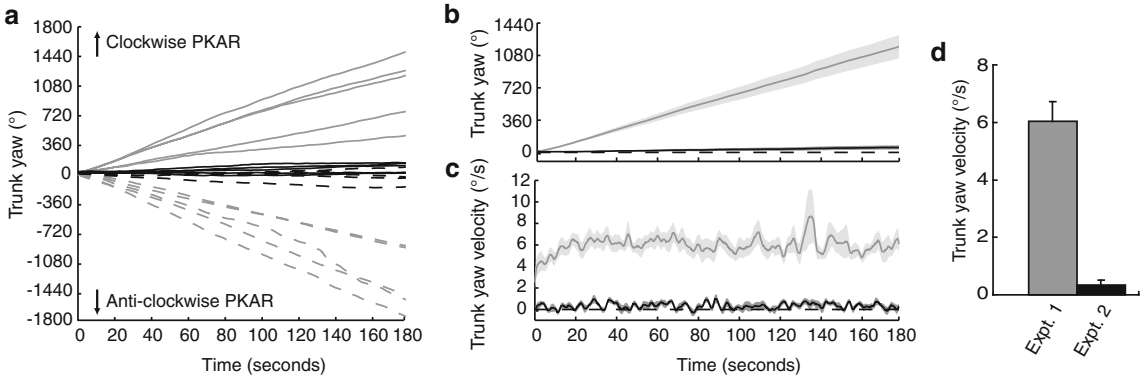

Fig. 2 Trunk rotation when stepping in place post-adaptation. **a** *Grey dashed* and *solid lines* show trunk yaw for subjects who experienced clockwise and anti-clockwise platform rotation, respectively (Experiment 1). *Black traces* show the equivalent data after static trunk-on-feet twist (Experiment 2). **b** Mean data for both experiments, after inversion of anti-clockwise PKAR. **c** Mean trunk yaw velocity. **d** Mean trunk yaw velocity between 30 and 180 s

this, subjects were stable and able to step in time with the metronome. Subjects occasionally looked down at their feet in order to remain in the centre of the rotating platform.

Following adaptation, all subjects displayed robust PKAR in a direction opposite to platform rotation (Fig. 2a; grey traces). Significant PKAR velocity was demonstrated ($6.05 \pm 2.16°$/s, $t(9) = 8.85$, $p < 0.001$; see grey traces in Fig. 2c, d). After 3 min of stepping in place, subjects had rotated by $1{,}186° \pm 414°$, on average (i.e., 3.29 revolutions; Fig. 2b). The mean angular velocity trace shows an initial acceleration for approximately 30 s, after which a steady rate of rotation is apparent for the rest of the 3-min period (Fig. 2c).

Subjects also demonstrated a significant fixed trunk-on-feet rotation in the same direction when standing still ($6.89° \pm 4.53°$, $t(9) = 4.82$, $p = 0.001$; Fig. 3a, c), indicating a significant postural reorientation after-effect. However, there was no significant relationship between the magnitudes of the two after-effects ($r = 0.06$, $p = 0.87$; see grey circles in Fig. 4).

During the adaptive period, all subjects showed an inadvertent rotation of the trunk with respect to the combined mean orientation of both feet, in a direction opposite to platform rotation ($9.61° \pm 6.37°$, $t(9) = 4.77$, $p = 0.001$). This change in average body segment alignment may explain the postural reorientation after-effect. However, there was no significant relationship between trunk rotation during the adaptive period and the subsequent postural reorientation ($r = 0.39$, $p = 0.27$).

Experiment 2: After-effects following static trunk twist

Throughout the static trunk-on-feet twist adaptive period, all subjects looked straight ahead and maintained the required posture.

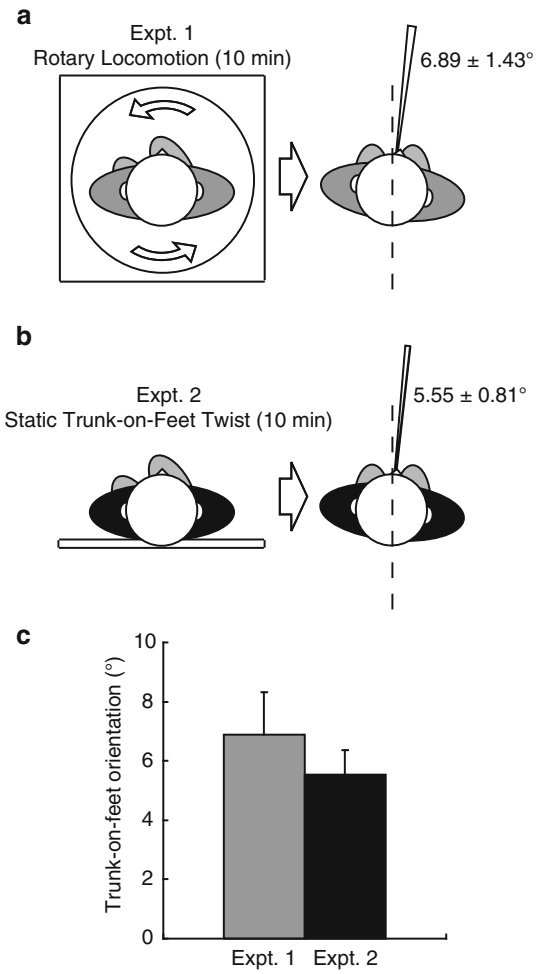

Fig. 3 Postural orientation when standing in place post-adaptation. **a**, **b** Trunk-on-feet orientation after Experiments 1 and 2, respectively. *Inset values* show mean angles ± SE, also represented by the *arcs*. **c** The same data in *bar chart*, for comparison

Following adaptation, PKAR velocity was not significantly different from rotation demonstrated at baseline ($0.35 \pm 0.55°$/s, $t(9) = 1.97$, $p = 0.08$; see black traces in

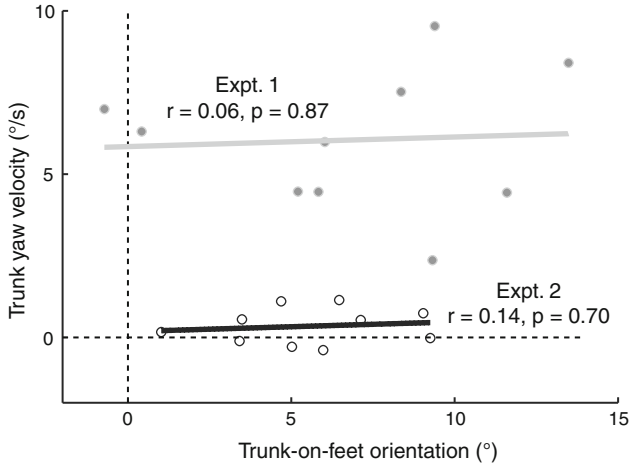

Fig. 4 Correlation between the magnitudes of postural and locomotor after-effects. *Grey and black circles* represent individual subjects following rotary locomotion (Experiment 1) and static body twist (Experiment 2), respectively. *Inset values* show the Pearson correlation coefficient (r) and significance (p) of the relationship in each experiment

Fig. 2c, d). After 3 min of stepping in place, only 3 of 10 subjects had rotated by more than 90° in the direction of trunk-on-feet twist during the adaptive period (Fig. 2a; black traces). Even in the subject who displayed the greatest PKAR velocity (1.14°/s), it was markedly less compared to following the adaptive period of rotary locomotion (4.47°/s).

Subjects did, however, demonstrate significant trunk-on-feet rotation in the same direction as during the adaptive period (5.55° ± 2.58°, $t(9) = 6.81$, $p < 0.001$; Fig. 3b, c). This indicates that although static body twist was sufficient to induce a significant postural reorientation, this after-effect did not automatically cause PKAR. Even the subject who demonstrated the greatest trunk-on-feet reorientation during standing (9.25°) demonstrated no PKAR (−0.02°/s). Furthermore, there was no significant correlation between the magnitude of postural reorientation and PKAR after-effects ($r = 0.14$, $p = 0.70$; see black circles in Fig. 4). There was no significant correlation between the magnitudes of postural reorientation induced by rotary locomotion and static body twist ($r = 0.20$, $p = 0.58$).

Discussion

Following a period of stepping on a rotating platform, two after-effects were induced. Firstly, subjects unconsciously turned in circles when stepping in place (PKAR). Secondly, they displayed a reorganized standing posture comprising a fixed rotation of the trunk over the feet (postural reorientation). Results to a second experiment showed that a prolonged static body twist was sufficient to cause a postural reorientation after-effect without inducing PKAR. This demonstrates that PKAR is not an automatic consequence of a reorganized posture and raises the possibility that they are due to separate mechanisms.

In accordance with previous studies, we demonstrated that robust PKAR and postural reorientation follow rotary locomotion. Subsequent to the adaptive period, all subjects displayed inadvertent rotation in a direction opposite to platform rotation when attempting to step in place without vision (Earhart et al. 2001; Gordon et al. 1995; Juergens et al. 1999; Weber et al. 1998). A gradual rise in rotation velocity occurred during the first 30 s of post-adaptation stepping, probably due to the vestibular perception of rotation initially opposing the tendency to rotate (Earhart et al. 2004; Juergens et al. 1999; Weber et al. 1998). One difference between our study and others using similar adaptation protocols was that we observed a lower rotation velocity (Earhart et al. 2002, 2004; Juergens et al. 1999; Weber et al. 1998). This is potentially because the adaptive period lasted only 10 min, whereas 15-min periods were used in some of these studies. It could also be due to the fact that, in our study, post-adaptation stepping was delayed by ∼1 min to allow for the measurement of postural reorientation. This delay may have caused some decay of the stepping adaptation. In addition to PKAR, when subjects were asked to stand with all body segments in alignment, they demonstrated a postural reorientation. They stood with a fixed rotation of the trunk over the feet by 6.9°, also in a direction opposite to platform rotation. This is consistent with the results of Scott et al. (2011) who reported trunk rotation of 8.4° following a 15-min adaptive period.

Scott et al. (2011) concluded from their findings that postural reorientation reflects transfer of PKAR to a non-locomotor task. Similarly, Hollands et al. (2007) suggested that the postural reorganization and PKAR are causally related. But we found no hint of correlation between the magnitudes of the two after-effects that followed rotary locomotion. As both feet remain in contact with the floor when standing, biomechanical constraints may have restricted the magnitude of postural reorientation more so than PKAR. However, the lack of correlation in the current study was not due to a consistent postural reorientation limit across subjects, or a lack of variance in either measure (see Fig. 4, grey circles). This finding suggests the two after-effects are not related. Furthermore, in Experiment 2, we found a static body twist to induce postural reorientation without inducing PKAR. A fixed rotation of the trunk was demonstrated, similar in magnitude to that in Experiment 1 (see Fig. 3). However, in contrast to Experiment 1, no significant PKAR occurred when subjects were asked to step in place (see Fig. 2). This finding shows that PKAR is not caused by postural reorientation. This is in accordance

with the results of Ivanenko et al. (2006). They asked subjects to actively oppose a rotational force applied to the pelvis for ~30 s. Following this adaptive period, subjects exhibited clear trunk reorientation, but did not turn when stepping in place. They did, however, exhibit curved trajectories when walking forward, suggesting possible differences in muscle synergies for stationary stepping and forward walking. Further research is necessary to ascertain whether postural reorientation and PKAR after-effects subsequent to rotary locomotion are caused by common or separate mechanisms (e.g., by studying their decay over a longer time period). Nonetheless, the current results clearly demonstrate that PKAR is not an automatic consequence of postural reorganization and, furthermore, raise the possibility they are caused by two distinct mechanisms operating in parallel.

Are postural reorientation and PKAR caused by separate mechanisms operating in parallel?

Following prolonged rotation between body segments, after-effects concerning their perceived orientation have previously been reported (Gurfinkel et al. 1989; Guerraz et al. 2006; Mars et al. 1998). Gurfinkel et al. (1989) described a so-called return phenomenon in which subjects perceive a slow displacement of their head towards the neutral position after holding it in a rotated position for several minutes. If the instruction had been to align the head with the trunk, as in the current experiment, these researchers would presumably have demonstrated a similar postural reorientation to the one we observed. The static adaptive period in the current study involved a prolonged trunk rotation. But we also found that during rotary locomotion, there was an average rotation of the trunk over the feet. It is therefore possible that the postural reorientation in both experiments can be attributed to proprioceptive adaptation as a result of a prolonged change in average trunk orientation during the adaptive period.

Such proprioceptive adaptation could be explained either by a peripheral or central mechanism. Peripherally, a prolonged change in the length of muscles for hip rotation (e.g., piriformis) may modulate subsequent muscle spindle discharge. If muscles acquire a passive stiffness by way of cross bridge reattachment when stretched or shortened (Morgan et al. 1984), the subsequent tension on sensory endings at an intermediate length is altered. This has been shown to lead to errors in limb position sense (Gregory et al. 1988; Winter et al. 2005). Therefore, it may explain the error in trunk alignment subsequent to prolonged body twist. However, cross bridges will become detached by a contraction or stretch (Proske et al. 1993). As a result, a peripheral effect such as this may be abolished by any movement of the muscle, potentially even when the subject was guided into position for post-adaptation trials.

The other possibility (not mutually exclusive) is central adaptation. This would involve reinterpretation of the pattern of sensory input corresponding to the perception of neutral body alignment. Such a mechanism has been invoked to explain a similar after-effect. Following adaptation to an inclined surface, Kluzik et al. (2005) showed that subjects unknowingly leant forwards during blindfolded standing. Similar to the current experiments, this postural after-effect was seen both after a dynamic (stepping) and static (standing) period of adaptation (Kluzik et al. 2005, 2007a). If movement of the legs and ankles was prevented during expression of the after-effect, subjects bent at the hips to lean forwards (Kluzik et al. 2007b). The authors, therefore, suggested a central adaptation, whereby the trunk-to-feet relationship is adapted rather than a single muscle or joint. In the current study, the postural reorientation after-effect may be explained in a similar way, whereby the signal for neutral trunk-on-feet *rotation* is reset.

Whether it is central or peripheral, a pure sensory adaptation provides one plausible explanation for the postural reorientation after-effect in both experiments. If this is the case, and prolonged trunk rotation during the adaptive period is indeed responsible for the subsequent postural reorientation in both experiments, then the complete absence of a stepping after-effect in Experiment 2 suggests that PKAR is caused by a different mechanism operating in parallel.

Different mechanisms may underlie postural reorientation following active and passive adaptation periods

An alternative explanation for our results is that the postural reorientation in both experiments is caused by different mechanisms. In support of this, there was a marked difference in response gain. Although similar postural after-effects were demonstrated in both experiments, the magnitudes of body twist during the adaptive periods were not equivalent. Postural reorientation of 6.9° was induced by a 9.6° twist during rotary locomotion. In contrast, in static conditions, a postural reorientation of 5.6° was induced by a much greater twist of 30°. This equates to a response gain of 0.72 in dynamic conditions compared to 0.19 for static conditions. Furthermore, there was no correlation between the magnitude of the postural after-effect caused by stepping and static twist. These differences raise the possibility of separate mechanisms underlying the postural after-effect in each experiment. One obvious difference between conditions is the presence of continuous motor output during the stepping condition, in contrast to the passive muscle stretch during body twist. Previous

research has established that active muscle contraction increases muscle spindle discharge due to α–γ motor neuron co-activation (Vallbo 1970). This would enhance proprioceptive signals during stepping, possibly explaining the increased response gain.

Additionally, continuous motor output may result in central neural adaptation, whereby the relationship between efference copy and expected reafference is remodelled (Held 1965). Such remodelling could contribute to both PKAR and postural reorientation after-effects following rotary locomotion. A major source of reafference during stepping would be length changes of hip rotator muscles, since trunk yaw rotation over the feet mainly occurs at the hip joint. However, other lower limb signals undoubtedly contribute to PKAR (e.g., more distal cutaneous, load and joint receptors; Wong et al. 2007), and these additional reafferent signals may account for the increased after-effect gain seen after stepping.

In summary, a period of stepping on a rotating platform simultaneously results in two after-effects, PKAR and postural reorientation. Although the precise mechanisms underlying these effects remain to be elucidated, our results demonstrate that PKAR is not an automatic consequence of reorganized posture.

Acknowledgments We thank Dr Mark Hollands for equipment use and Steve Allen for technical assistance. CJO is supported by the BBSRC.

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