

Stepping in circles: how locomotor signals of rotation adapt over time

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Key Points Summary

- While it has been well described that prolonged rotational stepping will adapt the podokinetic sense of rotation, the mechanisms involved are not clearly understood.
- By studying podokinetic after-rotations following conditioning rotations not previously reported we have shown that slower rotational velocities are more readily adapted than faster velocities and adaptation occurs more quickly than previously thought.
- We propose a dynamic feedback model of vestibular and podokinetic adaptation that can fit rotation trajectories across multiple conditions and data sets.
- Two adaptation processes were identified that may reflect central and peripheral processes and the discussion unifies prior findings in the podokinetic literature under this new framework.
- The findings show the technique is feasible for people with locomotor turning problems.

Abstract

After a prolonged period stepping in circles, people walk with a curved trajectory when attempting to walk in a straight line without vision. Podokinetic adaptation shows promise in clinical populations to improve locomotor turning, however the adaptive mechanisms involved are poorly understood. The first phase of this study asks: how does the podokinetic conditioning velocity affect the response velocity and how quickly can adaptation occur? The second phase of the study asks: can a mathematical feedback model account for the rotation trajectories across different conditioning parameters and different datasets?

Twelve healthy participants stepped in place on the axis of a rotating surface ranging from 4 to 20 deg.s^{-1} for durations of one to ten minutes, while using visual cues to maintain a constant heading direction. Afterward on solid ground, participants were blindfolded and attempted to step without rotating.

Participants unknowingly stepped in circles opposite to the direction of the prior platform rotation for all conditions. The angular velocity of this response peaked within one minute and the ratio of the stimulus-to-response peak velocity fitted a decreasing power function. The response then decayed exponentially. The feedback model of podokinetic and vestibular adaptive processes had a good fit with the data and suggested that podokinetic adaptation is explained by a short (141 s) and a long (27 minutes) time constant.

The podokinetic system adapts more quickly than previously thought and slower rotation is more readily adapted than faster rotation. These findings will have implications for clinical applications of the technique.

Introduction

When walking without vision in an open space, heading direction relative to the environment is formed primarily from the stepping motor command and the corresponding proprioceptive feedback – together considered the “*podokinetic*” sense. Vestibular semi-circular canal input is available during high acceleration rotations but the proprioceptive sense is available across a broad frequency band. Over short distances humans are able to accurately navigate straight (Rieser *et al.*, 1990; Mittelstaedt & Mittelstaedt, 2001) and curved (Takei *et al.*, 1996; Frissen *et al.*, 2011) trajectories without vision. However over time, everyone deviates from the desired direction (Toussaint *et al.*, 2008). This might be because the podokinetic signal of rotation does not have a fixed interpretation. Indeed studies have shown that the podokinetic sense will adapt according to experiences in the recent past; this was demonstrated after participants walked for two hours on a rotating platform using vision to maintain a constant heading direction in space (Gordon *et al.*, 1995). Once blindfolded and walking on solid ground these participants no longer walked straight ahead. Instead, they unknowingly walked in curved trajectories, opposite to the direction of the prior platform rotation. This aftereffect is known as *podokinetic after-rotation*, or PKAR.

Podokinetic conditioning is emerging as an effective therapy for locomotor disorders of turning. Parkinson’s Disease (PD) patients often have trouble with turning with straight-ahead walking less affected (Mancini *et al.*, 2015). Freezing of gait (FOG) episodes occur most frequently during turning and these symptoms increase the rate of falls and reduce mobility and quality of life (Nutt *et al.*, 2011). The magnitude of PKAR has been shown to be diminished in PD patients with FOG compared to PD patients without FOG and healthy controls (Nemanich & Earhart, 2016). This suggests FOG may be related to poor podokinetic adaptation mechanisms. A recent study showed

that ten repeated exposures to podokinetic stimuli in PD patients over 3 weeks led to an improvement in the magnitude of the PKAR and this capacity translated into improved overground curved walking (Godi *et al.*, 2017). Despite these promising therapeutic applications, the fundamental mechanisms underlying podokinetic adaptation are unclear and elucidating them could better inform locomotor therapy.

Studying the trajectory of the PKAR after-response over a range of conditioning parameters could shed light on the mechanism/s involved. There is a phase of increasing rate of turn over the first minute of PKAR; followed by a prolonged phase of exponential decline (Weber *et al.*, 1998; Jurgens *et al.*, 1999; Osler & Reynolds, 2012). The initial phase of rising angular velocity can be explained by vestibular attenuation of the podokinetic rotational signal. Once the vestibular signal has decayed and the angular acceleration rate falls below vestibular detection thresholds, the PKAR peaks within approximately one minute. It has been demonstrated that PKAR peaks almost immediately in people with bilateral vestibular loss (Earhart *et al.*, 2004) and in healthy participants with vestibular input negated by counter-rotation of the platform (Melvill Jones *et al.*, 2005). The prolonged phase of exponential decay is similar between conditions with, and without, vestibular feedback and therefore largely driven by podokinetic information (Earhart *et al.*, 2004; Melvill Jones *et al.*, 2005). The conditioning/response gain and time course of this adaptive process is unclear.

There has been one prior investigation into the behaviour of the podokinetic response across different conditioning velocities. Weber and colleagues (1998) report that the peak rotation of PKAR is always one third of the conditioning velocity, however only conditioning velocities of 11.25, 22.5, 45 and 90 deg.s⁻¹ were tested and this ratio was too high for the 90 deg.s⁻¹ condition, and too low for the 11.25 deg.s⁻¹ condition. Longer conditioning times resulted in PKAR that decayed more slowly and exponential fits applied directly to the PKAR curves suggest short- and long- time constants. Weber *et al.* also report that for the same conditioning velocity there is no difference in peak PKAR gain between 7.5 and 60 minutes of conditioning. Presumably, there must a minimum conditioning

time for a robust PKAR. Knowing the minimum conditioning time will be important if this method is to be used as a clinical tool for training locomotor turning in movement disorders (Godi *et al.*, 2017).

As the adaptive mechanisms of the podokinetic orientation sense are poorly understood, we measured PKAR following a more varied range of conditioning parameters than previously tested. We were interested to find out how quickly the podokinetic sense could adapt. We also were interested in investigating the conditioning/response velocity gain to determine which range of rotational velocities were more readily adapted. A comprehensive analysis of the PKAR response was performed by formulating a mathematical feedback model of stepping rotation that incorporated the observed properties of the podokinetic adaptive response together with vestibular semicircular canal input. The time constants of podokinetic adaptation operating within the feedback loop were estimated by incorporating PKAR responses across all conditions and included data from the Weber *et al.* (1998) study to ensure robustness.

Methods

Twelve healthy participants, six of each gender aged 23-58 years (mean=32.4) participated. Informed written consent was obtained from each participant. The study procedures conformed to the Declaration of Helsinki (except for registration in a database) and were approved by the Human Research Ethics Committee of the University of New South Wales (approval number HC05272).

Experimental setup

Barefoot participants were positioned over the axis of a servo-motor controlled platform (1.1 m diameter) embedded into the laboratory floor. Noise cancelling headphones limited acoustic orientation cues and provided a 2 Hz stepping rhythm. An Xsens MTi device was securely attached to a belt at the level of the sacrum (Xsens Motion Technologies, Enschede, The Netherlands). Data from

3D accelerometers, gyroscopes and earth magnetic field sensors housed within the XSens MTx device were used to calculate a drift-free yaw orientation signal in global coordinates (via the XSens Kalman filter). A custom-made LabView program (LabView 8.0, National Instruments, Austin TX) controlled the rotational velocity of the platform with a calibrated analog signal. This same program also synchronously collected heading data from the Xsens device at 25 Hz. From this data the yaw angular velocity was calculated at two second intervals.

Each trial was conducted on a different day to avoid possible carry-over effects and to prevent fatigue. To ensure participants did not make any translational movements during stepping, a smooth nylon cylinder, 10 cm in diameter and 10 cm in height was positioned over the axis. As the feet touched this reference participants remained over the axis without receiving orientation cues.

Baseline trials

Baseline podokinetic turning bias was recorded before each testing session. Participants were blindfolded and asked to step in place for one minute. Before the blindfold was removed the experimenter turned the participant randomly then aligned them in the original orientation to ensure participants were naïve of any rotation bias.

Podokinetic conditioning and after-rotation

Participants stepped in place over the axis of a rotating platform using visual information to remain aligned in space (Figure 1). In this way, the podokinetic signal of trunk-over-foot rotation was maintained at the rate of platform rotation: but in the opposite direction. In order to model podokinetic adaptation as a function of conditioning duration and conditioning speed, seven different conditions were tested. Five different conditioning durations (1,2,3,5,10 minutes) were tested while conditioning velocity was kept constant at 20 deg.s^{-1} . These durations were shorter and had smaller time increments between conditions than previous studies in order to more accurately model short-term podokinetic adaptation. Because it is unclear how the podokinetic response gain

behaves at lower conditioning speeds, an additional two conditions (10deg.s⁻¹ rotation for 3 minutes and 4 deg.s⁻¹ rotation for 10 minutes) were tested. Each condition was performed once, and the direction of platform rotation, and trial sequence were randomised between participants.

The platform had acceleration phases over five seconds to avoid suddenly destabilising balance. After the conditioning phase, participants were immediately blindfolded, and asked to commence stepping in place while maintaining constant heading direction. The delay between the conditioning and test phase was no more than a few seconds. PKAR was recorded for a minimum of five minutes and the test was stopped at a time when the participant faced the original direction. To gauge how reliable PKARs were, a subset of four participants were re-tested on the five 20 deg.s⁻¹ conditioning velocity trials with at least one week between sessions.

Data analysis

To remove oscillations associated with individual steps, angular velocity data was low-pass filtered at 0.2Hz with a 4th-order Butterworth filter. Directional bias in the mean angular velocity of baseline trials was assessed with a single sample t-test with zero as the reference value. To normalise for PK conditioning direction, PKAR responses that had conditioning with counter-clockwise platform rotation were inverted. Test-retest reliability of the PKAR magnitude (total degrees rotation after five minutes) was assessed with a partial Pearson's correlation controlling for subject ID.

A preliminary analysis of the profile of the PKAR decay was performed by fitting first-order exponential decay curves with nonlinear least squares to the velocity data. The first minute of the PKAR velocity trace was removed for this curve fit to remove the period where vestibular feedback was influencing the response. Exponential decay functions were of the form:

$$V(t) = a + V_0 e^{-t/b}$$

where a is the final asymptote, b is the decay time constant and $a+V_0$ is the ordinate intercept. Podokinetic gain was calculated as the ratio of the ordinate intercept of the fitted curve (i.e. the

estimated initial PKAR velocity if there was no vestibular feedback) and the conditioning velocity (platform rotation). The effect of conditioning time on the podokinetic gain and final asymptote of the 20deg.s^{-1} conditioning trials were compared with repeated measures ANOVAs. Contrasts tests compared differences between conditioning times. The effect of conditioning velocity on the podokinetic gain was initially explored by plotting these two variables. A decreasing power function of logged gain provided a high goodness of fit with the data as assessed by an adjusted R^2 value.

Based on the initial findings, a control systems feedback model of podokinetic and vestibular adaptations was developed to provide a more comprehensive account of locomotor rotation. Parameter estimation of the podokinetic adaptation processes was achieved with a non-linear best-fit of data from this experiment combined with the data from the study of Weber *et al.* (1998), a study that used similar procedures but with different conditioning times and velocities. The Weber *et al.* (1998) data were obtained from digitising the figures using Canvas X software (ADC Systems of America). A sensitivity analysis of the model parameters was performed. Monte Carlo sampling generated 200 samples with a normal distribution about the estimated parameter values. Partial correlations reported the relative influence of each of the model parameters on the predicted output of the model for each condition.

Data acquisition and preliminary processing were performed using LabView 8.0 software (National Instruments, Austin TX). Curve fitting, modelling and parameter estimation were performed with Matlab 2018a Simulink software (The Mathworks Inc., Natick MA). IBM SPSS Statistics 22 (Armonk, NY, USA) was used for statistical procedures with the a priori level of two-tailed significance set at 0.05.

Results

All participants completed the experiment without instability and remained over the platform axis. The mean rotational velocities of the baseline trials ranged from 0.81 deg.s⁻¹ clockwise to 0.64 deg.s⁻¹ counter-clockwise and across subjects were not statistically different from zero (mean=0.15 deg.s⁻¹ clockwise, SD=0.52, $p = 0.339$).

Podokinetic after-rotation

During PKAR, participants stepped in the direction that the trunk had rotated relative to the feet during the prior conditioning phase (Figure 2). All participants reported afterward they had not perceived any rotation and were quite convinced they had not deviated from the straight-ahead orientation. PKAR velocity peaked within approximately one minute before declining over several minutes. Test-retest reliability was high when controlling for subject ID (partial Pearson's $r = 0.882$, $p < 0.001$).

After the initial rise in PKAR (1 minute), exponential curves showed good fits with the data (Table 1). When the conditioning velocity was the same (trials of 20 deg.s⁻¹ conditioning), podokinetic response gains were not significantly different between trials of three, five or ten minutes of conditioning ($p=0.844$, $p=0.222$ and $p=0.271$ for 3 vs. 5, 3 vs. 10 and 5 vs. 10 respectively). This relationship is also apparent in the Weber *et al.* (1998) study, with the intercept of the fitted exponential curve not significantly different between 7.5 and 60 minutes of conditioning at 45 deg.s⁻¹ (Weber *et al.*, 1998). Our results showed that for one and two minutes of conditioning the podokinetic gains were significantly less than those for three or more minutes ($p < 0.001$ for both 1 vs. 3 and 2 vs. 3), suggesting that a time constant of podokinetic adaptation is likely to be between 2 and 3 minutes. It is also apparent from the table, that the highest asymptotes were for the longest conditioning durations, with 10 minutes of conditioning having a significantly higher asymptote than 5 minutes of

conditioning ($p < 0.001$). This suggests a 2nd-order adaptation process may be occurring over longer conditioning times.

Table 1. Exponential fit to PKAR curves

Conditioning		PKAR $V(t) = a + V_0 e^{-t/b}$				
Time	Velocity	a	V_0	b	Podokinetic Gain	
(min)	(°/s)	(95% CI)	(95% CI)	(95% CI)	Adj- R ²	(95% CI)
1	20	-0.20 (-0.36 – 0.03)	2.63 (2.53 – 2.74)	200 (172 – 254)	0.97	0.12 (0.10 – 0.14)
2	20	-0.06 (-0.32 – 0.21)	3.82 (3.35 – 4.28)	250 (215 – 280)	0.84	0.19 (0.15 – 0.22)
3	20	-0.40 (-0.69 – 0.11)	7.41 (6.94 – 7.89)	294.1 (275 – 315)	0.92	0.35 (0.32 – 0.38)
5	20	0.64 (0.13 – 1.15)	6.72 (5.79 – 7.35)	309.9 (215 – 378)	0.97	0.37 (0.30 – 0.44)
10	20	1.80 (1.51 – 2.09)	6.24 (5.83 – 6.65)	267.6 (254 – 283)	0.95	0.40 (0.37 – 0.43)
3	10	-0.10 (-0.50 – 0.25)	4.93 (4.85 – 5.0)	270.4 (261 – 277)	0.91	0.48 (0.43 – 0.53)
10	4	0.71 (0.42 – 1.10)	2.28 (2.03 – 2.53)	277.4 (265 – 290)	0.92	0.74 (0.61 – 0.88)

To investigate the relationship between conditioning velocity and podokinetic response gain, all trials with conditioning times of 3 minutes or more were considered (Figure 3). For slower conditioning velocities the relative velocity of the PKAR increased. Weighted linear regression of logged gain and velocity provided the best fit with no intercept, indicating that as the conditioning velocity approached zero the podokinetic gain approached one. The corresponding power function (f_v) is shown in Figure 3.

Feedback model of locomotor rotation

A feedback model of locomotor rotation (Figure 4) was proposed that incorporated the processes and interactions known to be involved:

- Podokinetic adaptation (PK) was described by more than one exponential function. The rationale for this was based on our initial analysis of exponential curve fits and Weber *et al.*'s (1998) conclusion. To determine whether a model with three podokinetic adaptation processes offered a better fit to the data than a model with two terms we compared two hierarchical models. Adjusted *R*-squared values for the 3-term podokinetic adaptation model were higher than the 2-term model for 3 of the 14 conditions, however the coefficients of partial determination were not significant ($p=0.171$, $p=0.688$ and $p=0.733$). Thus, the simpler model with two podokinetic processes was selected. The following expression for podokinetic adaptation was used in the final model:

$$PK(t) = G_s e^{-\frac{t}{\tau_s}} + G_L e^{-\frac{t}{\tau_L}}$$

where τ_s and τ_L are short- and long-term time constants and G_s and G_L are the corresponding weights.

- The function f_v scaled the podokinetic adaptive gain according to the velocity of stepping rotation.
- Vestibular transform equations described previously (Leigh *et al.*, 1981) that include peripheral canal, central velocity storage and adaptation operators were used in the model. Based on prior experiments in this population (St George *et al.*, 2011), the peripheral time constant (τ_c) was set to 7.2 s, the velocity storage time constant (τ_v) was set to 7.7 s, and the long-term adaptation time constant τ_a was set to 76 s.
- Any stepping rotation *during* the PKAR phase continued to pass through vestibular and podokinetic adaptive process, as podokinetic adaptation has been shown to occur even when the eyes are closed (Jurgens *et al.*, 1999).
- There is a binary operator (eyes open or closed) that switches between sensory channels used for orientation. With the eyes open the rotation signal is driven by the visual signal, and with the eyes closed vestibular and podokinetic channels are used for orientation. We have assumed that the

vestibular and podokinetic signals of orientation are ignored when vision is available given this healthy population in the well-lit laboratory. However, it is conceivable that with a noisy or unreliable visual signal (Deshpande & Patla, 2005), the vestibular and podokinetic signals would have more influence on locomotor rotation.

Podokinetic and vestibular signals are summed vectorially. Vestibular and proprioceptive inputs have previously been shown to combine with a weighted sum during walking (Frissen *et al.*, 2011) and for postural orientation (Hlavacka *et al.*, 1996; Mergner & Rosemeier, 1998).

[Figure 4]

The mean curves provided by Weber *et al.* (1998) were combined with our data to provide robust estimates of the unknown parameters in the model. A weighted non-linear least-squares optimisation across all 14 conditions of empirical data yielded the following estimates: $\tau_s = 141s$ and $\tau_L = 1,645s$ (27.4 minutes), $G_s = 0.99$ and $G_L = 0.35$. Standard errors provided by Weber *et al.* were used to calculate the total sum-of-squares from which high coefficients of determination were obtained for all conditions (Figure 5).

Sensitivity analysis showed that both the short-term and long-term PK time constants had a strong influence on the predicted PKAR. Not surprisingly, for conditions with shorter conditioning durations (1, 2, 3, 5, 7.5, 10, and 15 minutes) the short-term PK parameters had higher associations (R values of 0.85, 0.71, 0.74, 0.90, 0.63, 0.70, 0.34) compared to the long-term PK parameters (R values of 0.05, 0.17, 0.22, 0.15, 0.51, 0.48, 0.24). Whereas, for longer conditioning times (30, 60 minutes) the long-term PK parameters had more influence ($R = 0.89, 0.93$) than short-term PK parameters ($R = 0.50, 0.42$). The long-term vestibular adaptation term had very low influence across all conditions (τ_a R range 0.001-0.06). For PKAR output curves that included the initial rise time the vestibular canal and velocity storage terms had low associations with the predicted curve (τ_c R range 0.1-0.25 and τ_v R range 0.09-0.15) although when only the first minute of data was considered these

values increased (τ_c R range 0.22-0.41 and τ_v R range 0.13-0.25) which reflects the influence of vestibular process during the early phase of the PKAR.

Discussion

This study has explored the adaptive mechanisms involved in locomotor rotation. Visual cues were used to maintain heading direction while podokinetic signals were stimulated with a constant rotational signal. Without visual cues, locomotor rotation was driven by vestibular signals and the podokinetic signal. The extent to which the podokinetic signal had adapted toward the neutral position during conditioning is revealed in the after-rotation trajectories. The PKAR trajectories following multiple conditioning parameters across different datasets reveal a set of podokinetic adaptation principles previously unknown: slower locomotor turning is more readily adapted than faster turning, and adaptation can occur on shorter time-scales than previously thought. Furthermore, the notion of two parallel podokinetic adaptation processes suggested by prior studies is supported by our results and comprehensive control-systems modelling approach.

Weber *et al.* (1998) reported that the ratio of the peak PKAR velocity to conditioning velocity was one third, although acknowledged that this relationship broke down for conditioning velocities above 45 deg.s⁻¹ and they did not test at speeds slower than 11.25 deg.s⁻¹. Closer inspection of their data reveals that the highest gain was in fact at the lowest stimulus velocity and the lowest gain was at the highest stimulus velocity. When combined with the results of the current study, a much clearer relationship emerges. As the conditioning velocity increases, the gain of the peak PKAR decreases according to a negative power function. We can only speculate on how this occurs. The amount of the biomechanical turning may differentially affect peripheral somatosensory adaptation whereby increasing mechanical stresses on cutaneous, joint and muscle receptors create a progressive saturation of sensory and adaptation processes. A central adaptive mechanism may

reconcile slower podokinetic rotations as straight ahead more readily than fast podokinetic rotations. Velocity scaling to podokinetic stimuli is a novel finding of this study. However, a similar relationship is known to occur with full-field visual input, where central body schema of body position in space more readily accepts slower full-field visual rotations as motion of the self (Day *et al.*, 2016).

The results show that podokinetic adaptation can be explained by two time constants: a shorter time constant of the order of 2-3 minutes and longer time constant of the order of 26 minutes. This explains why after-rotations quickly decayed following just a few minutes of podokinetic conditioning and why there were sustained after-rotations following longer conditioning times. The Weber *et al.* study also report that two time constants describe the PKAR decay curve. However, their estimates (6-12 minutes and 1-2 hours) are much longer than ours because they fitted directly to the exponentially decreasing phase of the PKAR curve. Our estimates incorporate dynamic vestibular and podokinetic feedback that continues to occur during the PKAR phase. In addition, our estimates are based on 14 different conditions rather than one.

We speculate that the two decay time constants could represent two distinct adaptation processes. Several studies have suggested there could be two separate stored representations for movement in the nervous system (Morton & Bastian, 2004; Vangheluwe *et al.*, 2006; Galea *et al.*, 2007): one at a central, effector-independent level, and one at a task-specific, effector-dependent level. Evidence for both central and peripheral motor representations encoding podokinetic orientation can be seen in studies of inter-limb adaptation transfer. The thinking is that if podokinetic adaptation occurs through a central, limb-independent motor representation, then adaptation of one limb would generalize to unconditioned limbs. In contrast, if podokinetic adaptation is entirely through an effector-specific motor representation, transfer between a conditioned and an unconditioned limb would not occur. If podokinetic motor representations exist at both higher and lower levels, then an incomplete transfer of podokinetic adaptation across limbs

would be expected. A study that conditioned a single leg to podokinetic stepping rotation found afterward when hopping on the unconditioned leg participants rotated in the direction the conditioned leg had been exposed to (McNeely & Earhart, 2010). When the post-conditioning hopping was with the conditioned leg, there was greater rotation compared to hopping on the unconditioned leg (peak velocity of $7.95 \pm 1.41 \text{ deg.s}^{-1}$ vs. $5.59 \pm 1.17 \text{ deg.s}^{-1}$). These differences failed to reach statistical significance, however the direction of the discrepancy between limbs does suggest an incomplete transfer between conditioned and unconditioned limb. It is worth noting that because only the first two minutes of hopping after-rotation were recorded, according to our model, the short-latency adaptation process would be expected to dominate the response in this time period. Therefore, we speculate that the high response in the unconditioned limb reflects the short-term podokinetic adaptation, which is a central limb-independent process. If longer hopping after-rotations were recorded a greater disparity between the conditioned and unconditioned limbs may have emerged as the long-term adaptation process became more dominant.

Prism adaptation studies also suggest that locomotion orientation accesses a higher center of control. Prism adaptation of walking trajectory transfers to arm reaching but the reverse is not true: adaptation of arm reaching does not transfer to walking (Morton & Bastian, 2004). The cerebellum appears to be integral for higher-level visuomotor adaptations of the locomotor system. People with cerebellar dysfunction do not have a transfer between prism adaptation during walking and arm motion (Morton & Bastian, 2004). Furthermore, Earhart *et al.* (2002) show that the high initial velocity of PKAR is significantly less in patients with cerebellar degeneration when compared with normal participants, but cerebellar participants still have a sustained longer-term PKAR of similar decay profile as control participants (Earhart *et al.*, 2002). This result suggests a disruption of the short-term podokinetic adaptation but the long-term adaptation is intact in people with cerebellar damage. When removing the short-term podokinetic adaptation term from our model and applying the conditioning parameters of the Earhart *et al.* 2002 study (15 minutes at 45 deg.s^{-1}) the output

curve is similar to the example cerebellar participant provided (Earhart *et al.*, 2002). Although further testing is required, it is plausible that the short-term adaptation process involves the cerebellum by remodeling the relationship between efference copy of the motor output and expected reafference (Held 1965).

We propose that the long-term adaptation process likely involves receptor and spinal- level adaptations of the effectors involved in the conditioning movement. The sources of proprioceptive and somatosensory input that adapt through sustained stepping rotation include hip rotation as well many other sources (Wong *et al.*, 2007). This may be through use-dependent learning mechanisms where it is the repetition of the actual movement, rather than an error-signal, that underlies the learning changes (Wolpert *et al.*, 2011). Influence of use-dependent learning towards the last executed movement solutions have been found in a study that used visuomotor rotations to influence movement directions (Huang *et al.*, 2011).

Two studies (Jurgens *et al.*, 1999; Falvo *et al.*, 2009) have shown that 30 second exposure to visual cues during PKAR will halt the rotation. However once participants are blindfolded again the PKAR recommences with a similar decay profile at only a slightly decreased rate. This response is consistent with predictions of our proposed model because 30 seconds is insufficient time for the short-term adaptation mechanism to recalibrate to the visual signal. Our model also predicts Jurgens *et al.*'s reduced PKAR peak following rotations of *both* podokinetic and vestibular signals. This provides further evidence that our model integrates vestibular and podokinetic signals appropriately.

Although we replicated the study protocol used by Weber *et al.* as best we could, there may have been small differences in the PKAR curves related to unknown differences between studies. However, by combining the two datasets the quantitative estimates of the model should be more robust and less study-dependent. It is also worth noting that the parameter values identified in this

study are specific to a cadence of 2 Hz. Higher PKAR velocities will occur with higher cadences (Earhart & Horak, 2004).

The model assumes that both short and long-term podokinetic adaptation processes scale the rotational velocity signal by the same function (f_v). However, this function may not be necessarily the same for the short and long-term podokinetic processes. Our assumption offers a simpler model, and fits the data of the healthy sample, however future testing of clinical groups across varying conditioning velocities may reveal different velocity gain functions.

Training techniques that use podokinetic stimuli show promise in the treatment of motor disorders that affect locomotor turning (Godi *et al.*, 2017). As this study has shown that high-gain PKAR responses are evoked with low rotational velocities, training could be performed with slower platform speeds, which would be more agreeable to clinical groups with poor balance. Whether short-term or long-term podokinetic processes need to be engaged to improve turning is unknown. But potentially shorter, frequent podokinetic training sessions will improve turning to the same extent as longer sessions.

Summary

Locomotor signals of orientation adapt with sustained rotational stepping. A comprehensive analysis of PKAR to a range of conditioning parameters revealed that as the rotational stepping velocity increases, the adaptation becomes less complete. It was also shown that podokinetic adaptation is best explained by two adaptation time constants. We speculate that PKAR occurs through two adaptation mechanisms:

1. A central limb-independent adaptation with a time constant of 2-3 minutes that recalibrates expected and actual somatosensory information for straight-ahead stepping according

to the sense of orientation in space. When visual orientation cues are available they will govern the orientation sense.

2. A peripheral limb-dependent adaptation that occurs through sustained rotation in limb-specific somatosensors with a time constant of about half an hour.

The podokinetic dual-adaptation model we propose offers a theoretical framework to explain the findings of previous PKAR studies, particularly those concerning inter-limb-transfer, cerebellar patients and PKAR after periods of visual input. We encourage further testing of this model.

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Additional Information

Competing Interests

There are no competing interests.

Author contributions

The experiments were performed at NeuroScience Research Australia.

Conception or design of the work (RStG, RCF)

Acquisition, analysis or interpretation of data for the work (RStG, RCF, AAB, BLD)

Drafting the work or revising it critically for important intellectual content (RStG, RCF, AAB, BLD).

All authors; approved the final version of the manuscript, 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.

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Translational Perspective

After a person experiences a period of sustained rotational stepping, they walk with a curved trajectory when attempting to walk straight without vision. This adaptation of our sense of locomotor rotation (known as “podokinetic” adaptation), is a promising technique for improving locomotor turning in clinical conditions such as Parkinson’s Disease. This study sort to better understand podokinetic adaptive mechanisms by measuring rotational trajectories following podokinetic conditioning and forming a dynamic feedback model of podokinetic and vestibular adaptation processes. The results suggest that podokinetic adaptation occurs via two mechanisms; one that occurs quickly (2-3 minutes), and another that occurs over a longer time scale (~half an hour). We also show that slower rotational velocities are more readily adapted than faster velocities. These findings highlight the feasibility of the technique as a training or rehabilitation tool in people with disorders of turning. Benefits may occur with shorter conditioning times and slower rotational walking speeds than previously thought, which would be more agreeable to clinical groups with poor balance.

Figure 1. Experimental procedure

In the conditioning phase participants stepped in place over the axis of a platform rotating at a constant speed with vision available. Once the platform stopped the participant was blindfolded and they stepped in place attempting to maintain a constant heading direction.

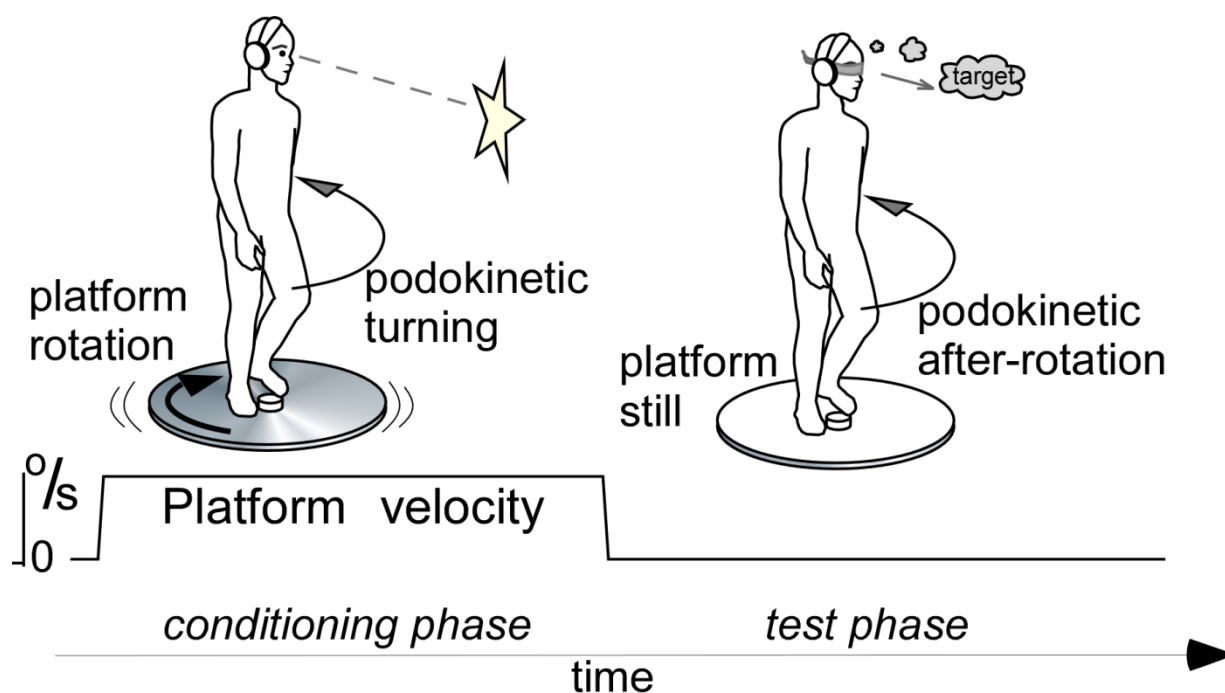


Figure 2. Example of PKAR raw data traces and exponential fits.

Example PKAR angular velocities of a participant following 20deg.s^{-1} podokinetic conditioning for 1, 2, 3, 5 and 10 minutes. Black data points are the first time the participant was tested on that condition and grey data points show the same condition repeated at least one week later. The red lines show the exponential function fitted to the mean data points (excluding the first minute of data) for this participant.

Conditioning duration: 1 min

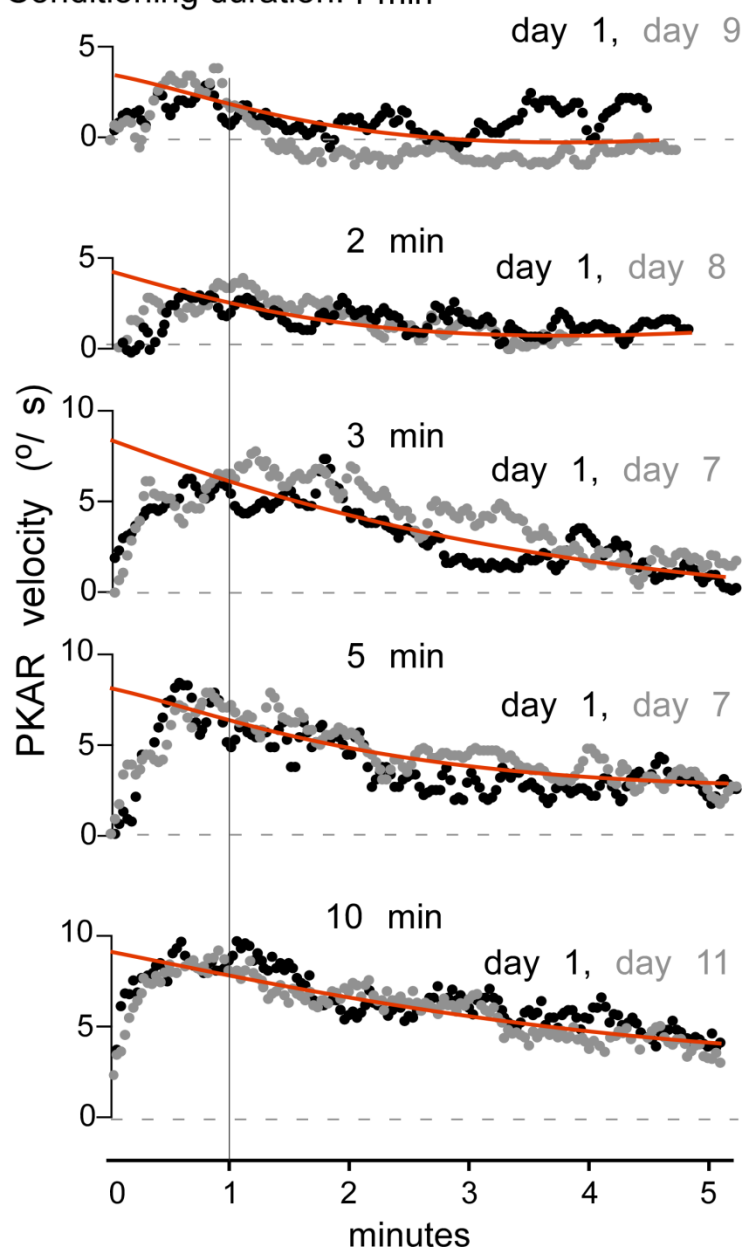


Figure 3. The effect of podokinetic conditioning velocity on the PKAR peak gain.

Filled data points are from this study and open data points are from the study by Weber *et al.* (1998). The number adjacent to each data point is the conditioning time which (after 3 minutes) appears to have minimal effect on the initial gain of the response. A power curve f_v provided the best fit to the data.

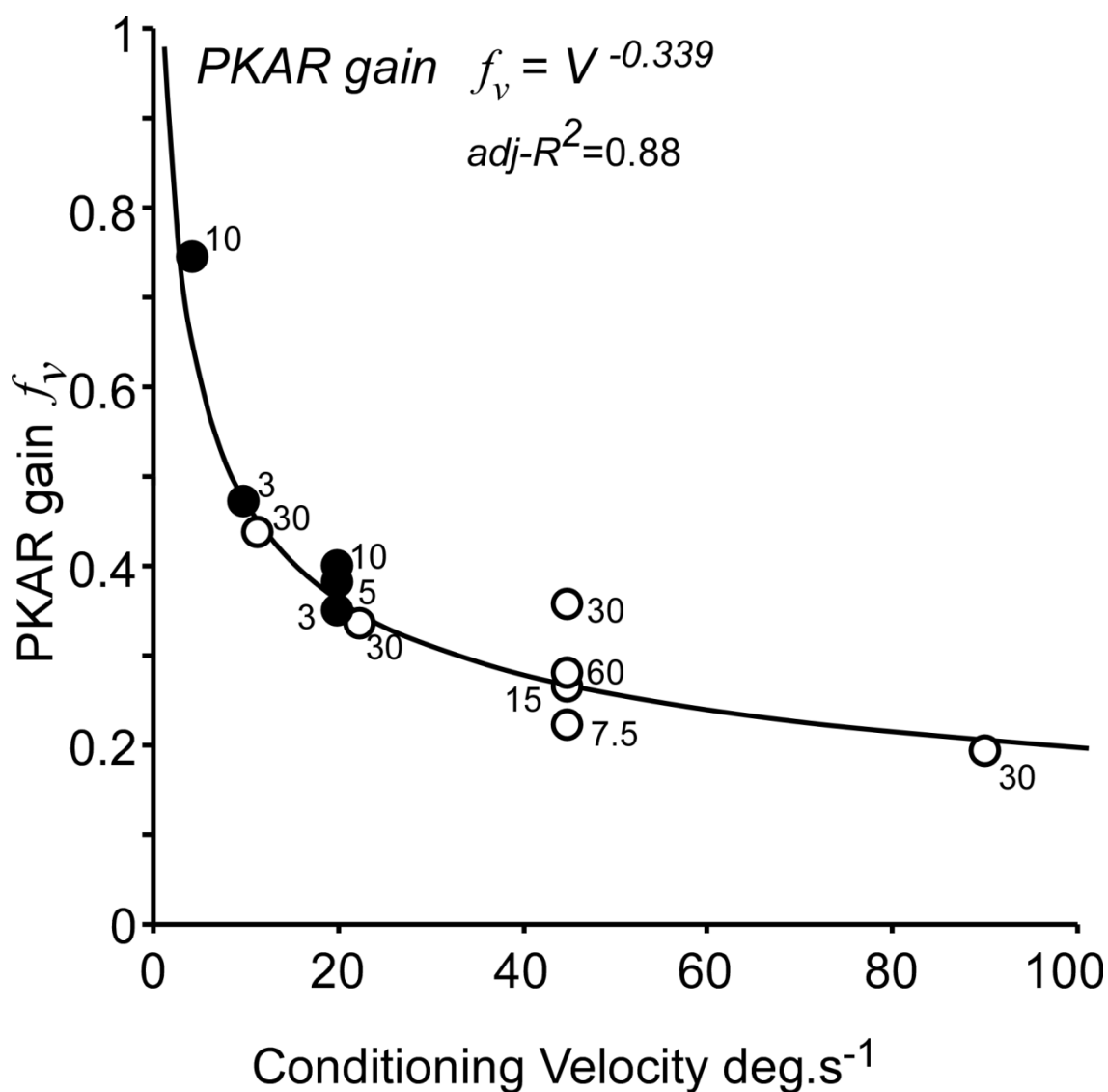
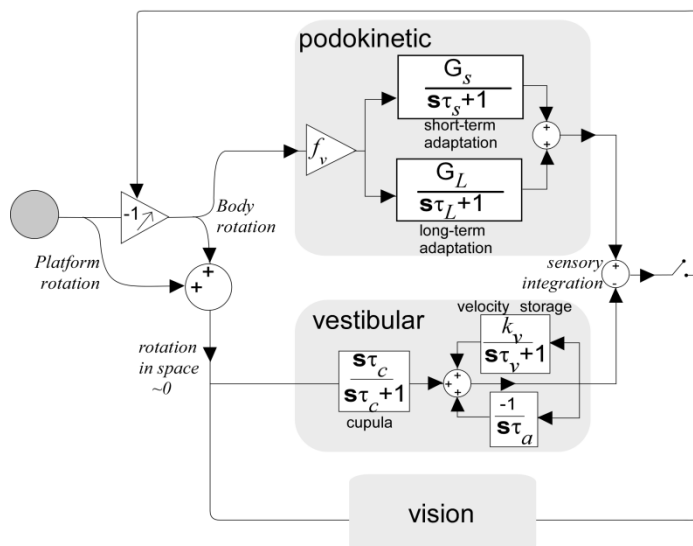


Figure 4. A feedback model of locomotor rotation.

A) During the podokinetic conditioning phase the platform rotated and vision was available. The controlled variable was rotational velocity relative to space which was the sum of the platform rotation and body rotation. Any error detected with vision was corrected by adjustments in body rotation velocity. To maintain constant heading direction, body rotation was the negative (-1) of the platform rotation. Body rotation relative to the feet underwent short and long-term podokinetic adaptation.

B) During the podokinetic after-rotation phase, vision was removed and the platform was stationary. The rate of body rotation in space was the result of the adapted podokinetic signal, and was attenuated by negative feedback through the vestibular system to evoke the sensation of no rotation in space.

A. Podokinetic conditioning



B. Podokinetic after-rotation

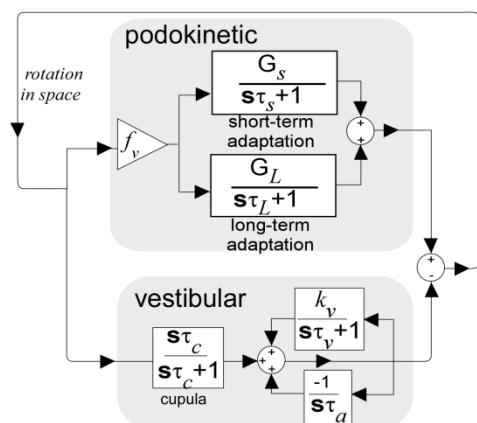
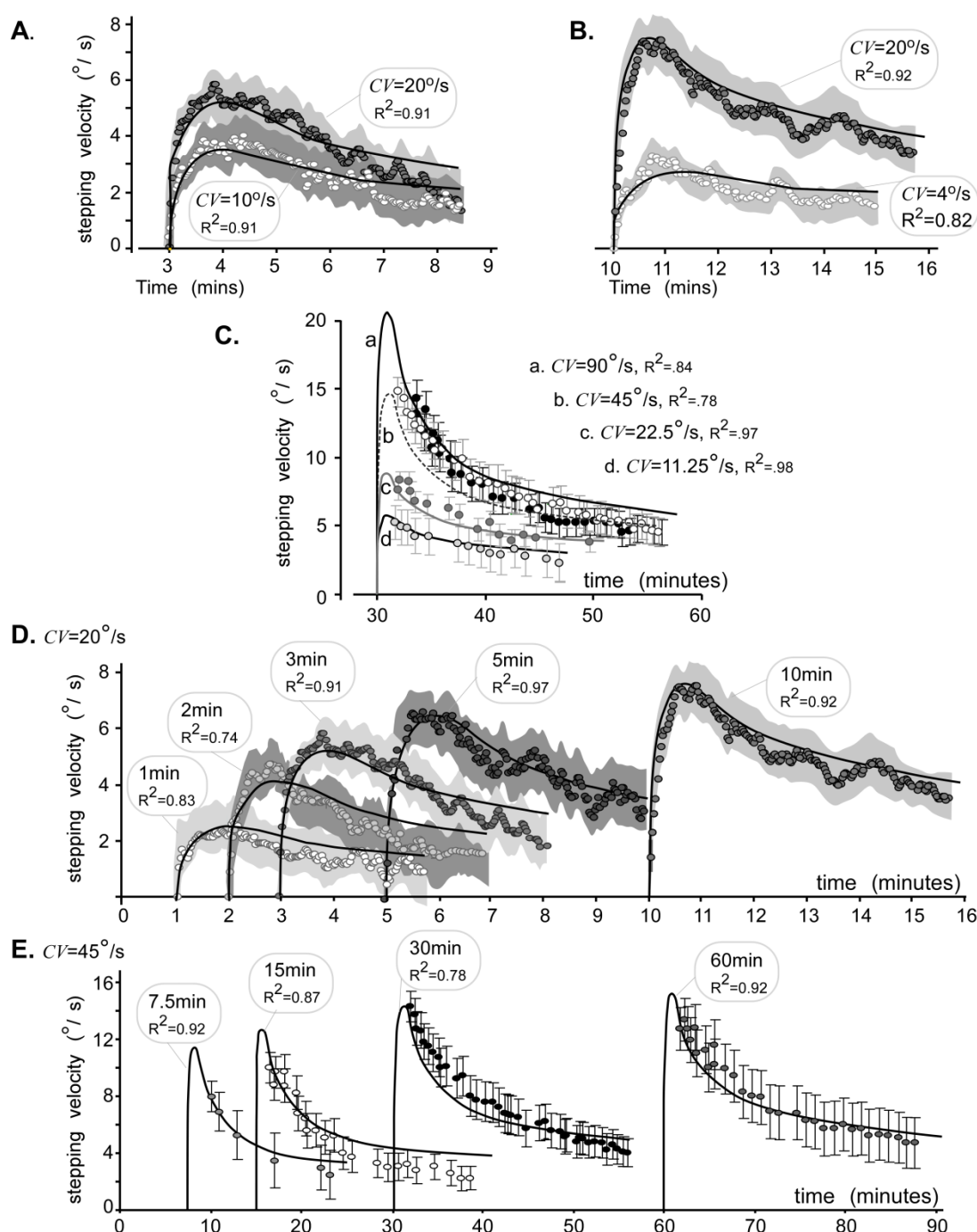


Figure 5. Experimental and model-predicted PKAR responses

The different conditioning velocities (CV) and durations for this study: A, B and D; and the Weber *et al.* study: C and E. The conditioning times are indicated by the start time of each of the curves on the abscissa. Solid lines represent the model predicted trajectories. The dots are the mean experimental PKAR responses and the shaded regions show the 95% confidence intervals for the current data. The 95% CI for the Weber *et al.* study were determined from their published standard errors (Weber *et al.*, 1998).





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