Locomotor adaptation is modulated by observing the actions of others

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Running Head: Locomotor adaptation is modulated by action-observation

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Abstract

Observing the motor actions of another person could facilitate compensatory motor behaviour in the passive observer. Here, we explored whether action observation alone can induce automatic locomotor adaptation in humans. To explore this possibility we used the "broken-escalator" paradigm. Conventionally this involves stepping upon a stationary sled after having previously experienced it actually moving (MOVING trials). This history of motion produces a locomotor aftereffect when subsequently stepping on to a stationary sled. We found that viewing an actor perform the MOVING trials was sufficient to generate a locomotor aftereffect in the observer, the size of which was significantly correlated with the size of the movement (postural sway) observed. Crucially, the effect is specific to watching the task being performed, as no motor adaptation occurs after simply viewing the sled move in isolation. These findings demonstrate that locomotor adaptation in humans can be driven purely by action observation, with the brain adapting motor plans in response to the size of the observed individual's motion. This mechanism may be mediated by a mirror neuron system that automatically adapts behaviour to minimise movement errors and improve motor skills through social cues, though further neurophysiological studies are required to support this theory. This non-verbal adaptive mechanism may have evolved to facilitate motor conformity within social groups with respect to environmental hazards or risks.

Key words

Locomotion, adaptation, learning, action observation, mirror neurons

Introduction

Adaptive behaviours are necessary to meet the pressures of physical and social environments (Kummer 2006). Current theories suggest that such patterned forms of behaviour in both humans and animals can be learnt simply by observing the actions of others (Akins et al. 2002; Herman 2012; Iriki 2006; Molnar-Szakacs et al. 2006). For example, observing another person perform reaching movements in a novel perturbing environment produces compensatory changes in force output (Wanda et al. 2013) and improves the accuracy of subsequent reaches by naïve observers (Brown et al. 2009). Observing another person slip during platform perturbations can also improve postural stability when naïve observers perform the same task (Bhatt and Pai 2008). However, it is unknown whether such learning based behaviour extends to locomotion.

In situations where we repeatedly encounter the same motor task, the brain generates sensorimotor predictions about the likely outcome of the event and accordingly adapts our motor plans (Shadmehr and Brashers-Krug 1997; Wolpert et al. 2011). This is an error-based motor learning process that quickly allows modification of motor strategies to maintain motor control in the face of an external perturbation (Bastian 2008). A specific example of such motor adaptation is how we learn to negotiate escalators. After repeatedly encountering a functioning escalator, we learn to step onto it by producing a predictive compensatory physical response to stabilise our balance. Such adaptive learning becomes apparent when we step onto a broken (stationary) escalator. The characteristic stumble produced is the result of an automatically generated forward trunk movement and faster gait that would have been required to negotiate a moving escalator. This has been termed the “broken escalator” phenomenon or locomotor aftereffect (LAE) (Reynolds and Bronstein 2003).

Such motor aftereffects are the remnants of compensatory movements developed in a perturbed environment which then occur automatically in an unperturbed environment. Although an aftereffect suggests that adaptive learning has taken place, to date, there is no data on whether an LAE can be generated by action observation alone or how any resulting aftereffect would scale to the size of the observed movement. Thus we sought to investigate the difference between adaptive learning induced by first-hand experience versus observation, as measured by the locomotor aftereffect with the “broken escalator” paradigm (Reynolds and Bronstein 2003). We were also interested in exploring whether locomotor adaptation following action-observation critically depends on viewing a perceived movement error (Osman et al. 2005) as with routine motor learning.

Materials and Methods

Participants

Thirty-six healthy individuals (27 male, mean=24.4 years age SD=4.0 years, age range 18-42) took part in the main study and were divided into three equally-sized groups of twelve. Participants provided written informed consent and were naïve to the purposes of the experiment. The study was approved by the local research ethics committee.

Equipment

The computer-controlled linear sled, running on a level track, was powered by two linear induction motors. Sled velocity was recorded with a tachometer (Reynolds and Bronstein 2003). Anterior-posterior trunk position and gait velocity was measured with a Fastrak tracking system (Polhemus, VT, USA) using a movement sensor secured over the C7 vertebra and sampled at 500 Hz. Step timing information was collected with pressure sensitive foot straps and a linear accelerometer attached to the sled.

Procedure

The research question was to establish if subjects (observers) would develop the broken escalator locomotor aftereffect (LAE) simply by observing an actor perform the locomotor task.

In the main investigation, the experimental sequence comprised three phases: PRE-OBSERVATION (5 trials, stationary sled), OBSERVATION (5 trials, observing an actor balance on moving sled) and POST-OBSERVATION trials (5 trials, stationary sled, locomotor aftereffect phase) in this order (Figure 1).

In the PRE-OBSERVATION and POST-OBSERVATION trials, observers stepped from a stationary platform onto a stationary sled. Subjects were prompted to walk forwards from a stationary stance by a single, brief auditory cue (beep), stepping with their right foot on to the fixed platform and then on to the sled with their left foot. Thereafter stopping and maintaining balance with both feet in line; three steps in all, right-left-right; see figure 2 in (Kaski et al. 2012). In the PRE-OBSERVATION and POST-OBSERVATION trials the sled does not move. PRE-OBSERVATION trials show the baseline response whereas the POST-OBSERVATION trials reveal the aftereffect.

In the OBSERVATION trials, observers sat and viewed the actor from a distance of 2m side on (to view anterior-posterior sway). The actor stepped upon the same sled in the same manner as described above, only this time the sled moved forwards in the direction of walking, moving along the linear track analogous to a moving walkway. Sled motion was triggered by the actor's first step forward from the 'start' platform onto the sled by breaking an infra-red light beam. After breaking the beam, the sled moves following a 600ms delay, travelling a distance of approximately 3.7m in 4.2s; maximum velocity of 1.4m/s was achieved after 1.3s, as in previous experiments (Reynolds and Bronstein 2003).

Here, in the OBSERVATION trials (moving sled), 24 OBSERVERS were randomly allocated to two subject groups, both with 12 subjects: Unstable actor observers, who viewed normal levels of postural sway (induced by sled motion); and Stable actor observers who viewed a higher degree of stability, Figure 2. This was to assess group differences when viewing a stable versus unstable actor. The actor's stability between the two conditions differed significantly (paired t-test $P<0.001$), see Figure 2. The same actor was used for both groups to perform all 5 moving sled trials for observers. Under conventional conditions in this experiment (Bunday et al. 2006; Reynolds and Bronstein 2003) subjects visibly sway during the moving sled trials, but gradually sway less when they repeat this task. The actor was trained to perform the experiment for the Unstable Observers realistically as a naïve person would; gradually swaying less as they repeated the task. Owing to the 'live' observation of the actor, the size of sway observed varied for each Observer. Participants sat in line with the actor's stationary starting position, viewing side-on motion. As a control condition, we tested a third group of 12 healthy OBSERVERS performing the same experiment, but this time they observed the experimental apparatus move in isolation without the presence of an actor (Sled Observers).

In the POST-OBSERVATION trials, the actor dismounted from the platform and observers were given the instructions "Step onto the sled as you did before. But this time the sled is not going to move and the motor is now going to be turned off. The sled will be stationary just as previously". The motor was audibly turned off, indicated by a key turning and the sound of the running motor ceasing. Each trial lasted 16 seconds after which subjects returned to the original starting position.

To evaluate whether the effects observed were due to inter-group differences in locomotor adaptation, the Stable actor observers and Unstable actor observers were also asked to perform the conventional 'broken escalator' paradigm on a separate occasion. Hence, the same subjects in the main investigation performed the conventional experiment. The conventional broken escalator LAE paradigm employed has been used in multiple previous publications (Bronstein et al. 2009; Reynolds and Bronstein 2003) but in summary, the conventional experiment comprises three stages: BEFORE

(5 trials, stationary sled), MOVING (5 trials, moving sled, adaptation phase) and AFTER trials (5 trials, stationary sled, locomotor aftereffect phase) in this order see (Kaski et al. 2012) figure 1.

-FIGURE 1 ABOUT HERE-

Data Analysis

Trunk overshoot in the PRE-OBSERVATION and POST-OBSERVATION trials was defined as the maximum forward deviation of the trunk relative to the mean final trunk position in the last 3 seconds of the trial. In OBSERVATION trials, trunk sway was measured as the maximum backwards—to-forwards (peak-to-peak) displacement after stepping onto the sled (Bunday and Bronstein 2008; Kaski et al. 2012). Gait velocity was calculated as the mean linear trunk velocity over a 0.5 second period prior to foot-sled contact. PRE-OBSERVATION trials 3-5 were averaged and used in the analyses as baseline performance. In the POST-OBSERVATION trials, trunk overshoot and gait velocity in trial 1 is referred to as an aftereffect.

We examined the data across groups with a [2x2] repeated-measures ANOVA with factors *phase* (PRE-OBSERVATION, POST-OBSERVATION) and *group* (Stable actor observers and Unstable actor observers). We used our customary approach to test for the presence of an LAE (Kaski et al. 2012; Patel et al. 2014) by comparing performance during the POST-OBSERVATION phase with PRE-OBSERVATION (i.e. the mean of PRE-OBSERVATION trials 3-5). Where appropriate post-hoc tests and correlations were performed, details are explained in the text. Paired statistics were corrected for multiple comparisons where appropriate.

Results

As seen in Figure 2 (top right), trunk overshoot in POST-OBSERVATION trial 1 was significantly larger in the Unstable actor observers compared to the Stable actor observers (P=0.004). The repeated measures ANOVA revealed significant main effects in trunk overshoot for *phase* (F[1,11]=33.09; P<0.001) and *group* (F[1,11]=10.43; P=0.008). A significant phase by group interaction was found (F[1,11]=8.99; P=0.012). Post-hoc analysis was used to elucidate specific effects. In the Unstable actor observers there was a significant increase in trunk overshoot in the first POST-OBSERVATION trial compared to baseline (P=0.002), demonstrating a trunk aftereffect in this group, but not in the Stable actor observers (P=0.1).

Gait velocity in POST-OBSERVATION trial 1 was faster in the Unstable actor observers compared to the Stable actor observers, though was only of trend level significance (P=0.08), as shown in Figure 2. The repeated measures ANOVA for gait velocity showed significant main effects of *phase* (*F*[1,11]=5.0; *P*=0.045) and *group* (*F*[1,11]=10.4; *P*=0.009). A significant phase by group interaction was also found (*F*[1,11]=5.65; *P*=0.039). Post-hoc analysis also showed a significant increase in gait velocity in the first POST-OBSERVATION trial compared to baseline in the Unstable actor observers (*P*=0.012) demonstrating a gait velocity aftereffect in this group, but not in the Stable actor observers (*P*=0.21).

Subjects who viewed the experimental apparatus move in isolation (Sled Observers) produced no significant trunk overshoot aftereffect (mean=1.44cm SD=1.47; *P*=0.38) or gait velocity aftereffect (mean=54.3 cm/s SD=5.47; *P*=0.44) in the first POST-OBSERVATION trial compared to baseline.

-FIGURE 3 ABOUT HERE-

In order to test whether the effects observed here were due to group differences in locomotor performance and adaptation, we re-tested the participants using the conventional 'broken escalator' paradigm (i.e., BEFORE, MOVING (with real exposure to the moving sled) and AFTER trials, see (Reynolds and Bronstein 2003)). A repeated-measures [2x2] ANOVA showed no significant main effect of *group* on trunk sway or gait velocity (Figure 3). As expected, both groups had a significant trunk overshoot and gait velocity aftereffect ($P \leq 0.002$), see figure 3. Therefore the effects of observation cannot be explained by differences in motor adaptation between the two observation groups. In addition, the trunk overshoot (P=0.029) and gait velocity (P=0.01) aftereffects were larger following the conventional experiment compared with observation.

-FIGURE 4 ABOUT HERE-

We then examined whether the size of each individual's trunk sway aftereffect was related to the size of the observed (actor's) sway during the OBSERVATION trials (mean trials 1-5), and found a highly significant positive correlation (Pearson's R=0.530, *P*=0.003), see Figure 4A, suggesting that increasingly unstable actors induce greater adaptation aftereffects in the observer.

It has previously been shown that an individual's trunk sway LAE is related to the degree of trunk sway they exhibit during the MOVING trials (Green et al. 2010). Thus, in the conventional broken escalator paradigm, the size of the aftereffects across the groups were positively correlated with the magnitude of their own sway in the MOVING trials (Pearson's R=0.550, *P*=0.008), shown in Figure 4B. Using a Fisher r-to-z transformation we found no significant difference between the two correlations (p>0.95, two-tailed).

The correlation between the size of the trunk overshoot aftereffect and the observed gait velocity during the OBSERVATION trials showed a trend towards significance (mean trials 1-5) (Pearson's R=0.399, *P*=0.053), whereas there was no correlation between the trunk overshoot aftereffect and actual gait velocity in the MOVING trials in the conventional experiment (*P*=0.65)

The gait velocity aftereffect was not significantly related to the observed (actor's) gait velocity (*P*=0.131) or sway (*P*=0.147) during OBSERVATION trials (mean trials 1-5).

-FIGURE 5 ABOUT HERE-

Discussion

Here we show that an adaptive locomotor learning process, one that is frequently experienced by commuters using underground transport systems, can be modulated by observing the actions of other individuals. We show for the first time that action observation alone is sufficient to produce a locomotor aftereffect. Remarkably, we found that the observer's locomotor plan is updated in proportion to the size of observed motion, inducing a similar effect to physically performing the conventional task. Critically, this effect is only conferred by observing another individual using the escalator; as observing the moving escalator (sled in this case) alone did not induce any aftereffect. These findings suggest that observing the behaviour of others is a critical avenue for developing and refining our motor programs.

Previous studies have shown that observing the behaviour of another person induces activity in brain systems similar to those activated when performing the action; a mechanism subserved by the mirror neuron system (Gallese and Goldman 1998; Kilner and Lemon 2013; Schieber 2013). This system is tuned specifically to biological (not robotic) motion from a member of the same species (Kilner et al. 2007; Kilner et al. 2003; Press et al. 2011). Thus, observing another person lifting heavy or light objects has been shown to modulate the accuracy of subsequent lifts, as well as altering motor cortico-spinal excitability (Buckingham et al. 2014). Evidence of observational learning effects after viewing arm movement errors have also been reported, with faster learning (Brown et al. 2009) and larger force corrections (Wanda et al. 2013) when observing a larger error. Intriguingly, after observing another person slip due to a sudden platform perturbation, subjects performing the same experimental paradigm had lower slip displacement and velocity and greater post-slip stability compared to a naïve group (Bhatt and Pai 2008). These results demonstrate that adaptation following action-observation critically depends on viewing a perceived movement error (Osman et al. 2005).

That an aftereffect is induced solely by observing instability in the actions of another (Stable actor observers and Sled observers did not generate an aftereffect) provides compelling evidence that the adaptive processes involved when observing an action may be the same as those employed when performing the action (Chong et al. 2008). Thus, it is possible that the observer generates new predictions about the task by covertly simulating the motor commands of the observed action (Wolpert et al. 2011). We suggest that the effects described here may be mediated by the mirror neuron system for motor control which automatically adapts motor behaviours to minimise the risk of falling and improve motor skills based on social cues. However, further studies employing neurophysiological or neuroimaging techniques would be required to confirm this possibility.

The LAE is often viewed as the result of an implicit risk assessment process based on the perception of threat; will the sled move or not? (Patel et al. 2014; Reynolds and Bronstein 2003). Consequently, subjects with larger levels of sway during the MOVING sled trials and observers who viewed larger levels of sway generated a greater aftereffect as the size of the potential hazard increased. A possible reason why Unstable actor observers generated a smaller aftereffect compared to the conventional experiment (trunk overshoot and gait velocity were significantly reduced), is that observation does not convey threat as strongly as physical performance. It follows that the Stable actor observers, who did not generate an aftereffect, did not perceive a significant risk associated with the task. Interestingly, patients with impaired vestibular or proprioceptive function are more unstable during MOVING trials, but do not exhibit a proportionally larger aftereffect (Bunday and Bronstein 2009; 2008). This would indicate that sensory feedback during the execution of actual MOVING trials may also contribute to the generation of an aftereffect. That this effect was related to trunk sway and not gait velocity suggests that the brain is selectively tuned to changes in postural sway since these are more closely associated with an increased risk of falling than gait velocity.

It is possible that the effects we report here may confer an evolutionary advantage. Automatically adapting locomotor behaviour through observing threats or hazards experienced by other members of a social group would provide a rapid mechanism for motor learning. It has been shown that in terms of the cultural beliefs and values held by different human social groups, the tendency to acquire the most common behaviour exhibited within a society is an adaptive strategy (Boyd and Richerson 1985). This convergence towards the most prevalent behaviour, termed ‘conformist transmission’, helps to maintain group identity and encourages competition between groups through natural selection (Henrich and Boyd 1998). Although conformist transmission has been most commonly applied to socio-cultural beliefs and learning through imitation, the findings we report here suggest that ‘*motor conformity’* can occur both subliminally and implicitly. The observers in this study only exhibited an LAE after they had viewed an unstable person stepping on to the moving escalator, whereas viewing the escalator alone or a stable person did not induce any aftereffect. Thus, after viewing the experience of another we are highly susceptible to adapting our behaviour to match. The advantage of such automatic motor adaptation is that learning is not constrained to the experiential, and can be conveyed quickly and efficiently throughout a group. This may have been particularly useful during collective activities where the terrain may have required locomotor adaptation. A limitation of the current study is that we do not know the extent to which the aftereffect observed here is modulated by fear (i.e., an emotional mechanism as previously suggested (Green et al. 2010)) as opposed to locomotor observation. Since mirror neurons have been shown to respond to emotion as well as movement (Fabbri-Destro and Rizzolatti 2008), it is possible that emotional factors may have some influence in inducing an aftereffect. Secondly, we do not isolate whether this aftereffect is driven by cortical or subcortical mechanisms. One approach to answering whether a particular cortical region is involved in this effect would be to use repeated transcranial magnetic stimulation to induce a virtual lesion over the corresponding cortical mirror neuron region. However, a significant challenge is that the brain areas activated in response to whole body movement constitute a distributed network, as has been noted in other studies (Bolognini et al. 2011; Keuken et al. 2011), therefore selecting the appropriate region within the network corresponding to the mirrored signal would not be straightforward.

One important distinction between this and other studies assessing the sequelae of motor observation is that the assessment of efferent motor action (i.e. the LAE) occurs after, not during, the observation phase. Previous research has indicated that the ‘broken escalator’ phenomenon is context specific (Reynolds and Bronstein 2004). Therefore, it would be interesting to test whether such observation-induced aftereffects are similarly environmentally specific, i.e. would the LAE generalise to a different locomotor context?

These findings raise a number of questions regarding the observation of locomotor tasks which future studies may wish to consider investigating. For example, the observers in this study were contemporaries of the actor, therefore we do not know whether observing a younger or older person perform the task would have a differential effect as has been suggested previously (Diersch et al. 2012). In addition, familiarity, gender bias or the extent to which a participant trusts the actor may also modulate the size of the effect (Newman-Norlund et al. 2009). There may also be clinical implications; does the observation-LAE alter with ageing or in neurodegenerative diseases? Locomotor action-observation could be an additional way of promoting or consolidating gait and balance training during rehabilitation (Bellelli et al. 2010).

Conclusions

We provide the first evidence that observation can generate a locomotor aftereffect, and that the degree of adaptation is proportional to the size of observed motion. This mechanism may confer an evolutionary advantage by automatically adapting locomotor behaviour in response to threats or hazards experienced by other members of a social group.

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Figures

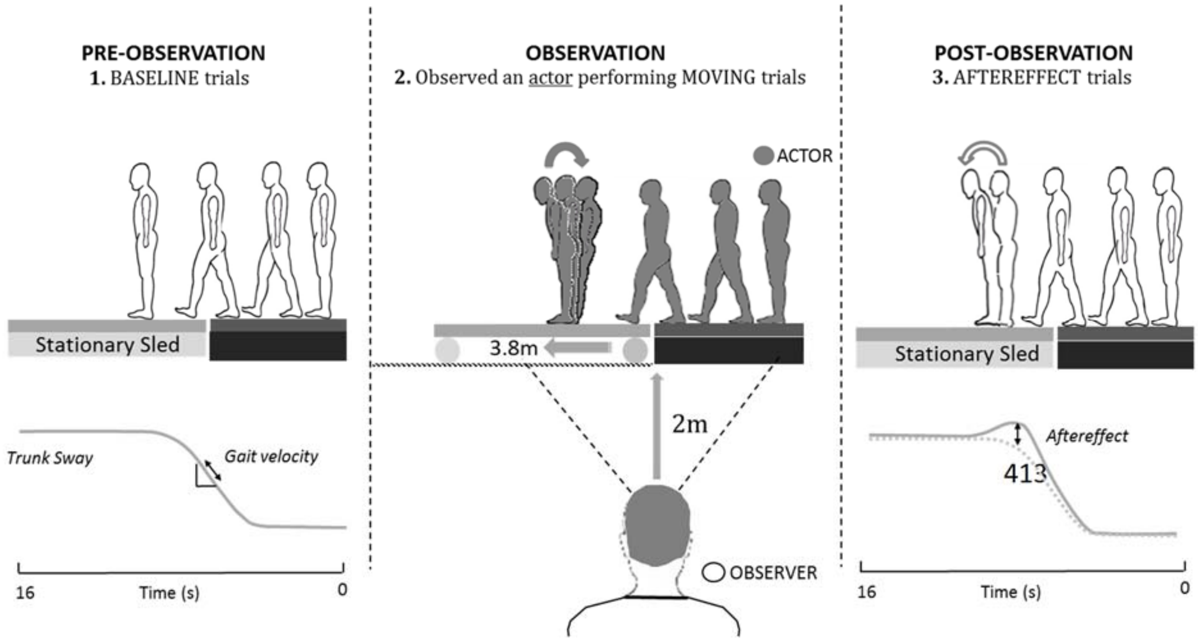

Figure 1: Experimental design. Subjects (n=24) were randomly divided into two equal groups: *Stable actor observers* performed PRE-OBSERVATION trials, then observed a stable actor balance upon the moving sled (OBSERVATION trials), before performing the POST-OBSERVATION trials. The *Unstable actor observers* performed the PRE-OBSERVATION trials, then observed an actor sway upon the moving sled (OBSERVATION trials), before performing the POST-OBSERVATION trials. The figure shows the experimental sequence (from left to right) performed by the Unstable actor observers whose results attest to action observation. There was an aftereffect (stumble) after viewing an unstable actor in the OBSERVATION trials as shown by the representative anterior-posterior trunk sway data.

Figure 2: Actor's sway in OBSERVATION trials

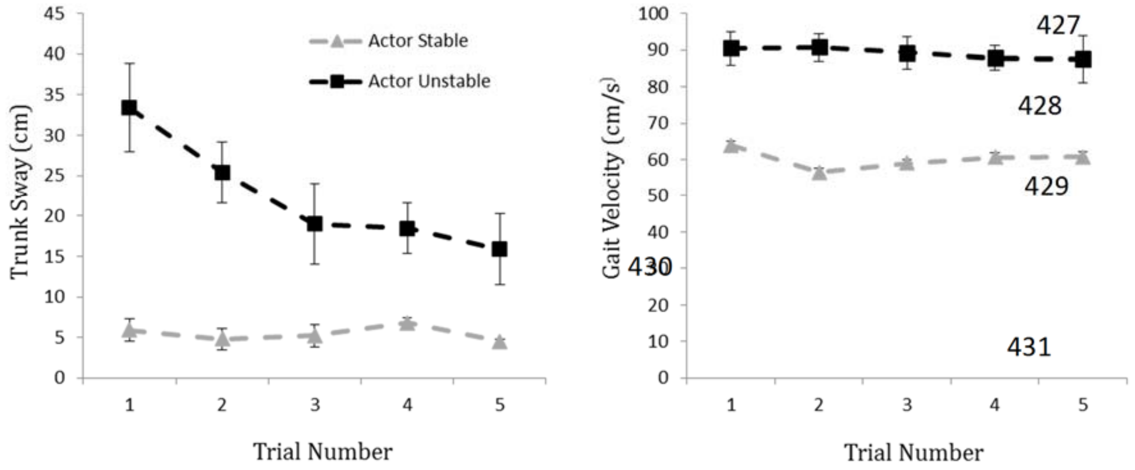

Figure 2: Trunk sway and gait velocity of the actor during OBSERVATION trials. Mean (+/- standard error) data of trunk sway and gait velocity of the actor during unstable (Actor Unstable, squares) or stable (Actor Stable, triangles) trials. The actor was trained to perform the experiment for the Unstable Observers realistically as a naïve person would; gradually swaying less as they repeated the task. In stable trials, the actor was trained to balance up on the moving sled well. The same actor was used for both groups to perform all 5 moving sled trials for observers.

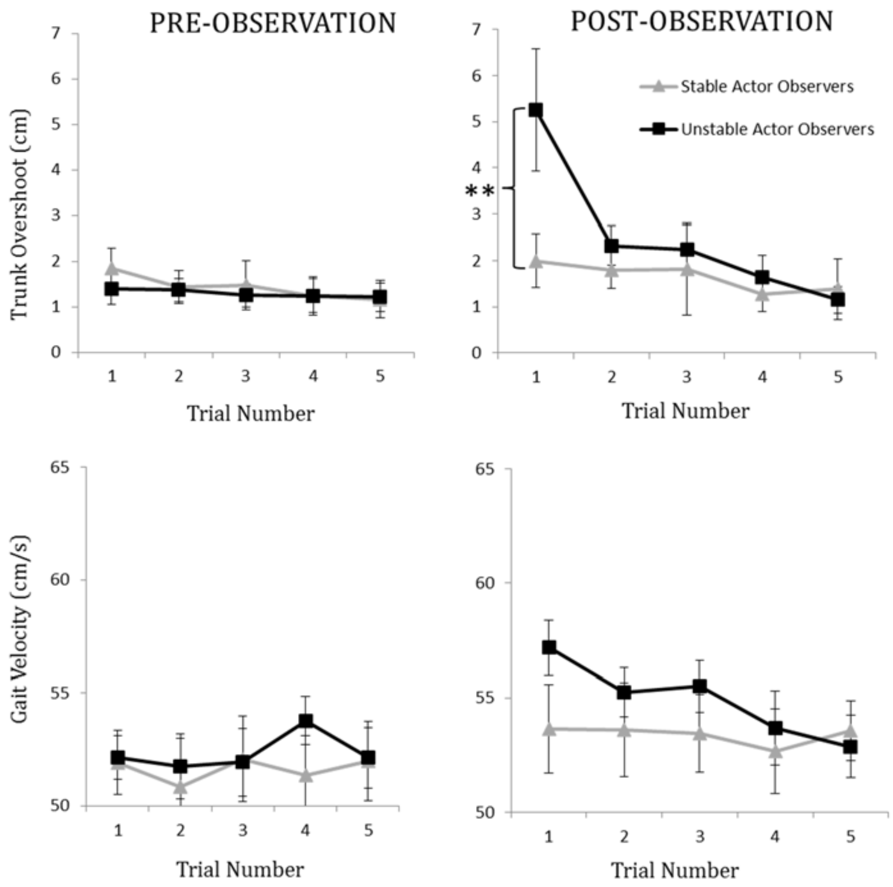

Figure 3: LAE for Stable and Unstable actor observers. Group mean (+/- standard error) data for Stable actor observers (triangles) and Unstable actor observers (crosses). The horizontal axis shows the trial number (1-5). The Unstable actor observers produced a significant aftereffect in both increased trunk overshoot and gait velocity in POST-OBSERVATION trials. Trunk overshoot in the first POST-OBSERVATION trial was also significantly larger in the Unstable actor observers compared to Stable actor observers, *****P*=0.004.**

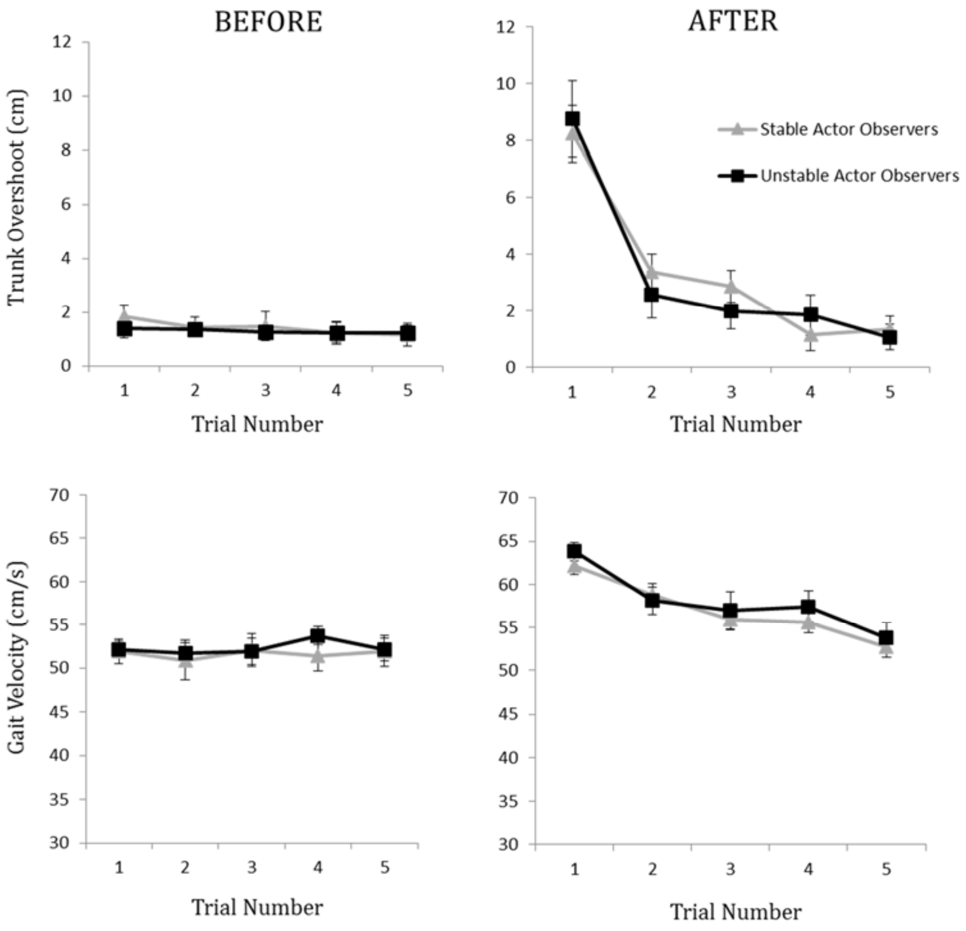

Figure 4: Performance on the standard broken escalator paradigm. Mean (+/- standard error) group data of BEFORE (left) and AFTER (right) trials for Stable actor observers (triangles) and Unstable actor observers (crosses) after physically performing the MOVING trials. The data show that both groups have an equal aftereffect demonstrated by a significant increase in trunk overshoot (top) and gait velocity (bottom) in the first AFTER trial.

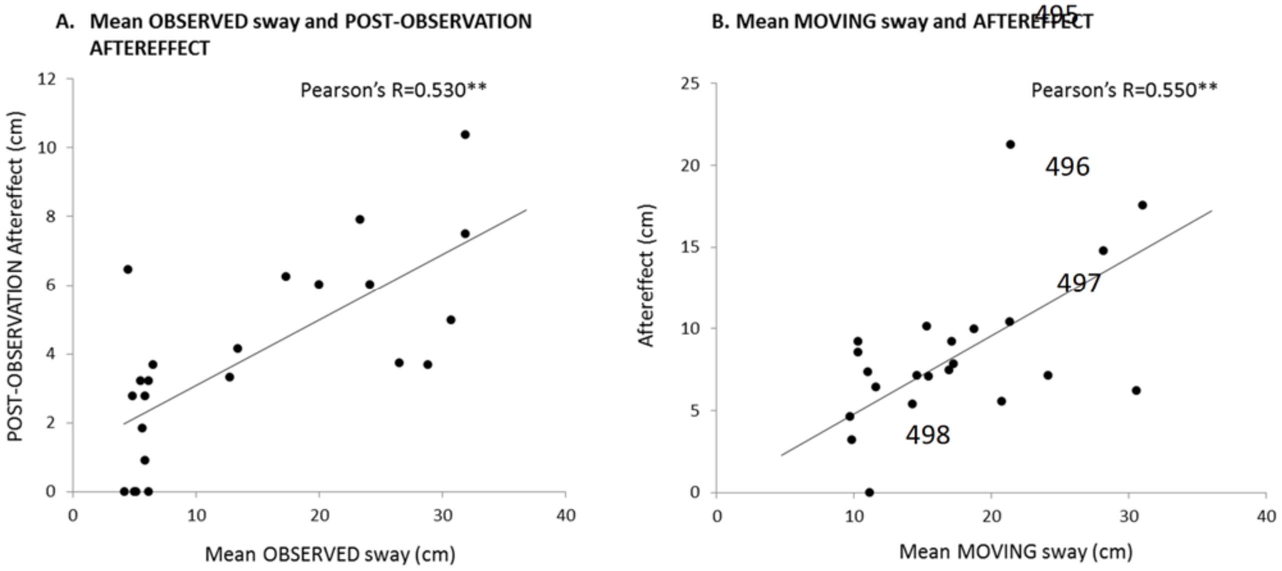

Figure 5: Associations between observation aftereffects and conventional aftereffects. (A) Correlation between the size of observed actor's sway in the mean OBSERVATION trials (average 5 trials) and the size of the trunk overshoot aftereffect (POST-OBSERVATION trial 1) for the Stable actor observers and Unstable actor observers. The figure shows that the size of the observed mean trunk sway in the OBSERVATION trials correlates with the size of the locomotor aftereffect (B) Correlation between the size of sway in the mean MOVING trials (average 5 trials, physically performed, conventional paradigm) and the size of the trunk overshoot aftereffect (AFTER trial 1) for the Stable actor observers and Unstable actor observers. The figure shows that the size of sway in the mean MOVING trials correlates to the size of the locomotor aftereffect. Together Figures A and B show that the size of the trunk overshoot aftereffect correlates to the level of sway in the MOVING trials, regardless of whether it is observed (A) or performed (B).