

1 **Locomotor adaptation is modulated by observing the actions of**
2 **others**

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12 **Running Head:** Locomotor adaptation is modulated by action-observation

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27 **Abstract**

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

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49 **Key words**

50 Locomotion, adaptation, learning, action observation, mirror neurons

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55 **Introduction**

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

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

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

85 depends on viewing a perceived movement error (Osman et al. 2005) as with routine motor
86 learning.

87 **Materials and Methods**

88 Participants

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

93 Equipment

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

100 Procedure

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

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

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

113 In the OBSERVATION trials, observers sat and viewed the actor from a distance of 2m side on (to
114 view anterior-posterior sway). The actor stepped upon the same sled in the same manner as
115 described above, only this time the sled moved forwards in the direction of walking, moving along
116 the linear track analogous to a moving walkway. Sled motion was triggered by the actor's first step
117 forward from the 'start' platform onto the sled by breaking an infra-red light beam. After breaking
118 the beam, the sled moves following a 600ms delay, travelling a distance of approximately 3.7m in
119 4.2s; maximum velocity of 1.4m/s was achieved after 1.3s, as in previous experiments (Reynolds and
120 Bronstein 2003).

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

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

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

146 (5 trials, stationary sled), MOVING (5 trials, moving sled, adaptation phase) and AFTER trials (5 trials,
147 stationary sled, locomotor aftereffect phase) in this order see (Kaski et al. 2012) figure 1.

148 -FIGURE 1 ABOUT HERE-

149 Data Analysis

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

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

165

166 Results

167 As seen in Figure 2 (top right), trunk overshoot in POST-OBSERVATION trial 1 was significantly larger
168 in the Unstable actor observers compared to the Stable actor observers ($P=0.004$). The repeated
169 measures ANOVA revealed significant main effects in trunk overshoot for *phase* ($F[1,11]=33.09$;
170 $P<0.001$) and *group* ($F[1,11]=10.43$; $P=0.008$). A significant phase by group interaction was found
171 ($F[1,11]=8.99$; $P=0.012$). Post-hoc analysis was used to elucidate specific effects. In the Unstable
172 actor observers there was a significant increase in trunk overshoot in the first POST-OBSERVATION
173 trial compared to baseline ($P=0.002$), demonstrating a trunk aftereffect in this group, but not in the
174 Stable actor observers ($P=0.1$).

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

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

186

187 -FIGURE 3 ABOUT HERE-

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

198 -FIGURE 4 ABOUT HERE-

199

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

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

210 The correlation between the size of the trunk overshoot aftereffect and the observed gait velocity
211 during the OBSERVATION trials showed a trend towards significance (mean trials 1-5) (Pearson's
212 $R=0.399$, $P=0.053$), whereas there was no correlation between the trunk overshoot aftereffect and
213 actual gait velocity in the MOVING trials in the conventional experiment ($P=0.65$)

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

216

217 -FIGURE 5 ABOUT HERE-

218

219 **Discussion**

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

229 Previous studies have shown that observing the behaviour of another person induces activity in
230 brain systems similar to those activated when performing the action; a mechanism subserved by the
231 mirror neuron system (Gallese and Goldman 1998; Kilner and Lemon 2013; Schieber 2013). This
232 system is tuned specifically to biological (not robotic) motion from a member of the same species
233 (Kilner et al. 2007; Kilner et al. 2003; Press et al. 2011). Thus, observing another person lifting heavy

234 or light objects has been shown to modulate the accuracy of subsequent lifts, as well as altering
235 motor cortico-spinal excitability (Buckingham et al. 2014). Evidence of observational learning effects
236 after viewing arm movement errors have also been reported, with faster learning (Brown et al.
237 2009) and larger force corrections (Wanda et al. 2013) when observing a larger error. Intriguingly,
238 after observing another person slip due to a sudden platform perturbation, subjects performing the
239 same experimental paradigm had lower slip displacement and velocity and greater post-slip stability
240 compared to a naïve group (Bhatt and Pai 2008). These results demonstrate that adaptation
241 following action-observation critically depends on viewing a perceived movement error (Osman et
242 al. 2005).

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

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

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

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

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

309 **Conclusions**

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

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407 **Figures**

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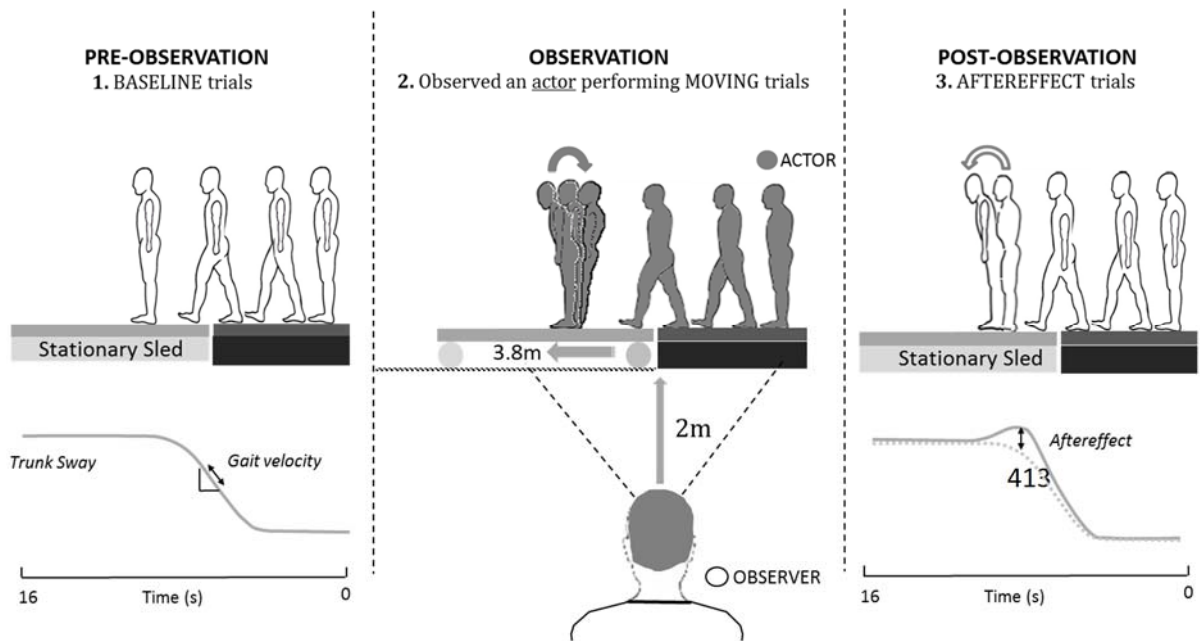
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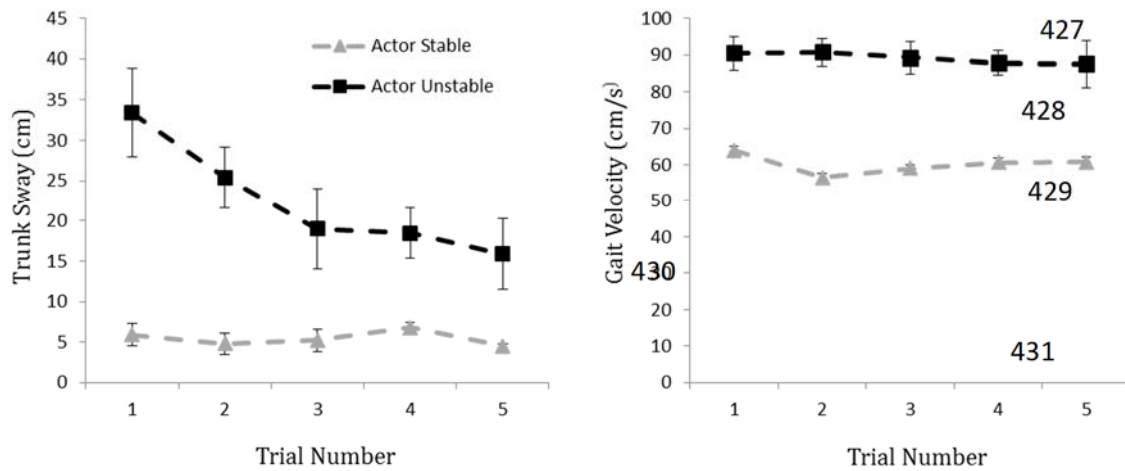


415 **Figure 1: Experimental design. Subjects (n=24) were randomly divided into two equal groups:**
416 ***Stable actor observers* performed PRE-OBSERVATION trials, then observed a stable actor balance**
417 **upon the moving sled (OBSERVATION trials), before performing the POST-OBSERVATION trials.**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

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Figure 2: Actor's sway in OBSERVATION trials



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

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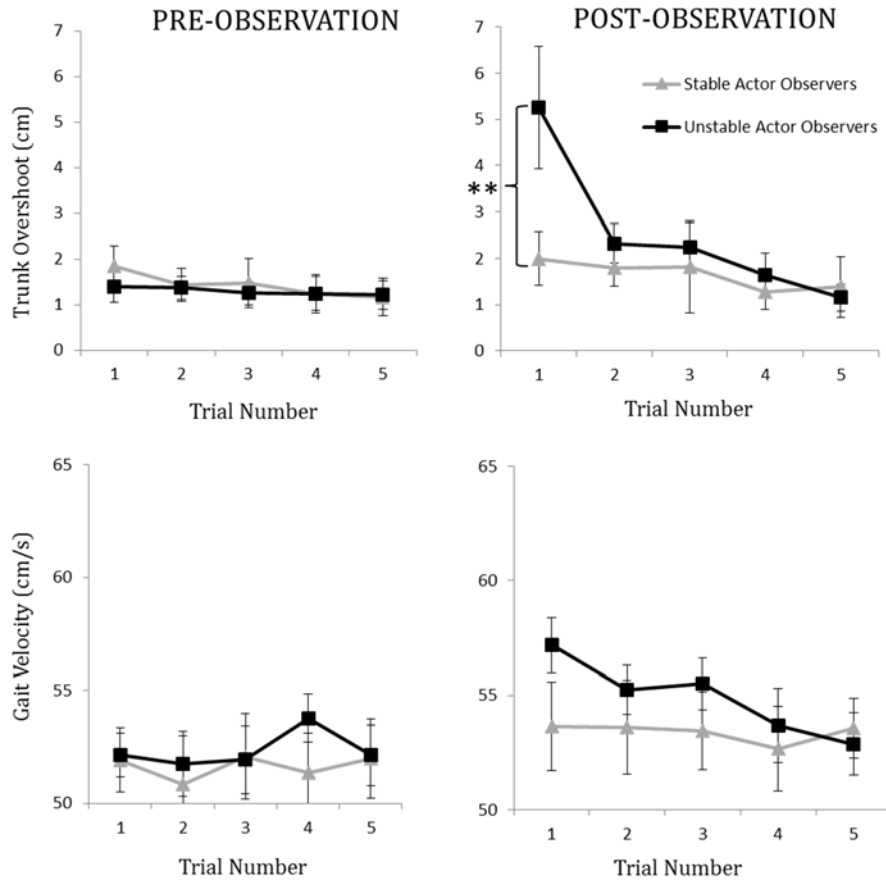


Figure 3: LAE for Stable and Unstable actor observers. Group mean (+/- standard error) data for Stable actor observers (triangles) and Unstable actor observers (crosses). The horizontal axis shows the trial number (1-5). The Unstable actor observers produced a significant aftereffect in both increased 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, ** $P=0.004$.

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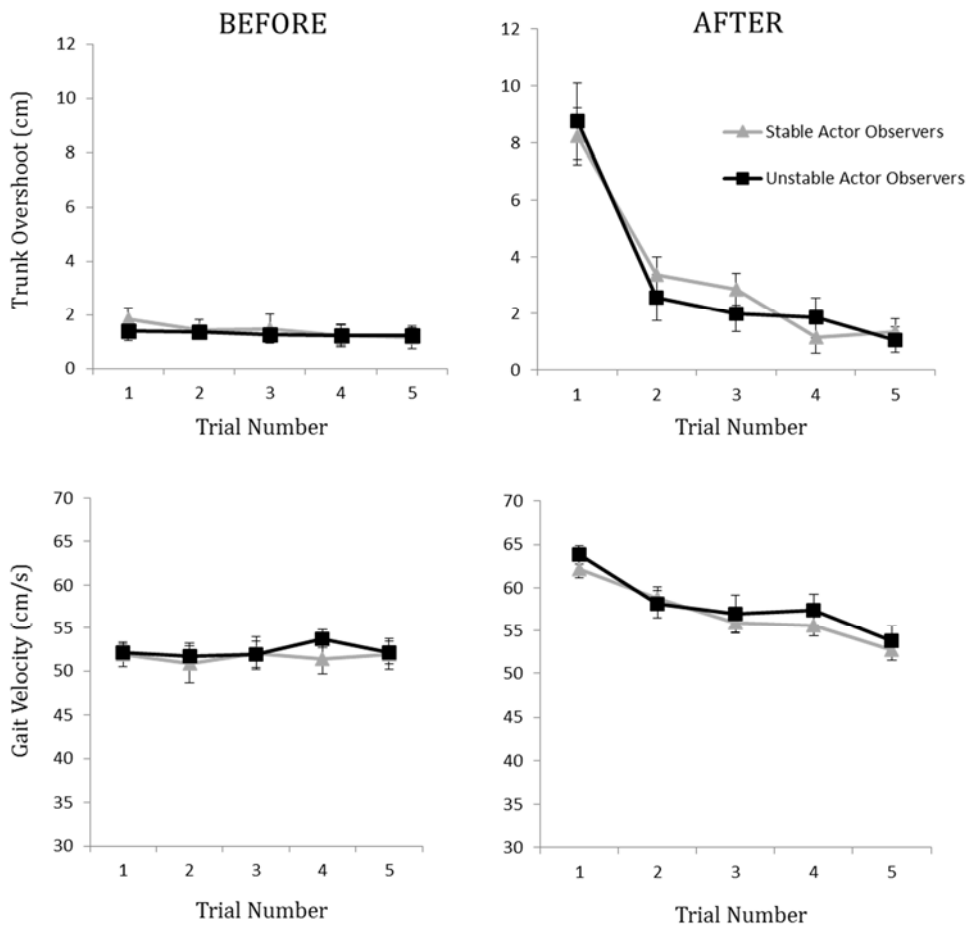
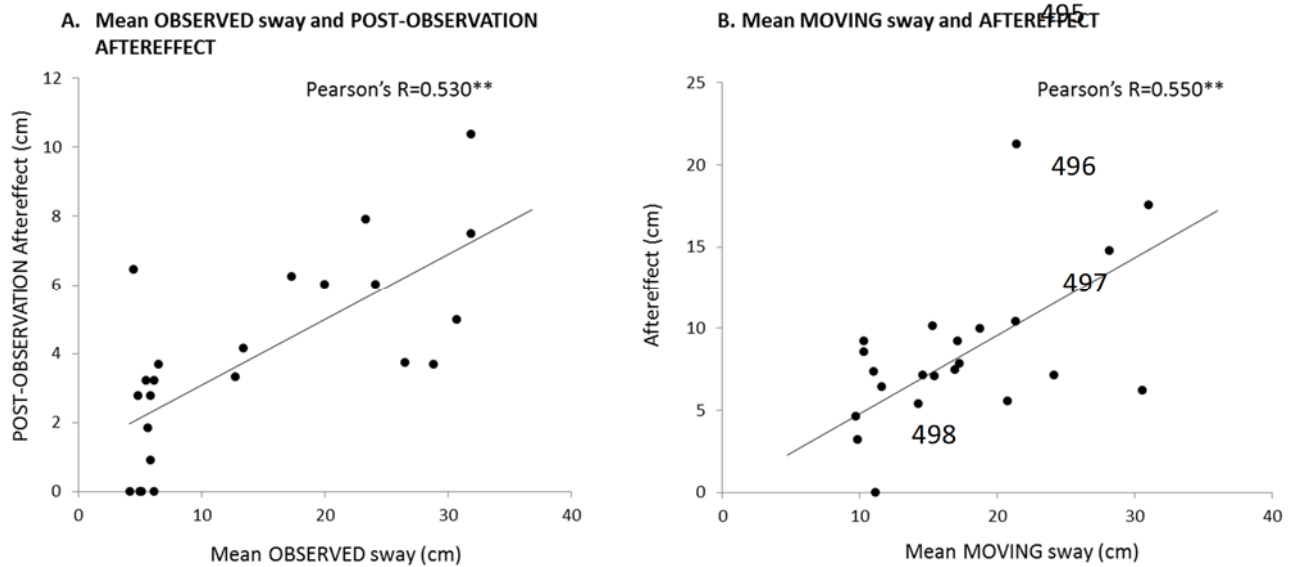


Figure 4: Performance on the standard broken escalator paradigm. Mean (+/- standard error) group data of BEFORE (left) and AFTER (right) trials for Stable actor observers (triangles) and Unstable actor observers (crosses) after physically performing the MOVING trials. The data show that both groups have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



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502 **Figure 5: Associations between observation aftereffects and conventional aftereffects. (A)**

503 **Correlation between the size of observed actor's sway in the mean OBSERVATION trials (average 5**

504 **trials) and the size of the trunk overshoot aftereffect (POST-OBSERVATION trial 1) for the Stable**

505 **actor observers and Unstable actor observers. The figure shows that the size of the observed**

506 **mean trunk sway in the OBSERVATION trials correlates with the size of the locomotor aftereffect**

507 **(B) Correlation between the size of sway in the mean MOVING trials (average 5 trials, physically**

508 **performed, conventional paradigm) and the size of the trunk overshoot aftereffect (AFTER trial 1)**

509 **for the Stable actor observers and Unstable actor observers. The figure shows that the size of sway**

510 **in the mean MOVING trials correlates to the size of the locomotor aftereffect. Together Figures A**

511 **and B show that the size of the trunk overshoot aftereffect correlates to the level of sway in the**

512 **MOVING trials, regardless of whether it is observed (A) or performed (B).**

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