Locomotor adaptation is modulated by observing the actions of others

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Locomotor adaptation is modulated by observing the actions of others. J Neurophysiol 114: 1538–1544, 2015. First published July 8, 2015; doi:10.1152/jn.00446.2015.—Observing the motor actions of another person could facilitate compensatory motor behavior 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 onto 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 behavior to minimize movement errors and improve motor skills through social cues, although further neurophysiological studies are required to support this theory. These data suggest that merely observing the gait of another person in a challenging environment is sufficient to generate appropriate postural countermeasures, implying the existence of an automatic mechanism for adapting locomotor behavior.

In situations in which 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 stabilize 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 that then occur automatically in an unperturbed environment. Although an aftereffect suggests that adaptive learning has taken place, to date there are 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 LAE 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 men, 9 women; mean age = 24.4 yr, SD = 4.0 yr, age range 18–42 yr) took part in the main study and were divided into three equally sized groups of 12. Participants provided written informed consent and were naive 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 were measured with a Fastrack tracking system (Polhemus) 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.

ADAPTIVE BEHAVIORS ARE NECESSARY to meet the pressures of physical and social environments (Kummer 2006). Current theories suggest that such patterned forms of behavior in both humans and animals can be learned 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 naive observers (Brown et al. 2009). Observing another person slip during platform perturbations can also improve postural stability when naive observers perform the same task (Bhatt and Pai 2008). However, it is unknown whether such learning-based behavior extends to locomotion.
Procedure. The research question was to establish whether subjects (observers) would develop the broken escalator LAE simply by observing an actor perform the locomotor task.

In the main investigation, the experimental sequence comprised three phases: Preobservation (5 trials, stationary sled), Observation (5 trials, observing an actor balance on moving sled), and Postobservation (5 trials, stationary sled, LAE phase) trials in this order (Fig. 1).

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

In the Observation trials, observers sat and viewed the actor from a distance of 2 m 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 forward 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 infrared light beam. After breaking the beam, the sled moves after a 600-ms delay, traveling a distance of ~3.7 m in 4.2 s; maximum velocity of 1.4 m/s was achieved after 1.3 s, 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 (Fig. 2). This was to assess group differences when viewing a stable versus an unstable actor. The actor’s stability between the two conditions differed significantly (paired t-test $P < 0.001$; see Fig. 2). The same actor was used for both groups to perform all five 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 naive 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 Postobservation trials, the actor dismounted from the platform and observers were given the following 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 s, after which subjects returned to the original starting position.

To evaluate whether the effects observed were due to intergroup 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 (5 trials, stationary sled, LAE phase) trials in this order (see Fig. 2 in Kaski et al. 2012).

Data analysis. Trunk overshoot in the Preobservation and Postobservation trials was defined as the maximum forward deviation of the trunk relative to the mean final trunk position in the last 3 s of the trial. In Observation trials, trunk sway was measured as the maximum backward-to-forward (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-s period prior to foot-sled contact. Preobservation trials 3–5 were averaged and used in the analyses as baseline performance. In the Postobservation trials, trunk overshoot and gait velocity in trial 1 are referred to as an aftereffect.

We examined the data across groups with a 2 × 2 repeated-measures ANOVA with factors (Preobservation, Postobservation) 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 Postobservation phase with Preobservation (i.e., the mean of Preobservation trials 3–5). Where appropriate, post hoc tests and correlations were performed; details are explained below. Paired statistics were corrected for multiple comparisons where appropriate.

RESULTS

As seen in Fig. 3, top right, trunk overshoot in Postobservation trial 1 was significantly larger in the Unstable Actor Observers compared with 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 × 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 Postobservation trial compared with baseline (P = 0.002), demonstrating a trunk aftereffect in this group, but not in the Stable Actor Observers (P = 0.1).

![Fig. 3. Locomotor aftereffect (LAE) for Stable and Unstable Actor Observers: group mean (±SE) data for Stable Actor Observers and Unstable Actor Observers. x-Axis shows the trial number (1–5). The Unstable Actor Observers produced a significant aftereffect in both increased trunk overshoot and gait velocity in Postobservation trials. Trunk overshoot in the first Postobservation trial was also significantly larger in the Unstable Actor Observers compared with Stable Actor Observers. **P = 0.004.](http://jn.physiology.org/Downloadedfrom)
Gait velocity in Postobservation trial 1 was faster in the Unstable Actor Observers compared with the Stable Actor Observers, though only of trend-level significance (P = 0.08), as shown in Fig. 3. 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 × 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 Postobservation trial compared with 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 = 1.44 cm, SD = 1.47; P = 0.38) or gait velocity aftereffect (mean = 54.3 cm/s, SD = 5.47; P = 0.44) in the first Postobservation trial compared with baseline.

To test whether the effects observed here were due to group differences in locomotor performance and adaptation, we retested 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 2 × 2 ANOVA showed no significant main effect of group on trunk sway or gait velocity (Fig. 4). As expected, both groups had a significant trunk overshoot and gait velocity aftereffect (P ≤ 0.002; see Fig. 4). 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 after the conventional experiment compared with observation.

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 Fig. 5A), 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 he or she exhibits during the Moving trials (Green et al. 2010). Thus, in the conventional broken escalator paradigm, the size of the aftereffects across the groups was positively correlated with the magnitude of their own sway in the Moving trials (Pearson’s R = 0.550, P = 0.008), shown in Fig. 5B. Using a Fisher r-to-z transformation, we found no significant difference between the two correlations (P > 0.95, 2-tailed).

The correlation between the size of the trunk overshoot aftereffect and the observed gait velocity during the Observation trials showed a trend toward 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).

**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 LAE. Remarkably, we found that the observer’s locomotor plan is updated in proportion to the size of observed motion, inducing an effect similar 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 behavior of others is a critical avenue for developing and refining our motor programs.

Previous studies have shown that observing the behavior 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. 2003, 2007; 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 has 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 because of a sudden platform perturbation, subjects performing the same experimental paradigm had lower slip displacement and velocity and greater postslip stability compared with a naive 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 that automatically adapts motor behaviors to minimize 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 with 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 2008, 2009). 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 behavior 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 behavior exhibited within a society is an adaptive strategy (Boyd and Richerson 1985). This convergence toward the most prevalent behavior, 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 onto 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 behavior 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 present 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. Second, 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 generalize to a different locomotor context?

These findings raise a number of questions regarding the observation of locomotor tasks that 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 aging 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 LAE, 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 behavior in response to threats or hazards experienced by other members of a social group. These data suggest that merely observing the gait of another person in a challenging environment is sufficient to generate appropriate postural countermeasures, implying the existence of an automatic mechanism for adapting locomotor behavior.

REFERENCES


