THE MOVING PLATFORM AFTEREFFECT:
LIMITED GENERALISATION OF A LOCOMOTOR
ADAPTATION

RF Reynolds\textsuperscript{1} & AM Bronstein\textsuperscript{2}

\textsuperscript{1} Sobell department of Motor Neurophysiology and Movement Disorders
Institute of Neurology
8-11 Queen Square
London WC1N 3BG, UK

\textsuperscript{2} Academic department of Neuro-otology
Division of Neuroscience and Psychological Medicine
Imperial College School of Medicine
Charing Cross campus
St Dunstans Road
London W6 8RF, UK

Corresponding author:
A.M. Bronstein (address as above)
Telephone: +44 (0) 208 8467523
Fax: +44 (0) 208 8467577
E-mail: a.bronstein@imperial.ac.uk

Running head: Generalisation of gait adaptation.
Abstract

We have recently described a postural aftereffect of walking onto a stationary platform previously experienced as moving, which occurs despite full knowledge that the platform will no longer move. This experiment involves an initial baseline period, when the platform is kept stationary (BEFORE condition), followed by a brief adaptation period when subjects learn to walk onto the platform moving at 1.2m/s (MOVING condition). Subjects are then clearly warned that the platform will no longer move, and asked to walk onto it again (AFTER condition). Despite the warning, they walk towards the platform with a velocity greater than that observed during the BEFORE condition, and a large forward sway of the trunk is observed once they have landed on the platform. This aftereffect, which disappears within three trials, represents dissociation of knowledge and action. In the current set of experiments, to gain further insight into this phenomenon we have manipulated 3 variables, the context, location and method of the walking task, between the MOVING and AFTER conditions, to determine how far the adaptation will generalise. It was found that when the gait initiation cue was changed from beeps to a flashing light, or vice-versa, there was no difference in the magnitude of the aftereffect, either in terms of walking velocity or forward sway of the trunk. Changing the leg with which gait was initiated, however, reduced sway magnitude by approximately 50%. When subjects changed from forward walking to backward walking, the aftereffect was abolished. Similarly, walking in a location other than the mobile platform did not produce any aftereffect. However, in these latter two experiments, the aftereffect reappeared when subjects reverted to the walking pattern used during the MOVING condition. Hence, these results show that a change in abstract context had no influence, whereas any deviation from the way and location in
which the moving platform task was originally performed profoundly reduced the size of the aftereffect. Although the moving platform aftereffect is an example of inappropriate generalisation by the motor system across time, these results show that this generalisation is highly limited to the method and location in which the original adaptation took place.

**Keywords:** Gait adaptation, Aftereffect, Generalisation.
Introduction

Acquisition of complex new motor skills is a remarkable property of the central nervous system. An important aspect of motor control is the ability to use these motor skills in different situations from those in which they were learned. Depending upon the nature of the task, generalisation may occur between different behaviours (Conditt et al., 1997), different contexts (Gandolfo et al., 1996), and across time (Goodbody & Wolpert, 1998) and space (Shadmehr & Moussavi, 2000). The extent to which a skill generalises can reveal the nature of the adaptation process itself. Generalisation may be detrimental as well as beneficial, and presumably the goal of the motor system should be to express a specific skill only in the appropriate circumstances.

This study concerns generalisation of locomotor adaptation. Previous studies on this topic have examined transfer of adaptive responses between legs and between different methods of locomotion. They offer mixed results. With regard to inter-limb transfer, Van Hedel et al. (2002) recently showed that learning to step over an obstacle with one leg is a skill which transfers to the other leg. However, hopping on a treadmill (Anstis, 1995) and stepping on a horizontally rotating platform (Earhart et al., 2002a) both produce aftereffects when attempting to hop on the spot and walk in a straight line, respectively, but only in the adapted leg. With regard to transfer of adaptation between methods of locomotion, it has been shown that the rotating platform adaptation transfers from stepping to hopping (Earhart et al., 2002b), and from forward walking to backward walking (Earhart et al., 2001). Conversely, learning to walk on a split belt treadmill with one leg moving faster than the other, does not transfer to the mirror condition (Prokop et al., 1995).
We have previously described an aftereffect of walking onto a moving platform (Reynolds & Bronstein, 2003). This aftereffect is analogous to the ‘broken escalator phenomenon’: anecdotal evidence suggests that many people experience an odd sensation of sway when walking onto a broken escalator even though they can see that the escalator is not going to move. In the laboratory, we used a paradigm where subjects initially learned to walk onto a moving platform and were then told that it would no longer move. Despite the warning, there was a clear aftereffect which most subjects reported as being similar to the broken escalator phenomenon. This aftereffect consists of an inappropriately high walking velocity and a large subsequent forward sway of the trunk when subjects walk onto the stationary platform previously experienced as moving. It occurred despite full knowledge that the platform will no longer move, and so represents dissociation between knowledge and action.

The purpose of the current study is to determine if this aftereffect generalises across different situations. Is it specific to the conditions during the adaptive period, or will it still occur if these conditions are altered? Specifically, we investigate whether the aftereffect occurs when the method, context and location of the walking task are changed between the MOVING condition, when subjects adapt to the moving platform, and the subsequent AFTER condition, when subjects are clearly warned that the platform will no longer move. In one experiment, the method of locomotion is altered by asking subjects to start walking with a different leg, thus changing the leg that strikes the platform. In another, a greater alteration in locomotion method is introduced, consisting of a transition from forward to backward walking. Finally, the location of walking is changed by asking subjects to start from a different position, thus confining the walking task to the fixed platform.
By examining the extent to which the aftereffect generalises, these experiments are intended to shed light upon the nature of the moving platform adaptation itself: Does the adaptation occur in limb, joint-based coordinates, or in an external, platform-based frame of reference? One would expect minimal generalisation across different methods of locomotion if the former is true, and maximal generalisation if the latter is true. The reverse pattern would be expected for generalisation across space: if the adaptation occurs in joint-based coordinates, one would expect it to generalise when the walking task is performed in other locations. In contrast, if it occurs in platform-based coordinates, it should be specific to the mobile platform, and one would not expect to observe the aftereffect when subjects walk elsewhere.

However, it is also possible that the pattern of generalisation could be affected by sensory cues not directly related to the task itself. Subjects may make implicit associations between such cues and the movement of the platform, perhaps independently of their declarative knowledge of the state of the platform, in a process akin to classical conditioning. To address this issue we performed an additional experiment where abstract sensory cues were manipulated between the MOVING and AFTER conditions. This consisted of changing the gait initiation signal from an auditory to a visual cue, or vice-versa, while the walking task remained unchanged.
Methods

Subjects

Ethical approval was given by the local committee. Fifty-four subjects gave informed consent to participate in the study (mean age=24, range=18-41). Eleven subjects were assigned to two each of groups for the leg change experiment. For the abstract context experiment, nine subjects participated in each group. Seven performed the Backward-walking experiment and another seven did the Fixed-platform experiment. All subjects were naïve with regard to the purpose of the experiments.

Apparatus

A mobile sled was powered by two linear induction motors, and moved with a plateau velocity of 1.2m/s (figure 1). The sled was 172cm long and 58cm wide. The distance between the subjects' starting position (as defined by the anterior boundary of the foot) and the front end of the fixed platform was 55cm. Sled movement was triggered by gait initiation by means of an infrared light switch at shin level. When subjects started walking, their leg passed through the beam, triggering the sled to move forward, in the same direction as subject progression. The second step takes the subject onto the sled, where they stop walking. Hence, the task consisted of a total of two steps. During MOVING trials, sled movement was initiated approximately 600ms before subjects made foot contact with it. The duration of sled movement was 4.2s. Sagittal trunk position was measured using a Fastrak electromagnetic tracking device (Polhemus, VT, USA). The sensor was placed over vertebral area C7 on the back, and the transmitter was attached to the sled. A second sensor was earth-fixed so that the movement of the sled could be subtracted when calculating trunk velocity. Step timing information was given by force sensors (Flexiforce, Tekscan, MA, USA)
placed inside the shoe under the first metatarsal-phalangeal joint and the heel. An accelerometer attached to the sled was used as a secondary corroborating measure of foot-sled contact. All signals were sampled at 250Hz.

**Protocol**

All subjects were shown the sled movement before the start of the experiment, so that they knew what to expect. There were three conditions in all the experiments, as follows: An initial baseline period during which the sled was kept stationary (BEFORE condition). This was followed by the MOVING condition, where subjects walk onto the moving sled. They were then explicitly warned that the sled would no longer move and asked to walk onto it again (AFTER condition). The purpose of all the experiments was to measure the presence and magnitude of any aftereffect which may occur. Therefore, the AFTER trials, and particularly the first AFTER trial, were the primary subject of analysis.

*Leg Change Experiment*

The protocols used for the four experiments are shown in Table 1. In the Leg Change Experiment, two groups of 11 subjects were compared. Both groups started walking with one leg during the BEFORE trials and changed to the other leg for the MOVING condition, when they adapted to the moving platform. Then, one group of subjects continued to start walking with the same leg as they had used during the MOVING condition. The other group changed leg, starting with the same leg as they had done during the BEFORE condition. For example, one subject might be given the order left, right, right, whereas a subject in the group who change legs between MOVING
and STATIONARY conditions might be given the order left, right, left. The two groups were further subdivided in order to remove any potential leg-specific effects.

Abstract Context Experiment

For the context experiment, the same experimental design was used, but instead of a change in leg, subjects experienced a change in the gait initiation cue between the MOVING and AFTER conditions. The two cues that were used consisted of three beeps or three flashes of a light bulb. The light bulb was situated just forward of, and to the side of the subject, at waist level. The flashing light was bright enough so that subjects did not have to look directly at it or even specifically attend to it in order to notice it flashing. The timing and duration of the beeps and the lights were exactly the same.

In both the Leg Change and Abstract Context experiments, subjects were told in advance that sometimes they would be asked to start walking with a different leg, or after a different cue, during the experiment. They were not told in advance when this would happen, however, and so they could not simply associate movement of the platform with the particular leg or cue before the experiment started. Although they were told of the order of the trials in advance (i.e. BEFORE, MOVING and AFTER conditions), it was also explained to them that they would be warned when the sled would be moving or stationary and that they did not need to remember this in advance. These instructions were given in order to make it less likely that subjects would feel the necessity to make conscious associations between the movement of the platform and the particular leg or context, since they did not need to predict whether it
would move or not. This made it more likely that any associations that subjects make during the experiment would be implicit rather than conscious.

*Fixed platform experiment.*

During the fixed platform walking, subjects walked in exactly the same way as when walking onto the sled, but sometimes their walking was restricted to the fixed platform (see figure 1). There were five fixed-platform trials during both the BEFORE and AFTER conditions. Obviously, the MOVING condition necessitated walking onto the sled. The first trials in the AFTER condition were fixed-platform trials, in order to see if the aftereffect would occur in this situation. Subjects then reverted to walking onto the sled five times to determine if this would cause further presentation of the aftereffect.

*Backward Walking Experiment*

The Backward Walking experiment followed the same design as the Fixed-platform experiment (see Table 1). Instead of walking on the Fixed platform, however, during the BEFORE and AFTER conditions subjects were asked to walk backwards onto the sled for five trials.

*Analysis*

For each trial, walking velocity was derived from the Fastrak trunk displacement signal. It was calculated as the mean velocity in a 0.5s time-window before foot-sled contact, which occurs at the second step after gait initiation. Foot-sled contact was derived from the force sensors worn inside the shoe. The signal from the accelerometer attached to the sled was used to confirm step timing. Forward sway was
calculated for all trials where the sled was stationary, as the maximum forward deviation of the trunk compared with final stance position (see trunk ‘overshoot’ in Figure 2). Forward sway during AFTER-trial 1 was normalised by subtracting the mean BEFORE value for each subject. Since the data were sometimes not normally distributed, or because distributions were of different sizes, non-parametric statistics were used throughout. This consisted of two-tailed Mann-Whitney tests for comparing groups, and one-tailed Wilcoxon signed ranks tests for within-subject comparisons. P<0.05 was considered significant. All graphs and numbers reported in brackets show standard errors of the mean unless otherwise stated.

Results

As a result of walking onto the moving sled, subjects experienced an aftereffect during the AFTER condition when the sled was kept stationary, in spite of the warning at the start of the trial. A typical example of this aftereffect, caused by adapting to the moving platform, is shown in figure 2 where AFTER trial 1 and 2 are compared with BEFORE values. This subject participated in the leg-change experiment, in the order left, right, right. A clear overshoot can be seen in the trunk displacement trace, indicating a forward sway of 15.0cm. By the second AFTER trial, trunk displacement returns to within $\pm 1.96$ s.d. of BEFORE-baseline values. This subject subsequently confirmed, as they all did, that he had heard and understood the verbal warning that the platform would no longer move. Results for each of the four generalisation experiments are now reported separately.
Leg Change Experiment

Figure 3 shows the results of the leg change experiment. One group changed their start leg between MOVING and AFTER conditions (‘change’), while the other used the same leg (‘same’). Mean walking velocities during baseline BEFORE trials were 0.66 and 0.55 m/s for these two groups, respectively (Figure 3A). Since subjects were free to walk at their own preferred pace, this difference is not particularly surprising. During the MOVING trials, however, both groups walked at a similar pace, as imposed by the movement of the sled. The difference became apparent again in the AFTER condition. During AFTER trial 1, both groups showed a significant increase in velocity above mean BEFORE values, meaning that the preceding MOVING trials induced an increase in walking velocity which partially persisted into the AFTER trials. These increases were 0.09 m/s (+0.021) for the ‘change’ group and 0.08 m/s (+0.029) for the ‘same’ group. Within three trials, this returned back to baseline levels for both groups. There were no significant differences in walking velocity between the two groups that could not be accounted for by the initial difference in the baseline value.

Figure 3B shows Forward Sway for both groups during trials where the sled was stationary (i.e. BEFORE and AFTER; not applicable to MOVING trials). Mean BEFORE values were almost identical: 1.38 cm (+0.06) and 1.40 cm (+0.10) for ‘same’ and ‘change’ groups, respectively. During AFTER trial 1, the aftereffect can clearly be seen in both groups, with forward sway values of 9.20 cm (+1.50) for ‘same’ and 5.20 cm (+2.09) for ‘change’. For statistical comparison of this effect, these values were normalised with respect to the mean BEFORE value for each subject, yielding 7.82 cm (+1.46) for ‘same’, and 3.81 cm (+1.94) for ‘change’. These
values are significantly different (U=28, p=0.034). Consideration of individual subject results reveals greater difference between the two groups (see figure 3D). In the ‘change’ group, 8 of the 11 subjects did not have any considerable aftereffect (i.e. greater than 2 S.D. of baseline sway), and the mean value of 3.81cm resulted from the remaining three subjects who did experience an aftereffect. It should be noted that these three subjects did not have any obvious distinguishing common factor which might set them apart from the other subjects in the group, such as being taller, older or walking faster. In contrast to the ‘change’ group, all but one of the 11 subjects in the ‘same’ group showed an increase in sway ranging from 3 to 15 cm. These results show that changing the start leg between the MOVING and AFTER conditions caused an attenuation of the mean aftereffect size, and also reduced the likelihood of each subject experiencing any aftereffect.

Abstract Context Experiment

This experiment followed the same design as the Leg Change experiment, except that the change was in the cue used to tell the subject to start walking (either three beeps or three flashes of a light). Both groups similarly displayed an aftereffect in the form of an increase of walking velocity during AFTER trial 1, although there were no significant differences in walking velocity between the two groups in any of the three conditions (Figure 4A).

Both groups also displayed an aftereffect in terms of Forward Sway, shown in figure 4B. The values during AFTER trial 1 were similar, being 13.27cm (±3.25) for ‘same’ and 12.38cm (±2.98) for ‘change’. This gave Normalised values of 11.59cm (±3.63) for ‘same’, and 9.90cm (±2.84) for ‘change’ (Figure 4C). These values were not
different, statistically (U=38, p=0.863). A glance at the histograms also tells us that individual variation in normalised forward sway was similar in both groups, with the majority of subjects in both groups showing an aftereffect (figure 4D). These results show that a change in abstract context between the MOVING and AFTER conditions had no influence upon the magnitude of the aftereffect.

**Fixed-platform Experiment**

During the fixed-platform experiment, the BEFORE and AFTER conditions included five trials in which subjects only walked on the fixed platform. Figure 5A shows Walking Velocity during the Fixed Platform experiment. When the walking task was confined to the fixed platform, this did not affect walking velocity as compared with walking onto the sled, either during the BEFORE or AFTER conditions. During the AFTER condition, there was no increase in walking velocity above BEFORE levels which would be indicative of an aftereffect. This was true both during the fixed-AFTER trials and the sled-AFTER trials.

The results are similar for Forward Sway (Figure 5B). There is no increase in Forward Sway during fixed-AFTER trial 1. However, when reverting to walking onto the sled (sled-AFTER trial 1), three of seven subjects displayed a clear increase in sway above baseline (sled-BEFORE) of 4.47cm, 7.03cm, and 5.53cm. This led to a group mean forward sway of 3.14 cm during sled-AFTER trial 1. This increase was not quite significantly above the mean sled-BEFORE value of 1.49cm (z=1.52, p=0.064).
Backward-Walking Experiment

During this experiment the BEFORE and AFTER conditions included five trials where subjects walked backwards onto the sled. Otherwise, the experimental design was the same as the Fixed Platform experiment.

Overall, the results are similar to those of the Fixed Platform experiment (Figure 6). There were no significant changes in walking velocity during the BEFORE condition (Figure 3.9A). However, during the backward-AFTER condition, it can be seen that there is a small dip in walking velocity in the first trial, relative to the subsequent four trials. Indeed, a Friedman’s rank test reveals a significant effect of trial number upon walking velocity during the backward-AFTER condition (Chi-squared=9.58, p=0.048). The reason for this difference is not apparent, although it may conceivably be due to cautiousness when reverting to backward walking. There was no increase in forward sway during backward-AFTER trial 1. However, 4 of seven subjects did show a forward sway greater than 3cm (8.04, 3.21, 5.70 & 14.60cm) when they reverted to forward walking onto the stationary sled. This resulted in a mean Forward Sway of 5.11cm during forward-AFTER trial 1, significantly greater than the baseline forward-BEFORE mean value of 1.43cm (z=2.197, p=0.014).

Hence, like the fixed-platform experiment, no subjects showed a large forward sway when they walked differently than during the MOVING trials. When they reverted to walking in the same manner as during the MOVING trials, however, some subjects did show a large sway indicating that the aftereffect had been stored for subsequent release.
Discussion

In a series of experiments we have investigated the extent to which the moving platform aftereffect generalises to different situations. This involved introducing changes between the moving condition, where subjects adapted to the moving platform, and the subsequent stationary condition, where subjects were warned that the platform would no longer move. When the gait initiation cue was changed from beeps to a flashing light, or vice-versa, there was no reduction in the magnitude of the aftereffect as measured by the degree of forward sway or walking velocity, compared with a control group. However, when the leg with which gait was initiated was changed, the forward sway response was absent in most subjects. When subjects were asked to change from forward to backward walking, it was abolished in all subjects. When the walking task was performed somewhere other than the mobile platform (restricted to the fixed platform), there was also no aftereffect. An interesting additional finding was that some subjects in the backward-walking and fixed platform experiments exhibited a weak aftereffect when subsequently asked to walk onto the stationary platform again in the same way that they had done so during the MOVING condition. This shows that the adaptive behaviour had been stored for later release.

Location and Method of walking are crucial for the Aftereffect

Some basic conclusions can immediately be made on the basis of these results. Firstly, it is clear from the abstract context experiment that subjects did not learn, either consciously or implicitly, to associate their behaviour with abstract event-related cues. This is despite the fact that there was a highly salient change in the gait initiation signal between the MOVING and the AFTER conditions. This means that
there was no element of classical conditioning involved in learning the walking task. This agrees with previous findings which showed that subjects could not use abstract cues to help them switch between two adaptive motor tasks, at least during the early stages of motor learning (Gandolfo et al., 1996). Secondly, the expression of the adaptive behaviour used to walk onto the moving platform was highly specific to the manner in which people walked. When they changed the leg with which they started walking the aftereffect was much reduced, and when they changed to backward walking the aftereffect was abolished. Thirdly, the adaptive behaviour was highly specific to the location, because the aftereffect did not occur when subjects were asked to walk anywhere other than onto the sled. Therefore, in order to fully elicit the aftereffect, two conditions must be met: the subject must walk onto the same surface that was previously experienced as moving, in the same way that they walked onto it when it was moving. If conditions deviate from these two prerequisites, it seems as if the motor system is no longer ‘tricked’ into expressing the behaviour which was appropriate for the moving platform and which is no longer appropriate.

There are no subconscious associations between abstract cues and platform movement.

One might hypothesise that the broken escalator phenomenon may be the result of associations that we make between sensory cues in the environment and movement of the escalator. Here, the fact that a change in the gait initiation cue had no influence upon the size of the aftereffect would suggest that such an association is not responsible for the experimental aftereffect. This finding has two implications: Firstly, it is of interest in itself, because it shows that there is no process akin to classical
conditioning occurring, which could have been responsible for the aftereffect.
Secondly, it has an implication for the interpretation of the other results reported here:
The other experiments involved introducing various changes in the task between the
MOVING and AFTER conditions. These changes caused loss or attenuation of the
aftereffect. It was possible that this could have been due to abstract sensory cues,
rather than the changes in the walking task per se. For example, by changing the leg
with which one initiates gait, one not only alters the effector used to perform the task,
but one also provides a simple sensory cue which could signal change. If, during the
MOVING trials there was subconscious association between the movement of the
platform and such cues, then a change in this cue could potentially cause loss of the
aftereffect. The null result observed in the abstract context experiment shows that the
marked effect we observed when the method of walking was changed cannot be
attributed to such non-specific subconscious associations. Instead, it must be directly
related to the performance of the task.

Of course, it should be noted that the broken escalator phenomenon and our
experimental aftereffect may not be entirely analogous. One obvious difference is the
timescale of adaptation: people may spend years walking onto escalators, whereas the
experiment involved only relatively brief exposure to the moving platform. Hence the
potential for forming subconscious abstract associations may well exist if the
adaptation period is sufficiently long.
The Aftereffect is not due to stereotyped behaviour

It is conceivable that the moving platform aftereffect is simply the consequence of the motor system becoming locked or trapped into a stereotypical behaviour due to prolonged repetition of the same walking task. However, the results from the backward-walking and fixed-platform experiments suggest that this is not the case. During the backward-walking experiment subjects walked forwards during the MOVING condition and then backwards in the AFTER condition, displaying no aftereffect. When they subsequently walked forwards onto the stationary platform, three of them displayed a small but significant aftereffect. This means that an intervening period of different motor activity was not sufficient to cause ‘washout’ of the aftereffect. During the fixed-platform experiment, subjects walked in the same way during the AFTER condition as they had done immediately before during the MOVING condition and yet there was no aftereffect. Also, the aftereffect reappeared when they reverted to walking onto the sled. Hence, given these findings, simple stereotyped behaviour seems unlikely as an explanation.

Although we showed a small degree of transfer of the aftereffect to the mirror condition, when the gait initiation leg was changed, it did not transfer from forward to backward walking. The reverse situation was not investigated because it was deemed unsafe to walk backwards onto the moving platform. This raises the possibility that the aftereffect did not present itself during backward walking due to basic differences in the method of locomotion, rather than being due to a learning phenomenon. However, the results show that for three subjects the aftereffect was stored up during the backward-walking phase for subsequent release when they walked forward again.
Therefore it is unlikely that the aftereffect was simply masked during the backward walking trials.

**Situational/Geographical context is crucial**

The interesting and unique aspect of the moving platform aftereffect is that it occurs despite full knowledge that the platform will no longer move. It therefore represents a dissociation of knowledge and action. Although this knowledge does reduce the extent of generalisation as compared with an unpredictable change, we have previously shown that there is no active attempt to suppress the aftereffect as a result of the warning of stationarity (as shown by no increase in lower-leg muscle cocontraction which would be indicative of cautious behaviour; Reynolds & Bronstein, 2003). In the current experiments, one crucial factor in eliciting the aftereffect is location; the subject must walk onto the sled for it to occur, and if he/she walks somewhere else in the room, it doesn't. Intuitively, this might seem obvious. For example, the analogous effect which many people report when walking onto a broken escalator only occurs in that specific context where there is an escalator. It clearly does not transfer to other situations. However, this finding introduces a potential paradox. On the one hand, the aftereffect occurs *despite* the fact that the ‘high-level’ declarative brain is aware that the platform will not move. On the other hand, the aftereffect does not occur in different places *because* the declarative brain is aware that you are in a different place. Therefore the conscious, declarative CNS seems capable of suppressing the incorrect motor response in one situation (when you know that you're not walking onto the sled), but not in another (when you know that the sled will not move). An answer to this paradox may simply be that ‘situational’ or...
'geographical' context (purely sensory based) is far more salient information than an instruction from an experimenter (cognitively based).

**The nature of the adaptation determines the extent of transfer**

Previous studies examining generalisation of gait adaptation show mixed results. Van Hedel et al (2002) found that obstacle avoidance during gait was a skill that readily transferred to the opposite leg. Anstis (1995) reported an aftereffect of hopping on a treadmill which manifested as a forward drift when subjects subsequently attempted to hop on the spot. This aftereffect did not transfer to the opposite leg. Similarly, Earhart et al (2002a) showed that the gait trajectory aftereffect which occurs after prolonged stepping on a rotating surface does not transfer between legs. Also, split belt treadmill locomotion, where one leg is moving faster than the other, is a skill which does not transfer to the mirror condition (Prokop et al., 1995). In the current experiment we have shown very limited transfer of the moving platform aftereffect to the mirror condition (i.e. when subjects changed the leg with which they start walking). Van Hedel et al. (2002) attributed the discrepancy between their own finding and other experiments as possibly being due to differences in the way the CNS adapts to tasks involving leg flexor verses leg extensor muscles. They argued that leg flexor tasks may be more likely to generalise because the flexor muscles display less bilateral coupling than the extensors. The moving platform task in the current study predominantly involves the leg extensor muscles, since greater propulsion forces are required when stepping onto a forward moving surface. However, since we have shown only limited transfer of the aftereffect between legs, our results neither support nor contradict this hypothesis. Another factor which may affect transfer of adaptation is the relative contribution of proximal versus distal
musculature: if the trunk muscles predominate over leg muscles in coping with the postural perturbation, then perhaps there would be more transfer of skill between legs. Since only 3 of 11 subjects showed a considerable aftereffect when they changed leg, then this low level of transfer would suggest that leg muscles are primarily involved.

However, it seems more likely that differences between these various findings are due to more basic differences in methodology. In particular, one cannot directly compare adaptation per se with the aftereffects of adaptation if the motor task is not the same in both conditions. Indeed, if the task has been changed, the experiment is studying generalisation of adaptation by definition, which is the subject of this study. The other major difference concerns the nature of the adaptation process itself. Running on a treadmill results in an aftereffect (Anstis, 1995) but does not involve the acquisition of a new skill since subjects were presumably already capable of running on a treadmill. Therefore the aftereffect is likely to be due predominantly to sensory/perceptual adaptation rather than motor learning (Durgin & Pelah, 1999), and this is confirmed by the anomalous perception that subjects have of jogging on the spot when in fact they are moving forward. Walking on a split belt treadmill or rotating surface also results in perceptual changes (Jensen et al., 1998; Gordon et al., 1995). The fact that these aftereffects do not generalise to opposite legs is consistent with a specific sensory channel becoming recalibrated. For example, when hopping on a treadmill, proprioception signals from that particular leg may be recalibrated and so the aftereffect will only occur when that particular leg is used. In contrast to this, learning to step over obstacles or coping with a transient gait perturbation (such as in the current study) are skills which probably do not involve sensory recalibration. Hence, these adaptations may be more likely to generalise because they are not
restricted to a given sensory channel from one leg. This might explain why Van Hedel et al observed transfer of skill from one leg to the other, whereas other experiments did not. Nevertheless, here we have also shown little transfer of the aftereffect when subjects changed starting leg, even though it is unlikely that the moving platform task induces sensory recalibration. However, it must be remembered that the experiment described here involves inhibition of an inappropriate motor response, when subjects are warned of the change in context. This cannot be directly compared with a situation where subjects are actively trying to transfer a skill from one leg to another, such as occurs during obstacle avoidance.

**The Pattern of generalisation suggests learning in a joint- and muscle- based reference frame**

Previous experiments which have examined generalisation of motor learning have observed that learning can either be specific to the limb used to perform the task (Earhart *et al.*, 2002a) or alternatively may readily be transferred between limbs (Schulze *et al.*, 2002; Imamizu & Shimojo, 1995), with the extent of transfer depending on the paradigm used (Choe & Welch, 1974; Criscimagna-Hemminger *et al.*, 2003). Also, changing the method of the task may or may not abolish the learned response (Thut *et al.*, 1996; Conditt *et al.*, 1997; Earhart *et al.*, 2001; Baraduc & Wolpert, 2002). Just as when changing the limb used, such a change of method can require the use of different muscles, or different patterns of muscle activity to perform the task. Here, in the leg-change experiment 8 of 11 subjects showed no aftereffect. Also, when the walking method was changed to backward walking, there was no aftereffect. Both these results suggest that the learning is represented by the CNS in a
way which is specific to the effectors used to perform the task. In other words, the pattern of generalisation suggests learning in a joint- and muscle-based frame of reference (Gandolfo et al., 1996). From a teleological perspective this is perhaps surprising. Given a potential threat to one's balance, all that should matter is whether the support surface will move or be still, irrespective of the exact manner in which you walk on to it. However, despite the observed specificity with regard to walking method, in the fixed platform experiment there was no aftereffect when walking elsewhere even though the same effectors were being used to perform the task. Therefore, although the adaptation is specific to the manner in which the task was performed, a change in location can signal to the subject that the learned response is no longer appropriate. This signal must operate beyond the level of conscious awareness, since we have shown that knowledge is not enough in itself to abolish the aftereffect.

Hence, the greater the deviation from the method of walking onto the moving platform, the lesser the aftereffect. Such context-specificity has been demonstrated for different types of motor learning, including adaptation of reaching (Baraduc & Wolpert, 2002; Seidler et al., 2001) and the vestibular-ocular reflex (Shelhamer et al., 1992).

**Conclusion**

Although the moving platform aftereffect occurs despite full knowledge of the changing trial condition, it shows very limited generalisation to other situations. It is quite specific to the mode of locomotion, and only occurs when walking onto the mobile sled. It is therefore very context-specific. However, changing abstract
contextual cues had no effect. This means that only changes which directly affect the walking task itself have any influence.

Reference List


Figure Legends

Figure 1. Experimental apparatus and task. A. The walking task is shown. In this example, the person has initiated gait with the right leg. During the MOVING condition, the sled moved forward, as indicated by the arrow. Sled movement was triggered using a light switch mechanism and moved according to the velocity profile shown in B. The backward-walking and fixed-platform walking tasks are shown in C and D, respectively.

Figure 2. Trunk Displacement. The grey solid bar shows +1.96 s.d. of trunk displacement for the 10 BEFORE trials, for a subject who participated in the leg-change experiment. AFTER trials 1 and 2 are shown by the solid and broken lines, respectively. There is a 15cm forward sway, as indicated by the trunk overshoot. The timing of foot-sled contact is shown by the vertical dashed line. The cartoon at the top shows the approximate state of the subject across time; after stepping onto the sled, the subject stops walking and stands in place.

Figure 3. Walking Velocity and Forward Sway during leg change experiment. One group changed the gait initiation leg between the MOVING and AFTER conditions. The other group maintained the same leg. A, Mean Walking Velocity. B, Mean Forward Sway. C, Normalised Forward Sway during AFTER trial 1. The ‘change’ group showed twice as much sway as the ‘same’ group. D, Frequency distributions of data in graph C, showing that most subjects in the ‘same’ group exhibited a forward sway greater than 2.5cm whereas 8 subjects in the ‘change’ group did not. N=11 for both groups.

Figure 4. Walking Velocity and Forward Sway during context experiment. One group experienced a change in the gait initiation cue between the MOVING and AFTER conditions, the other group did not. A, Mean Walking Velocity. B, Mean Forward Sway. C, Normalised Forward Sway during AFTER trial 1. There was no statistical difference in sway between the groups. Frequency distributions of data in graph C, showing that most subjects in both groups swayed more than 2.5cm. N=9 for both groups.

Figure 5. Fixed-platform walking. For some trials during the BEFORE and AFTER conditions, walking was confined to the fixed platform. In the other trials, they walked onto the sled. A, Mean Walking Velocity, and B, Forward Sway. N=7.

Figure 6. Backward-walking. For some trials during the BEFORE and AFTER conditions, subjects were asked to walk backward onto the stationary sled. A, Mean Walking Velocity, and B, Forward Sway. N=7.
Table 1. Protocol for the generalisation experiments. The protocols for all four experiments are shown. The BEFORE trials provided baseline data, when the sled was kept stationary. During MOVING trials, subjects adapted to the moving sled. During the AFTER trials, subjects were warned that the sled would be kept stationary again. The Number of trials in each sequence is shown in brackets. For the ‘Leg’ and ‘Context’ experiments, two groups were compared. One group experienced a change between MOVING and AFTER conditions, the other did not. These groups were further subdivided into two groups to control for leg- or stimulus- specific effects. The ‘Backward’ and ‘Fixed’ experiments used repeated measures designs.
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