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Aftereffects from jogging

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Abstract. After running for 60 s on a treadmill, a runner who attempted to jog in place on solid ground inadvertently jogged 152 cm forwards. One-legged hopping on the treadmill produced an aftereffect in the same leg, but not in the other leg, and this non-transfer suggests a peripheral neural site. Judgments of velocity and slope were affected; running on a backward-moving or an uphill-sloping treadmill made a stationary test treadmill seem to move forwards and a horizontal test treadmill seem to slope downhill. These aftereffects suggest an automatic gain control process.

Key words: locomotion -- gait -- adaptation -- aftereffect

Introduction

Running is no clockwork reflex but an adaptive skill. Runners constantly adjust their running to the local terrain, shortening their stride uphill, picking their way over rough ground and so on. Reviews of these adaptive processes can be found in Desmedt (1976), Herman, Grillner, Stein and Stuart (1976), Howard (1982), and Patla (1991). Patla, Armstrong and Silvera (1989) have measured the time course of such adaptive processes during a single stride. We now report adaptive changes in gait, namely negative aftereffects, after running on an exercise treadmill, a conveyor belt device that carries the runner backwards at the same speed as (s)he runs forwards. Following adaptation by a 60 s run on a treadmill, a runner who dismounted on to solid ground showed various gait-contingent aftereffects. While standing still, no aftereffects were noticed. However, as soon as the runner attempted to walk or run on the ground, (s)he had an illusion of being apparently borne forwards, as if on invisible wheels. In particular, when asked to jog in place with eyes closed, (s)he actually jogged forwards without being aware of it.

Measuring the jogging-in-place aftereffect

The runner adapted to the treadmill by running on it for 60 s at a speed of 8 km/h, with eyes closed (to rule out visual components such as optic flow) and holding the handrail (to avoid being flung off backwards). (S)he dismounted from the treadmill and "jogged in place" with eyes closed on solid ground.
This jogging, supposedly in place, was measured with a carpenter's spring-loaded flexible steel measuring tape clipped to the back of the runner's belt. If (s)he moved forward or backwards, the measuring tape spooled or unspooled from its canister, and it was videotaped in close-up by a TV camcorder. The amount of "creep" —

inadvertent forward motion of his body — was measured off-line afterwards to the nearest 0.5 cm from the videotape with the aid of a freeze-frame.

Normally each foot would repetitively strike the same spot on the ground; this was true for control runners who had merely run around the block. However, after running on the treadmill our runners jogged forward through a mean distance of 152 cm in 15 s (Fig. 1). They were completely unaware of this forward motion until they bumped into the wall or else opened their eyes. Running backwards on the treadmill produced a backward aftereffect (Fig. 1), and running sideways produced a sideways aftereffect (not shown). These forward, backward and sideways effects also occurred with eyes open and no handrail.

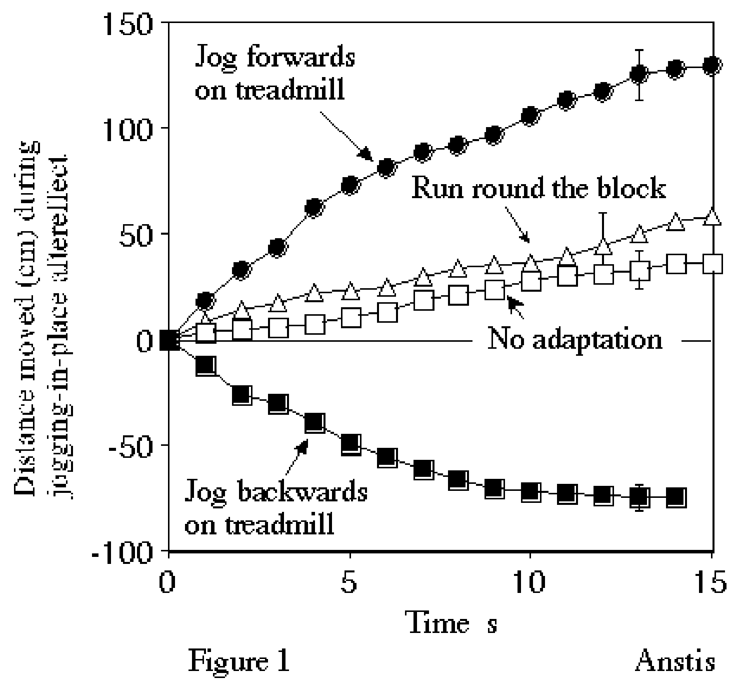

Figure 1. After running forwards (backwards) on a treadmill, runners attempted to jog in place with eyes closed, and inadvertently jogged forwards (backwards). This aftereffect was not found in control conditions of running around the block or without prior running. Typical SE bars are shown. All data are means of four runners for one trial.

Time course and storage of the aftereffect.

Runners stepped off the treadmill after 60s and then jogged in place, either immediately or else after standing still for 15, 30, 60 or 120 s. Eyes were closed throughout. The order in which delay times were presented was randomized across subjects. Result (Fig. 2): The inadvertent forward motion was greatest for zero delay, and decreased as the delay was progressively increased to 120 s. Thus, the stored aftereffect gradually dissipated over the course of a minute or two.

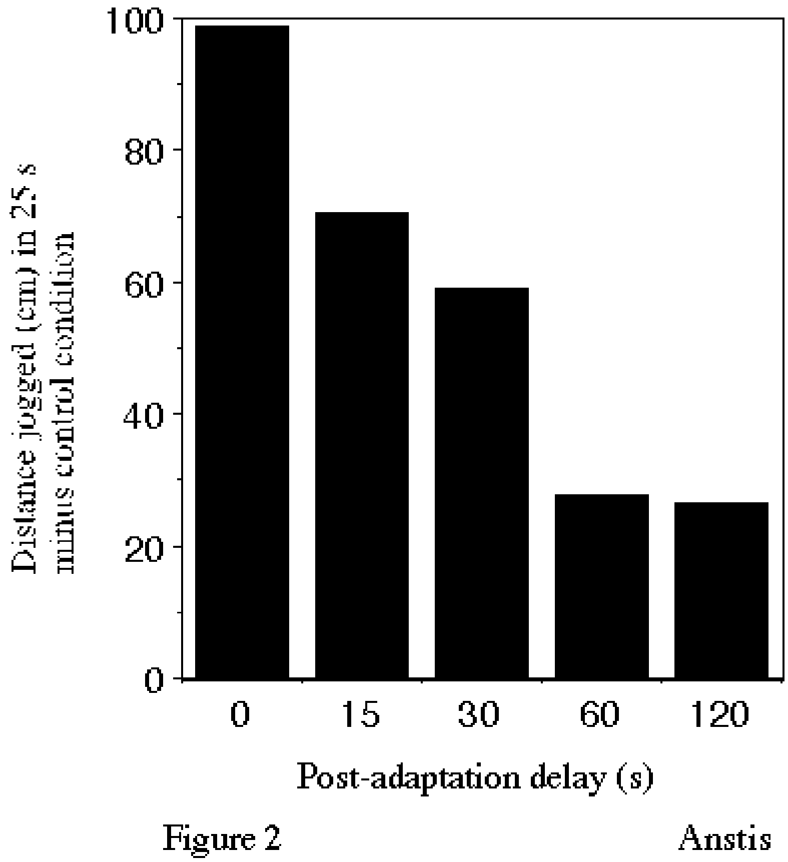

Figure 2. After running on the treadmill, runners stood still for 0-120 s before attempting to jog in place. Aftereffects declined with increasing delay.

No inter-limb transfer of the aftereffect.

To examine the neural site of these aftereffects, we borrowed a technique used in studying the negative aftereffect of visual motion, in which one gazes at a rotating pattern with one eye, then views a static test pattern with either the same or the other eye (Moulden 1980). Viewed with the same eye, the test pattern appears to rotate strongly backwards: viewed with the other eye, it seems to rotate backwards but with about half the strength (Anstis and Duncan 1983). This suggests that both monocularly and binocularly driven cortical pathways are involved (Anstis and Moulden 1970: Raymond 1993).

The runner hopped on his or her preferred leg on the treadmill for 30 s at a speed of 5 km/h. This slow speed was used because hopping is very fatiguing. The runner then dismounted and hopped in place on solid ground with eyes closed, using either the same (adapted) leg or the other (unadapted) leg on different trials. In the resulting aftereffect (Fig. 3), the runner inadvertently hopped forward through 118 cm when the same leg was used (showing bipedal gait was not necessary), but *not* when the other leg was used. (There was a small forward motion on the opposite leg, but this did not differ significantly from zero: $t=0.81$, $df=3$, $p<0.4$).

This failure of the aftereffect to transfer across legs suggests a peripheral rather than a central neural site. Thus the adaptation could not be visual or vestibular, but must occur in those parts of the nervous system that control each leg separately.

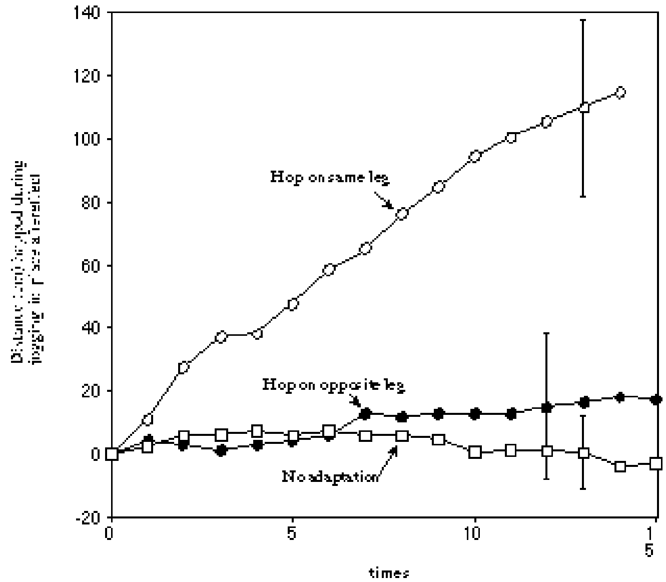

Figure 3 Anstis

Figure 3. Hopping on the treadmill on one leg procuded an aftereffect in the same leg, but not in the opposite (unadapted) leg.

Judgments of ground velocity and slope underwent adaptation.

After a 30s run at 8 km/h on a treadmill, a stationary test treadmill felt as though it was moving forwards. This aftereffect was nulled out by moving the test treadmill slowly backwards until a speed was found at which it felt stationary. Eyes were closed throughout. The test mill felt stationary when it was actually moving backwards at 2.29 ± 0.24 km/h (mean and SE of five runners). This was 28.6% of the adapting treadmill velocity. After a run on a treadmill that sloped upwards, a horizontal test treadmill felt as though it sloped downhill. This aftereffect was nulled out by sloping the test treadmill slightly upwards until it felt level. Adaptation to an uphill slope of 4° made the same 4° slope feel horizontal (Fig. 4), a negative aftereffect of 100%. Adaptation to an uphill slope of 8° made an uphill test slope of 5° feel horizontal.

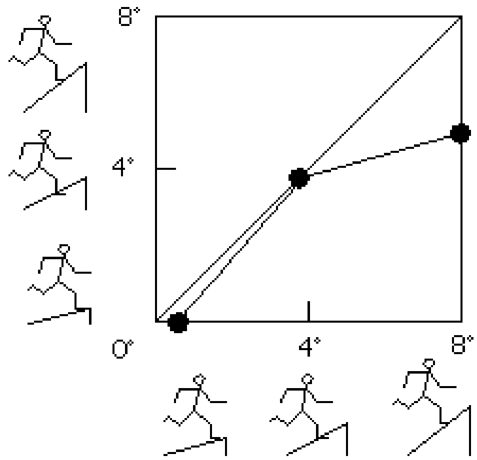

Figure 4 After walking on a treadmill that sloped 4° or 8° uphill, a horizontal treadmill felt as though it sloped downhill, and a nulling procedure showed aftereffects of 4° and 5° respectively.

Conclusions

What is the neural site of these aftereffects? They are clearly not visual, since they occurred when the eyes were closed. Since the two legs adapted independently we can rule out central components such as vestibular adaptation -- the aftereffects occurred, not necessarily within the leg itself, but at least within the neural pathways that control each leg separately. Since running around the block produced no significant aftereffects, the adaptation must specifically counteract the backward motion of the treadmill. We conclude that running on the treadmill adapts those neural pathways that compare the muscular effort of swinging each leg forwards (or backwards) with the resulting postural position of each leg (Houk, Keifer and Barto 1993). The backward motion of the treadmill produces an artificial mismatch between motor output and normal postural feedback, for which the adaptation compensates or nulls out by adjusting internal gain parameters to bring output and feedback back into line. But once the runner steps on to solid ground these newly adjusted parameters are now inappropriate and manifest themselves as an aftereffect, which dissipates as the parameters automatically update to match the solid ground. So these new aftereffects reveal the continuous neural recalibration of the gait control system.

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