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Abstract

Anstis (1995) described an aftereffect following treadmill running in which people would inadvertently advance when attempting to run in place on solid ground with their eyes closed. Although originally induced from treadmill running, the running-in-place aftereffect is argued here to result from the absence of sensory information specifying advancement during running. In a series of experiments in which visual information was systematically manipulated, aftereffect strength (AE), measured as the proportional increase (posttest/pretest) in forward drift when attempting to run in place with eyes closed, was found to be inversely related to the amount of geometrically correct optical flow provided during induction. In particular, Experiment 1 (N=20) demonstrated that the same aftereffect was not limited to treadmill running, but could also be strongly generated by running behind a golf-cart when the eyes were closed (AE = 1.93) but not when the eyes were open (AE = 1.16). Conversely, Experiment 2 (N= 39) showed that simulating an expanding flow-field, albeit crudely, during treadmill running was insufficient to eliminate the aftereffect. Reducing ambient auditory information by means of earplugs increased the total distances inadvertently advanced while attempting to run in one place by a factor of two, both before and after adaptation, but did not influence the ratio of change produced by adaptation. It is concluded that the running-in-place aftereffect may result from a recalibration of visuomotor control systems that takes place even in the absence of visual input.

Introduction

Visual information during normal locomotion serves not only to guide the direction of movement (Cutting, 1986; Warren & Hannon, 1988), but also to monitor the results of action. Various kinds of optically-induced visuomotor adaptations, such as sensorimotor accommodation to shifted or inverted optical information, can be understood in terms of adjustments to novel correlations between the control of action and the sensory consequences of those actions (CS Harris, 1963). This paper addresses a recent aftereffect reported by Anstis (1995) produced in the absence of visual feedback. With their eyes closed throughout the experiment, participants who had run on a treadmill for 60 s would inadvertently advance when attempting to run in one place back on fixed ground. No such aftereffect followed normal running outdoors, and so it was concluded that the effect was due entirely to a postural readjustment to the backward movement of a treadmill belt, without the involvement of vision. In the present paper we present new evidence on the conditions producing this aftereffect which suggests instead that it is a visuomotor adaptation that takes place even in the explicit absence of visual information.

Because the specification of the adaptation conditions necessary to produce it is what is under investigation, we will refer to the aftereffect according to its expression, and call the resulting illusory sense of running in place, when actually advancing, the running-in-place aftereffect (RIPAE). Let us emphasize that the illusion here is that the individual has a "visceral" sense of running in one location, when they are actually drifting forward. We will address the question of why is it produced by treadmill running.

Consider that the relative motion of treadmill belt and runner is, *a priori*, qualitatively identical to that between runner and road. Nevertheless, the differences between these two running conditions may still contribute to the RIPAE. The most obvious difference would at first appear to be the effects of the movements of running on the vestibular otoliths: running at an approximately constant velocity would produce small, periodic changes in linear acceleration. The vestibular system is also important generally for the control of postural stability, for instance to minimize sway, primarily in the absence of vision.

On the other hand, arguments against significant vestibular involvement are somewhat more compelling. Because vestibular sensitivity is specific to acceleration, the stimulation from running at a constant velocity on fixed ground (i.e. changes from constant absolute motion) and that from treadmill running (i.e. changes from constant "zero" absolute motion) is likely to be very similar. And, if these stimulations were primarily responsible, they should lead to a similar amount of aftereffect in the two conditions (they do not: Anstis, 1995). Furthermore, the vestibular system on its own (or even with accompanying proprioceptive information) seems unable to accurately control running speed and direction. It is easily confirmed, for example, that hands-free running on a treadmill with the eyes closed, which requires maintaining a constant speed and direction, is not possible without quickly stepping off the treadmill, losing balance and falling off (authors' personal observations!). A system which is not able to sensitively control running speed or direction, is unlikely to mediate the kind of adaptation that leads to a robust directional running aftereffect like the RIPAE.

To remain stable on a treadmill requires either visual input, or holding onto the handrails if the eyes are closed. If vestibular inputs are not involved, then only the respective sensory and motor patterns from these factors can contain the important differences between treadmill running and running on fixed ground. To investigate the importance of visual information in generating the RIPAE, we consider whether a quantitatively similar aftereffect can also be generated on fixed ground (rather than only on a treadmill) when normal optical flow is reduced or eliminated. We also test whether the introduction of simulated optical flow while running on a treadmill is sufficient to eliminate the RIPAE, and whether holding onto the treadmill rails is important.

Anstis argued that the adaptation leading to the RIPAE involved non-visual aspects of the gait control system specifically applicable to running on a treadmill (i.e. an adjustment of muscular output to postural feedback: Anstis, 1995). We postulate that this effect may represent instead a more general recalibration, one involving control of motor output to primary sensory input, and mediated particularly by adjustments to visuomotor "expectancies" concerned with updating self-position during locomotion (cf. Pelah and Barlow 1996).

The task of running in place with eyes open is easily controlled by vision under normal circumstances. At the same

time, in the absence of visual feedback, running in place may still be controlled accurately enough by application of the normally calibrated relationship between locomotor action and normal visual feedback. However, visuomotor or other sensory expectanciesinvolved in locomotion may be recalibrated by treadmill running, since the perception of self-motion leading to advancement correlated with running is reduced or eliminated. During the testing phase, the runner's goal is to act in such a way as to *receive* (if their eyes were open) zero optical flow; whereas the runner's sensory experience from the treadmill is that to *produce* no optical flow requires running forward. Thus, the experience would tend to adjust the calibrated point for zero flow (i.e. zero self-motion) to some positive forward velocity or acceleration of the runner with respect to the surface beneath his feet.

In contrast to the above, Anstis's hypothesis for a motor-based recalibration only, and one specific to treadmill devices, predicts no effect from normal running and therefore no effect of the presence or absence of optical flow during normal running. In short, the testing of normal running in the absence of vision is crucial to the examination of the motor-only hypothesis. In Anstis' (1995) experiments, the presence or absence of forward motion with respect to solid ground during adaptation was confounded with the presence or absence of normal optic flow. The experiments reported here are designed to test this hypothesis against our postulated general sensory recalibration hypothesis by measuring the RIPAE in response to systematic manipulation of the normal relationships between optical flow and running.

Experiment 1: Running in the real world

If the RIPAE is due to a general recalibration of motor output in response to primary sensory input, and is not specific to moving surface devices like treadmills, then it ought to be possible to induce it by running on fixed ground in the absence of optical flow (i.e. with eyes closed). To test this, we developed a paradigm of running while holding onto a bar attached to the back of a moving golf cart. (Some of these results were previously presented in brief by Pelah et al., 1997.) The golf cart paradigm provides the same enforced relative motion between runner and surface as that which occurs on a treadmill. However, it further allows us to examine any specific effects of running on treadmills (since here running is on fixed ground) and especially the role of visual information specifying self-movement. This can be done by contrasting normal visual information observable with eyes open with the absence of visual updating produced by closing the eyes while running behind the golf-cart. Durgin and Pelah (1998) have already reported that the RIPAE is greater following treadmill running with eyes open than with eyes closed, whereas precisely the opposite pattern of results is predicted by our hypothesis following a golf-cart run in which vision will correctly indicate self-movement. On the other hand, the explanation proposed by Anstis (1995) would predict no RIPAE from the golf-cart, with eyes either open or closed.

Methods

With subject committee approval, twenty Swarthmore undergraduates (paid for their participation) individually ran while holding onto a horizontal bar, 1.3 m above the ground, attached to a golf cart driven at an approximately constant speed of 9 km/h over a 1 km route. Ten of the participants were required to keep their eyes closed while they ran; the other ten viewed the prevailing optical flow (which was only partly obstructed by the back of the golf cart). Running in this way was surprisingly unobjectionable even with eyes closed, and our participants reported no discomfort with this task. The experiments were conducted in daylight on a winding, tree-lined campus road, and no specific fixation instructions were given. Participants were told beforehand of the route to be taken, a familiar road for most of them which looped back to the original testing location.

To assess the RIPAE we measured the net distance that each participant advanced while attempting to run in place (in the same outdoor location) with eyes closed for a period of 20 s. Distance measurements were taken both before and after the run behind the golf cart. For each measurement, the participant was led to an unseen mark, instructed to run in place, and their advance after 20 s marked and measured to the nearest cm. After the pre-run measurement we ensured that participants were not made aware that they had actually advanced by leading them a

short distance away from the test location with their eyes still closed. For purposes of analysis, we considered the change in distance advanced as the logarithm of the ratio between measures after and before adaptation (cf. Durgin, 1996). Statistical analyses of aftereffect strength were therefore computed on differences of logarithms (i.e. logarithms of ratios). We will report mean distances measured in tables, however, and will normally describe the size of an aftereffect as a geometric mean ratio (i.e. the ratio corresponding to the mean difference of logarithms), because those magnitudes will be easier to interpret.

Because we suspected that auditory localization information might also influence the RIPAE, half of our participants (five in each condition) were adapted and tested while wearing earplugs. The sounds in the testing environment were ambient noises of birds and occasional lawnmowers or cars in the distance, but perhaps the most important sound used for localization without earplugs arose from the footfalls of the participants as they attempted to run in place. There was a dense wood about 2 m to the right of the test route. Echoes of the footfalls against the nearby trees, etc., were minimized by the earplugs. The noise of the golf cart itself during adaptation permeated the auditory environment, but this noise was modified by changes in the surrounding environment and probably still signaled motion in the absence of earplugs. With earplugs, the internal vibrations of the footfalls and the (subjectively distant) low frequencies of the engine noise constituted the subjective auditory environment.

Because earplugs dramatically increase the amount of inadvertent forward advance both before and after adaptation, the data summarized in Table 1 depict the conditions in which earplugs were worn, so as to enable comparison with subsequent experiments in which they were employed. Table 2 depicts the conditions in which hearing remained unobstructed in this and subsequent experiments. The details on variants of the main golf-cart paradigm and additional experiments are described along with their results in the text that follows.

Results and discussion

Assuming that a gain-control mechanism (Craik 1938) was implicated, we defined RIPAE strength as the logarithmic change in distance traveled inadvertently. Figure 1 shows that aftereffect strength was strongly modulated by visual information [$F(1,16)=5.8$, $p<.05$], but not by auditory information [$F(1,16)<1$]. These results support our visuomotor hypothesis and contradict two aspects of Anstis's (1995) motor-based interpretation: First, since the aftereffect could be produced by the golf-cart paradigm, backward motion of the running surface is not required. Second, the strong modulation of the aftereffect by vision argues that the absence of visual input in Anstis's experiment did not redress the anomalous absence of visual flow produced by treadmill running.

Figure 1. Aftereffect of running behind a golf cart is expressed as geometric mean ratio between the distances advanced over a period of 20 sec after and before the golf-cart run (intervals on the ordinate are logarithmic). Each bar represents the data of 5 participants. Standard error bars are shown. Ear plugs reduce variability in this measure (by increasing overall distances; see Figure 2), but do not influence aftereffect strength. Visual information during running strongly influences the size of aftereffect.
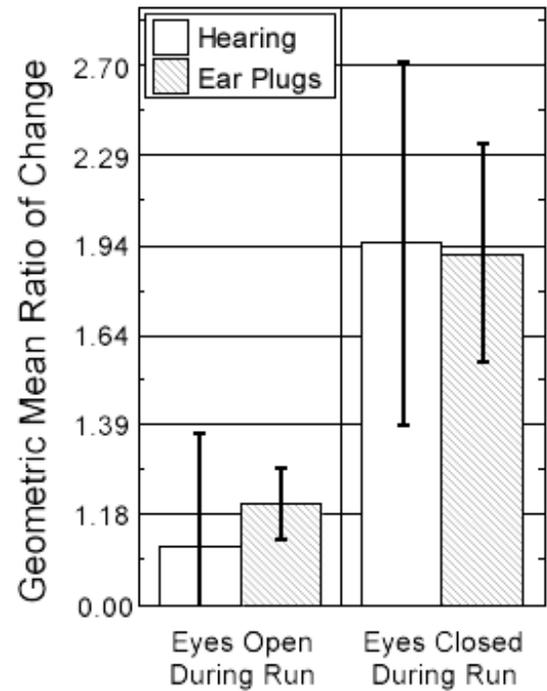
It is of some interest that the reduction of auditory information greatly increased the absolute distances traveled (collapsed across runs before and after adaptation) by a factor of 2, as shown in Figure 2, [$F(1,16)=9.3$, $p < .01$]. Thus it would appear that auditory information could be used to help maintain stasis in the absence of vision, though it apparently played little role in the adaptation process itself. The failure of audition to modulate effect size during eyes-open adaptation is not surprising, since visual updating of position would presumably dominate. If the underlying system for tracking self-position in the environment is multi-modal, however, some effect of audition might have been anticipated for eyes-closed adaptation. Admittedly, the experimental conditions were not ideally suited for assessing this, however.

Figure 2. The effect of using earplugs on the task of running in place with eyes closed is illustrated here by comparisons of total distance traveled in 40 sec (20 s before plus 20 s after the adapting run) for each of the four groups of participants. Standard error bars are shown. Auditory information is apparently quite useful for maintaining stasis with eyes closed. Overall inadvertent advance in its absence overshadows the effects of the adaptation itself.
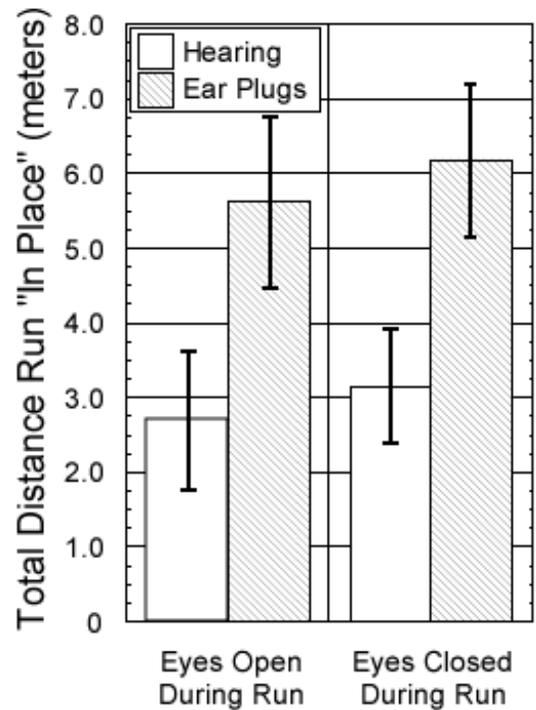
Effects of reduced peripheral vision

It could be argued that the golf cart mimics a treadmill too closely in that both devices require the observer to hold onto a bar while running. This might have produced postural adaptation in the eyes-closed running conditions that could have accounted for the aftereffect. We therefore devised an experiment requiring adaptation without the bar. We used the same procedure and route for normal running as in the previous experiment (but without the golf cart), and used restrictive goggles to eliminate peripheral vision beyond about 40 deg from the fovea. For ten new participants (again, half adapted and tested with earplugs, half without) the geometric mean ratio of change in inadvertent advance was 1.34, which is intermediate between the eyes-closed (1.93) and eyes-open (1.16) conditions of the previous experiment. This is consistent with the visuomotor hypothesis because the quantity of appropriate optical information was intermediate between those conditions. Average distances are shown in Table 1 for those tested with earplugs, and in Table 2 for those tested without.

Table 1: *Distances inadvertently advanced during a period of 20 s, in the absence of hearing and vision, before and after adaptation in each of the experiments reported here (mean ◆ standard error).*

Adapted Visual Status	N	Mode	Test Surface	Before (m)	After (m)
Eyes Closed	5	Golf Cart	Pavement	2.17 ◆ 0.46	4.00 ◆ 0.67
Eyes Open	5	Golf Cart	Pavement	2.56 ◆ 0.53	3.06 ◆ 0.63
Restrictive Goggles	5	Free Run	Pavement	2.64 ◆ 0.61	3.69 ◆ 0.47
Ganzfeld Goggles	5	Free Run	Grass	1.58 ◆ 0.51	3.92 ◆ 1.39
Eyes Open	5	Free Run	Grass	2.12 ◆ 0.60	2.62 ◆ 0.70
Ganzfeld Goggles	5	Treadmill	Carpet	2.12 ◆ 0.51	3.94 ◆ 0.48

Table 2: *Distances inadvertently advanced during a period of 20 s, in the absence of vision only, before and after adaptation in several experimental conditions (mean � standard error).*

Adapted Visual Status	N	Mode	Test Surface	Before (m)	After (m)
Eyes Closed	5	Golf Cart	Pavement	1.10 � 0.30	2.05 � 0.53
Eyes Open	5	Golf Cart	Pavement	1.14 � 0.43	1.58 � 0.49
Restrictive Goggles	5	Free Run	Pavement	2.11 � 0.39	2.55 � 0.45
VR -- Eyes Closed	10	Treadmill	Carpet	1.33 � 0.81	2.53 � 0.29
VR – No Flow	10	Treadmill	Carpet	0.96 � 0.14	2.96 � 0.30
VR – Normal Flow	10	Treadmill	Carpet	0.88 � 0.26	2.38 � 0.43
VR – Fast Flow	9	Treadmill	Carpet	1.27 � 0.26	3.23 � 0.30

Free running with unstructured visual input

In the previous condition subjects nevertheless experienced some visual information about their forward advance. In order to produce a condition of more normal locomotion with visual information signaling a complete absence of optical flow, we had five new participants (young adults from the Cambridge community) run in a large well-mown grassy field for 45 s while wearing translucent "ganzfeld" goggles that provided unstructured light to the eyes. As a control, five additional subjects ran the same course and time but without the goggles. The ganzfeld adaptation produced a much stronger RIPAE (the geometric mean ratio of change was 2.45), than the control group using normal vision (1.38), $[t(8) = 2.40, p < .05]$. Rather than closing their eyes, both groups wore the ganzfeld goggles during testing as well and all subjects wore earplugs. For comparison, a further group of five participants were tested in the same manner after running on a treadmill with the ganzfeld goggles for 45 sec, and these also showed strong RIPAEs, with a geometric mean ratio of 1.99. Average results for each group are shown in Table 1. As with the previous experiment, this result suggests that holding onto treadmill rails (or golf-cart bar) is not essential for producing the RIPAE. More generally, these findings provide further support for the visuomotor hypothesis because the aftereffect was still produced with free running in the presence of unstructured visual input but an absence of optical flow.

A note of discrepancy

There is something of a discrepancy between Anstis's (1995) pre-adaptation observations and our own. Even in the absence of earplugs, we typically found more than 1 m of forward advance over a period of 20 s before adaptation, whereas Anstis found less than 0.5 in 15 s. Furthermore, although not strictly discrepant, our post-adaptation distances also tend to be longer than those he reported by an amount that cannot be explained by the difference in test time. In addition, although we did not measure it, we observed no tendency toward deceleration during the inadvertent advance before and after adaptation, whereas Anstis recorded a clear deceleration in the adapted condition. If anything, we felt that runners tended to accelerate, even in the absence of earplugs. It may be that the spring-loaded measuring tape which Anstis had attached to the back of his runners during testing served to decelerate and thus slow their progress, though alternative accounts of these apparent differences (e.g., involving the acoustics or running surface of Anstis's particular testing situation) are also possible.

Experiment 2: Running in a virtual world

We have thus far framed our hypothesis primarily in terms of a correlation between locomotor activity and optical flow, but have made little effort to distinguish optical flow, *per se*, from any number of other sources of information of self-motion provided by vision and other sensory systems. We considered therefore whether providing simulated optical flow to a treadmill runner, for example by means of a virtual reality (VR) system, would be sufficient to reduce the RIPAE.

Method

To test this hypothesis we used an LCD projector to display the video image of a texture-mapped moving circular tunnel onto a back-projection screen mounted in front of a treadmill. The simulated tunnel was 3 m in diameter, and viewed from a height of 1.7 m. The texture on the tunnel was a high-contrast grayscale image which provided clear motion signals. The projected image, which was viewed from a distance of 1 m, subtended approximately 120 degrees of visual angle horizontally, and 90 degrees vertically, and was centered approximately at the eye-height of the runner.

Thirty-nine Swarthmore students, who had not participated in any other of the experiments were divided among four adaptation conditions. All adaptations involved running on the treadmill for 90 s at 9 km/h. Hearing was unobstructed. The visual information during adaptation was either (1) none -- eyes closed, (2) a static tunnel, (3) a normal speed (9 km/h) tunnel, or (4) a triple-speed (27 km/h) tunnel. Light from the projection screen dimly illuminated the participants' surroundings, including the treadmill itself and the frame of the projection screen. Runners wore an occluder over their left eye thus viewing the stimulus monocularly. Those who required them wore corrective lenses.

It is to be noted that a display of this type fails to capture aspects of natural optical information, and that none of our participants experienced any illusion that they were actually moving within the tunnel. First, because the image was not yoked to the runner's activity, vertical parallax produced by the up and down motion of the runner's head and horizontal parallax produced by any swaying conflicted with expected signals of self-motion and depth. Moreover, individual pixels were clearly visible in the LCD projection, providing a further indication of a flat static screen. Finally, our runners were, of course, holding onto the rail of the treadmill in order to avoid falling off the back, and may have thus maintained a strong sense of stasis. Nonetheless, our display contained plenty of optical flow information which was roughly consistent with forward motion. If the RIPAE is governed entirely by the registration of optical flow, *per se*, then the display should be sufficient to reduce the amount of RIPAE.

As in all previous experiments, each participant was required to attempt to run in place on fixed ground with eyes closed for 20 s both before and after adaptation, and did not learn of their inadvertent advance until the conclusion of the experiment. Because of the use of the VR system, participants had to walk a few meters after adaptation between the adaptation area and the test area. This route was maneuvered with eyes closed but measurement was somewhat delayed.

Results and discussion

The data, which are summarized in Table 2, under "VR," showed strong aftereffects in all conditions. However, no statistical differences were detected between conditions in the analysis of log ratios of change in the distance inadvertently advanced. It may be that the sharp conflict between visual cues specifying motion in the VR display and those specifying stasis (e.g., motion parallax) rendered the displays equivalent to eyes-closed conditions. Consistent with an earlier report (Durgin and Pelah 1998), aftereffect strength with eyes open in the absence of flow (the geometric mean ratio of change equal to 3.31) is somewhat greater than with eyes closed (2.42). However, these groups differ reliably only if the analysis is computed on the arithmetic difference scores of the pre- and post-test for the two groups, [t(18) = 2.44, p < .05]. Apart from this, it would appear that the system underlying the calibration process is not responsive simply to optical flow, *per se*. Merely manipulating the speed of optical flow,

without creating a compelling sense of self-movement, is apparently insufficient to alter the amount of the RIPAE.

General Discussion

The results summarized in Tables 1 and 2 show an unmistakable pattern. All participants tested with earplugs tended to advance by about 2 m prior to adaptation. Those who were then adapted *without* normal visual information on self-motion advanced by about 4 m afterwards. Those adapted *with* normal visual information advanced by only about 3 m afterwards. A partial restriction of visual information produced an intermediate quantity of subsequent advance. Similar patterns, but with shorter distances both before and after adaptation, were found without earplugs. Running on fixed ground did not seem to differ from running on a treadmill in producing a RIPAE. However, the mere provision of crudely simulated optical flow is apparently insufficient to reduce the amount of aftereffect.

It is evident therefore that visual information available during running can modulate the amount of recalibration, but that the presence of optical flow *per se* is apparently insufficient to do so on its own. Moreover, Stuart Anstis (personal communication) has recently found that the RIPAE can be generated in congenitally blind individuals who presumably do not have visuomotor expectancies. The question remains then whether the recalibration that generates the effect is one that is controlled by the flow of information within a single dominating sensory modality (i.e. vision in the sighted) or rather one that is mediated by a coordinated multi-modal neural system that perhaps tracks self-progress through the environment.

Anstis (1995) reported that after hopping on a treadmill, attempts to hop in place demonstrated a RIPAE in the leg used during adaptation but not in the other leg. Anstis argued from this failure of inter-limb transfer that the effect must involve peripheral pathways only. This finding, however, is also consistent with visuomotor adaptation, because it is possible in such adaptation to recalibrate a single effector with respect to changes in visual input. Indeed, visuomotor adaptations are normally specific to the effector that is used during adaptation. This occurs, for example, in the classic case of adaptation to prism goggles which displace the visual world (see CS Harris 1963; Lackner 1981). Active reaching misses its visual target when first wearing the goggles but motor responses quickly adjust to become aligned with the shifted optical information; a compensatory aftereffect is also produced in the opposite direction when the goggles are later removed. Because this effect is a response to a mismatch between vision and action it is clearly a visuomotor adjustment. The important point however is that if reaching is limited to a single hand, the other hand will show little if any learning, and only the adapted hand will show the compensatory aftereffect when the goggles are removed (CS Harris 1963). A recent PET imaging study has localized the site of adaptation to the posterior parietal cortex but only to the contralateral side of the reaching limb (Clower et al. 1996). Thus, the adaptation is not only limb-specific but probably also takes place at a central cortical site.

Recalibration may occur when expected patterns of sensory correlation do not hold (Andrews 1964; Barlow 1990). Barlow (1990) has argued that contingent aftereffects, in general, reflect a technique for efficient coding of sensory information by encoding only departures from normal correlations (see also Durgin 1996; Durgin and Proffitt 1996; Helson 1964). Other formulations of contingent aftereffects include the notion of error correction with respect to an internal standard (e.g. Dodwell & Humphrey 1990) or the elimination of crosstalk between sensory channels (Anstis 1975). Barlow's (1990) formulation differs from these in supposing that recalibrations are the adjustment of the normal ("expected") correlation, rather than a correction for unwanted correlations (cf. Helson 1964). Since sighted people seldom engage in locomotor activity without vision, perhaps the usual co-occurrence of action and vision is so strong that the visuomotor system is not able to treat the absence of visual information about visual flow (i.e. eyes closed) as entirely different from specification of zero optical flow.

Pelah and Boddy (1998) have recently described a complementary result for modulatory effects of locomotor activity on visual motion adaptation. They found that a motion aftereffect to expanding optical flow was reduced when exposure occurred during walking on a treadmill. No such diminution was found with contracting flow, suggesting

that only the expected correlation between forward locomotion and expanding flow fields reduces visual motion adaptation. LR Harris et al (1981) have previously shown that a similar reduction of motion aftereffects can occur when an observer is passively rolled forward and back with expanding flow presented during the forward leg of the movement. Evidently, therefore, reduction of the motion aftereffect can occur either from correlated vestibular information of self-motion (Harris et al 1981), or by correlated motor activity even in the absence of actual self-motion (Pelah and Boddy 1998). In the present experiments, vestibular information regarding self-motion behind the golf-cart was apparently insufficient to eliminate adaptation.

The RIPAE may turn out to have a similar explanation to that proposed by Pelah and Barlow (1996) for a visual illusion in which treadmill running, by virtue of the absence of optical flow, produces a visual sensation of accelerated forward motion when later walking on fixed ground. Pelah and Barlow measured this effect by having participants attempt to maintain a constant perceived visual velocity while repeatedly walking a constant distance. Because perceived visual velocity was initially heightened by the aftereffect, participants had to accelerate their walking speed over time as the effect wore off in order to maintain the same perceived flow speed. Importantly, the participants in that study were well aware that they were physically accelerating; it was simply the only way they could maintain the same visual impression. These kinds of motor-contingent visual illusions seem to be a complement to the RIPAE. Although the RIPAE can be generated and tested with eyes closed, it may normally involve a kind of vision-contingent calibration of motor signals based on the absence of appropriate, and perhaps convincing, visual flow information during adaptation.

Our experiments have shown that in the presence or absence of audition, altered visuomotor experience affects the attempt to run in place with eyes closed. Thus, runners seem to depend on implicit visuomotor expectancies even in the absence of vision, which is consistent with the idea that such expectancies are normally useful for predicting the outcomes of action prior to receiving visual feedback. Modifications of these visual expectancies can affect later actions performed in the absence of visual feedback (cf. Rieser et al. 1995).

It remains possible that participants in all of our various conditions adopted abnormal gait when running with unusual visual feedback (cf. Dietz et al. 1994; Konczak 1994; Prokop et al. 1997). However, the fact that aftereffects are increased when running on a treadmill with eyes open compared with eyes closed (Durgin and Pelah 1998) suggests that the data from the golf-cart experiment cannot be interpreted simply in terms of gait adjustments to blind running. Moreover, our open-field ganzfeld experiments have shown that holding the treadmill bar (or golf-cart bar) is not a necessary condition for adaptation. It therefore seems that altered visual feedback, rather than anomalous gait, plays the pivotal role in inducing the aftereffect even when the eyes are closed.

Closing the eyes can sometimes prevent progression of change in visual adapted state. For example, recovery from contingent adaptation in the McCollough effect is halted (adapted state is maintained) during periods of sleep (MacKay and MacKay 1974; 1975). Moreover, contrast threshold elevation following spatial frequency adaptation is also stored unchanged during periods of visual inactivity when the eyes are closed (Thompson and Movshon 1978). Although the above effects are purely visual, it is nevertheless surprising to find visuomotor adaptation actually taking place in the absence of vision. However, it seems from the present case that closing the eyes while moving disrupts the normal correlations between active locomotion and visual feedback, and that the activity of the legs is apparently sufficient to drive visuomotor adaptation even in the absence of vision. Anstis (1995) reported that the RIPAE dissipated after a minute or two of standing with eyes closed. Since standing is still an active motor process, however, it would be interesting to know whether lying down following adaptation might result in longer storage and whether visual information during this period is of any consequence. It is apparent from the evidence presented here that closing ones eyes is insufficient to disengage processes underlying this kind of visuomotor adaptation.

We have argued that the RIPAE is the result of visuomotor adaptation despite being generated in the absence of explicit vision, or that perhaps a more general recalibration takes place involving multi-sensory feedback relevant to the updating of body location. Because of the possibility that gait parameters may be affected by visual information during running (e.g. Dietz et al. 1994), gait adjustments cannot be ruled out as an additional factor. However, there

is a clear tendency for the strength of the aftereffect to change according to the amount of appropriate and convincing visual flow during adaptation. Providing an unusual relationship between effector activity and the resulting perceptual information about self-motion (or a lack thereof), recalibrates a system that is apparently able to control running in one place with the eyes closed.

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Author Notes