

Research Article

NOT LETTING THE LEFT LEG KNOW WHAT THE RIGHT LEG IS DOING: Limb-Specific Locomotor Adaptation to Sensory-Cue Conflict

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Abstract—We investigated the phenomenon of limb-specific locomotor adaptation in order to adjudicate between sensory-cue-conflict theory and motor-adaptation theory. The results were consistent with cue-conflict theory in demonstrating that two different leg-specific hopping aftereffects are modulated by the presence of conflicting estimates of self-motion from visual and nonvisual sources. Experiment 1 shows that leg-specific increases in forward drift during attempts to hop in place on one leg while blindfolded vary according to the relationship between visual information and motor activity during an adaptation to outdoor forward hopping. Experiment 2 shows that leg-specific changes in performance on a blindfolded hopping-to-target task are similarly modulated by the presence of cue conflict during adaptation to hopping on a treadmill. Experiment 3 shows that leg-specific aftereffects from hopping additionally produce inadvertent turning during running in place while blindfolded. The results of these experiments suggest that these leg-specific locomotor aftereffects are produced by sensory-cue conflict rather than simple motor adaptation.

How do people know how fast they are moving? How do they know if they are moving? Standing in one place is easy, even with eyes closed, but what about running in place, or hopping? In fact, in the absence of visual and auditory localization information, when people attempt to run in place, they tend to drift forward without realizing it (Durgin & Pelah, 1999). Moreover, after running on a treadmill (Anstis, 1995) or on solid ground with eyes closed (Durgin & Pelah, 1999), there is a dramatically increased tendency for forward drift, which can amount to several meters in a 20-s period. Anstis argued that this aftereffect is specifically due to motor adaptation involving postural adjustments peculiar to treadmill running. Durgin and Pelah, however, suggested that it is due to locomotor recalibration associated with adaptation to conflicting sensory information (cues) about self-motion, specifically, an absence of visual motion signals. In this article, we explore the limb-specificity of such aftereffects, one of the chief findings thought to favor Anstis's motor-adaptation explanation, and show that the evidence actually supports the sensory-cue-conflict account.

In previous publications, we have referred to this cue conflict as "sensory conflict" in order to emphasize the role of visual input in the calibration of locomotor control. However, the set of signals that may be in conflict could include efference copy, so we use the more generic term "cue conflict" here. We often refer to "sensory-cue conflict" in particular, to emphasize the role of perception in the recalibration of action. By cue, we mean specific information that can be used to estimate the value of some motor or perceptual variable (e.g., rate of self-motion). Many separate sources of information (cues) are normally available for use

in estimating self-motion. Presumably these various cues are integrated, but in normal locomotion, visual feedback is likely to be highly weighted. Indeed, visual signals are normally so conspicuous during locomotion that their absence, even when the eyes are closed, may constitute a cue (absence of expanding optical flow) specifying nonmotion. Our general account is consistent with the notion of an "internal model" (e.g., Wolpert, Ghahramani, & Jordan, 1995) of the self in space, but our emphasis is on the recalibration produced by discrepancies between various sources of information normally relevant to updating the internal model of the self in space.

To understand how sensory-cue conflict can arise during locomotion, consider that locomotor-control systems are designed to produce specific amounts of self-motion. These control systems therefore need to estimate the amount of self-motion that will be produced by a certain kind of motor activity, and then calibrate themselves using sensory feedback obtained when that motor activity is actually performed. Treadmill running produces cue conflict between the estimate of self-motion provided by the locomotor system (which predicts that running will produce forward movement) and the feedback received from other sensory systems, such as vision or the vestibular system (which indicates that no movement is taking place). It is this conflict between the expected feedback (the locomotor estimate) and the actual feedback (the absence of appropriate visual motion signals) that could produce a shift in the locomotor estimate of self-motion (an aftereffect).

An alternate account of aftereffects from treadmill locomotion is that the locomotor systems simply acclimate to a particular motor pattern (e.g., forward thrust) and persevere in producing that pattern. This is a version of a simple motor theory of adaptation. Anstis's (1995) discussion of this theory includes the idea that there may be inconsistent feedback concerning the posture of the leg following a stride on a treadmill, for example, but the emphasis of his account is that visual information is irrelevant to these forms of locomotor adaptation.

Anstis's (1995) case for simple motor adaptation was based on three distinct findings. First, adaptation to treadmill running can be accomplished with eyes open or closed. This seemed to distinguish it from the kind of visuo-motor recalibration reported by Rieser, Pick, Ashmead, and Garing (1995; but cf. Durgin, Pelah, & Amiruddin, 1998). Second, the aftereffects occurred only for treadmill running and did not occur for normal running. This argument has been countered by a later finding that normal running with eyes closed does produce a running-in-place drift aftereffect (Durgin & Pelah, 1999), although running with eyes open does not. This later finding is consistent with a sensory-cue-conflict account. Anstis's third piece of evidence was that one-legged hopping on a treadmill produced inadvertent drift when subjects later attempted to hop in place on the same leg with eyes closed. Crucially, it seemed, this aftereffect occurred only for the leg originally hopped on. Anstis argued that the failure to transfer to the nonadapted leg demonstrated that this was a purely motor aftereffect, by analogy to visual aftereffects that do not show interocular transfer.

Visual aftereffects that do not show interocular transfer are often

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regarded as occurring at a locus in the visual stream preceding the combination of the eye signals (Blake, Overton, & Lema-Stern, 1981). However, it is not clear that the analogy from interocular transfer to interlimb transfer is appropriate. Calibration of an individual limb with respect to other sensory information would still be functionally useful (Harris, 1963). Thus, even if adaptation is limb-specific, it still could, in theory, be induced by discrepant visual signals. Most likely, it is (cortical) motor control of the limb that has been altered during adaptation, not the limb itself. Therefore, a single leg could be recalibrated with respect to novel sensory feedback registered in the cortex.

The cue-conflict hypothesis suggests that the locomotor aftereffects under discussion occur because treadmill locomotion entails motor activity in the absence of normal sensory feedback. Indeed, whether the eyes are open or closed on a treadmill, there is an absence of the sensory feedback normally associated with locomotion. In neither case does one have the experience of moving forward. Because locomotion without sensory feedback about self-motion is a rare experience for most people, there is no reason to expect the perceptuo-motor control systems to be prepared for it.

To pit the sensory-cue-conflict hypothesis against the motor hypothesis, we adapted subjects to one-legged outdoor hopping with or without a blindfold. The simple motor theory states that vision is irrelevant and that the blindfold manipulation should have no effect. According to this simple account, there would be no aftereffects in either adaptation condition because of the lack of a treadmill. We reasoned, in contrast, that hopping while blindfolded would produce cue conflict because of the absence of normal visual feedback about self-motion, and that blindfolded subjects would therefore show aftereffects. Upon testing this hypothesis, we were somewhat surprised to observe that forward hopping without a blindfold also seems to involve cue conflict—for the leg that is not doing the hopping.

EXPERIMENT 1: OUTDOOR HOPPING

The purpose of this experiment was to test whether forward hopping could produce leg-specific aftereffects under conditions of sensory-cue conflict. Specifically, we hypothesized that during hopping, absence of the visual signals usually concomitant with self-motion represents a limb-specific sensory-cue conflict.

Method

Subjects

Because hopping without support is quite strenuous, we recruited male and female athletes (members of the Swarthmore College swim team) to participate in exchange for money toward their annual team fund drive. Ten college-age students participated.

Design

Each subject was adapted to hopping along an outdoor track on one leg (randomly selected) while wearing a blindfold and on the other leg without wearing a blindfold. (Opaque swimming goggles lined with black felt served as a blindfold.) Order of adaptation condition was counterbalanced across subjects and crossed with which leg was adapted first. Both before and after adaptation, the amount of inadvertent forward advance made when attempting to hop in place on each leg was measured in centimeters.

Procedure

After being informed of the requirements of the experiment and signing consent forms, subjects were asked to hop for 20 s in place on each leg while blindfolded. This was done in order to familiarize subjects with the experimental task and to establish baseline performance. Stickers were placed on the track to mark subjects' starting and stopping points for the stationary hopping task, but subjects were not permitted to see the stickers or to otherwise receive feedback about their inadvertent motion. For adaptation, subjects were then asked to hop along the track for 30 s either with or without a blindfold. In the blindfolded condition, an experimenter ran ahead of the subjects and guided them vocally.

Upon completion of adaptation, subjects were immediately instructed to stop and put on a blindfold (or keep it on). They were then tested on the blindfolded stationary hopping task for 20 s on each leg. The adapted leg was always tested first, because the adaptation state of this leg was expected to be primarily altered by the manipulation of visual feedback. Following a brief rest, the second adaptation period and posttest measurements of drift were undertaken. Subjects were then debriefed.

Results and Discussion

For each subject, inadvertent drift following adaptation was computed in centimeters per second. We had predicted that there would be heightened drift only in the adapted leg and only in the blindfolded adaptation condition. The mean drift rates for each of the four cells of the design are shown in Figure 1. As expected, drift in the adapted leg was greater following blindfolded adaptation (5.3 cm/s) than eyes-open adaptation (4.0 cm/s), $t(9) = 2.02$, $p < .05$, one-tailed. When subjects were blindfolded during adaptation, drift was also greater in the adapted leg (5.3 cm/s) than in the nonadapted leg (3.3 cm/s), $t(9) = 2.0$, $p < .05$, one-tailed. Thus, the principal cue-conflict condition (motor activity without visual feedback) differed in the expected manner from both of the non-cue-conflict conditions, (a) motor activity with visual feedback and (b) neither motor activity nor visual feedback.

To our surprise, however, in the no-blindfold condition, there was an apparent reduction in drift for the nonadapted leg (1.8 cm/s) relative to the adapted leg, $t(9) = 2.7$, $p < .05$, two-tailed. This nonadapted/no-blindfold condition can be regarded as involving cue conflict in a different direction: visual feedback specifying self-motion in the absence of appropriate motor activity (the other leg is not hopping). In other words, it seems as if locomotor recalibration of the nonadapted leg resulted because the locomotor calibration system was not prepared to treat the visual feedback as being specific to the leg doing the hopping. Just as the locomotor system is probably not prepared for extended locomotion without appropriate visual feedback, it is likely that it is not prepared for extended periods of single-limb locomotion. Despite the fact that the unused leg was not actually hopping, it was an active participant in the locomotor task (supplying balance, etc.), and the cortex received concomitant optic flow appropriate to self-motion without the leg having to do much work. (In Anstis's, 1995, experiments on treadmills, there would have been no opportunity for such a contingency, because there was never any sensory feedback specifying self-motion.)

Thus, all of these results are consistent with cue-conflict theory. The leg-specific drift in stationary hopping performance produced by adaptation to hopping is produced by sensory-cue conflict, not by the motor activity of forward hopping itself.

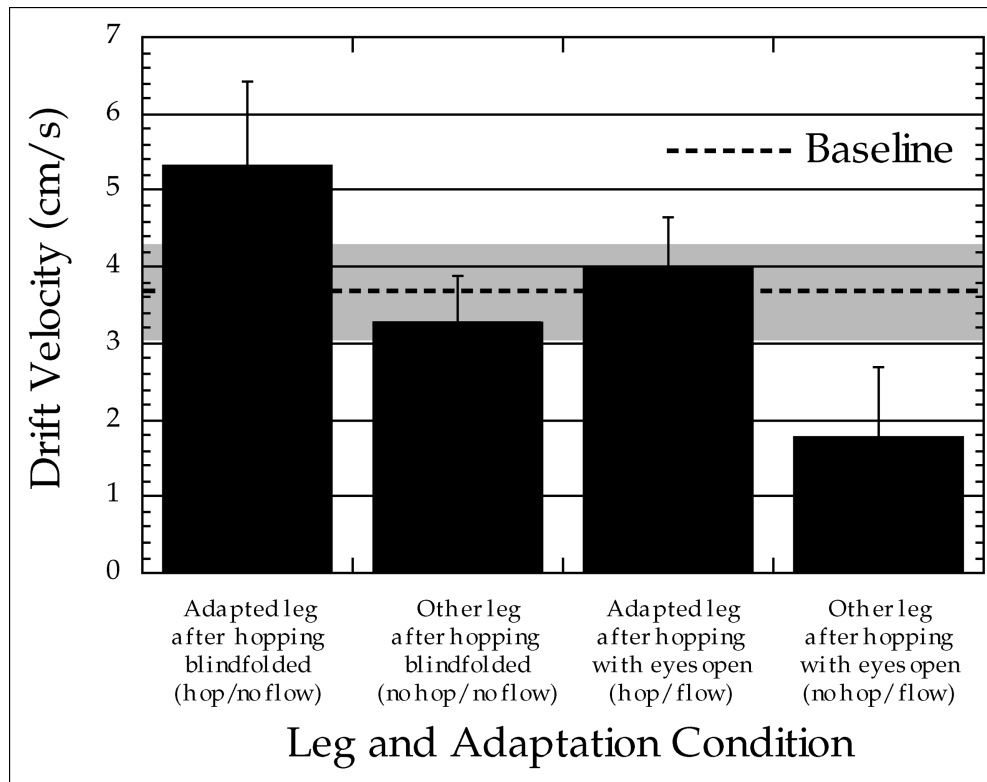


Fig. 1. Results of Experiment 1: Average forward velocity of inadvertent drift during blindfolded hopping in place following adaptation. Average baseline drift is shown as a dashed line within a gray band representing standard error. Postadaptation drift is shown as a function of leg tested (adapted vs. other leg) and visual experience during adaptation (visual flow, no visual flow).

EXPERIMENT 2: TREADMILL HOPPING

A second consequence of the cue conflict present during stationary treadmill locomotion is shown by subjects' overshoot in a blindfolded walking-to-target task (Durgin et al., 1998; Rieser et al., 1995, Experiment 2). After walking on a treadmill for several minutes with their eyes open, subjects walked too far (by about 10%) when asked to walk to a previewed target while blindfolded (Rieser et al., 1995). Considering these results and the results of Experiment 1, we decided to test whether adaptation to one-legged hopping on a treadmill (cue conflict) would produce a leg-specific aftereffect on efforts to hop to a visually previewed target while blindfolded.

To ensure that any overshoot on the hopping-to-target task resulted from locomotor recalibration rather than mere fatigue from the effort of hopping, we conducted a control experiment after completion of the main experiment. In the control experiment, subjects hopped in place on an unmoving treadmill belt during the adaptation period—a situation without sensory-cue conflict.

Method

Subjects

A total of 30 college-age male and female students participated. Because less strenuous hopping was required than in Experiment 1 (because of the presence of treadmill rails for support), the students

who were paid to participate were selected without regard to athleticism. Twenty subjects were in the main experiment. An additional 10 participated in the control version of the experiment with no cue conflict. All were paid for their participation.

Design

The cue-conflict experiment was designed to test whether hopping on a treadmill (5 kph) would produce leg-specific overshoot in later attempts to hop (blindfolded) to a previewed target location. Four different target distances were used during a pretest, two for each leg (6.0, 6.5, 8.5, and 9.0 m). Short and long distances were alternated, with order and hopping leg counterbalanced. Hopped distances were measured in centimeters and expressed as proportions of the target distances. Subjects were then adapted (twice) to hopping on the treadmill for 30 s and tested immediately afterward each time with distances of 7 or 8 m on either the adapted or nonadapted leg. The first target distance and first leg tested were crossed and counterbalanced across subjects. One leg and one target distance were tested after the first period of adaptation. The other leg and target distance were tested after the second adaptation period. Note that in this experiment, the same leg was adapted twice so that the effect on each of the legs could be assessed immediately following adaptation.

For the no-conflict control condition, the same design was used except that the treadmill belt was stationary during adaptation.

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Apparatus and procedure

All treadmill adaptation occurred with eyes open to maximize sensory information about the absence of forward motion. A Landice 8700 treadmill was set to 3.2 mph (5 kph) or turned off. During adaptation, subjects held onto the treadmill rails for support and stability. All hopped-distance testing was done with environmental sounds masked by music played through radio headphones (to prevent auditory localization) and vision masked by a blindfold (opaque swimming goggles lined with black felt). While previewing the distance to be hopped, subjects stood with both feet on the floor and the blindfold raised above their eyes. They then lowered the blindfold and commenced hopping toward the target location. While hopping toward the target, subjects gripped a small piece of plastic pipe that slid freely along a taut guide wire to prevent veering.

Prior to the start of their participation, all subjects were provided with 3 to 5 min of unstructured practice. They were allowed to hop to self-selected targets without vision using a duplicate guide-wire setup in a room separate from that used for the experiment. Following practice, subjects performed the four pretest distance trials without feedback. These were followed by the two adaptation periods interleaved with the two posttest distance trials, all without feedback. The 20 experimental subjects were tested first. The control experiment was conducted immediately afterward with 10 additional subjects.

Results and Discussion

For the experimental group, the average pretest hopping distance was 95% of the target distance. As illustrated in Figure 2, students later overshoot the target distance when tested on the adapted leg and did not overshoot when tested on the nonadapted leg. Planned comparisons showed that the posttest distance ratio on the adapted leg (1.07) was greater than the pretest distance ratio (0.95), $t(19) = 4.04, p < .01$, as well as greater than the posttest distance ratio on the nonadapted leg (0.99), $t(19) = 2.56, p < .05$. The nonadapted leg did not differ reliably between posttest and pretest, $t(19) = 1.20, n.s.$ In other words, hopping on the treadmill-adapted leg demonstrated a leg-specific overshoot aftereffect.

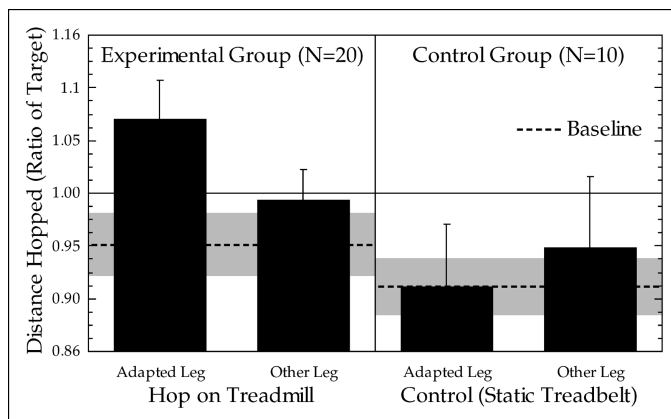


Fig. 2. Results of Experiment 2: Average distance hopped (as a proportion of the target distance) on the adapted leg and the other leg in the main cue-conflict experiment (left) and no-conflict control experiment (right). Average baseline distance hopped is shown as a dashed line within a gray band representing standard error.

For subjects adapted to simply hopping on a stationary treadmill, distance ratios hopped on the adapted leg (0.91) did not differ from the pretest distance ratio (0.91), $t(9) = 0.157, n.s.$, or from distances hopped on the nonadapted leg (0.95), $t(9) = 0.853, n.s.$ That is, there was no aftereffect in the absence of cue conflict between locomotor activity (hopping in place) and sensory feedback (in this case, the perception of staying in place). The mere effort of hopping in place did not produce a change in the calibration of hopping, without vision, to a visually previewed target.

Taken together, the results of Experiments 1 and 2 demonstrate a second form of leg-specific locomotor adaptation to cue conflict.

EXPERIMENT 3: TRANSFER TO TWO-LEGGED LOCOMOTOR ACTIVITY

Experiment 2 demonstrated differential calibration of the two legs from treadmill hopping. The purpose of Experiment 3 was to test whether the different calibration states of the two legs would be expressed when both legs were used together. In particular, we expected that adaptation to treadmill hopping would produce a tendency to rotate away from the adapted leg during attempts to run in place while blindfolded.

Method*Subjects*

A total of 20 college-age male and female students participated.

Design and procedure

To test how the separate leg calibration states might affect bipedal locomotor performance, we asked subjects to run in place while blindfolded before and after adapting to treadmill hopping. We measured inadvertent drift (both forward drift and lateral drift with respect to their initial orientation) and angular turning during 20 s of blindfolded running in place. Hearing and vision were blocked during testing, as in Experiment 2.

Adaptation consisted of 30 s of hopping on a treadmill at 5 kph. Leg of adaptation was randomized across subjects.

Results and Discussion

Changes in orientation and drift were coded so that positive values indicated movements consistent with the hypothesis that subjects would turn away from the adapted leg.

Results are shown in Figure 3. As predicted, there was a positive overall change in orientation (12.8°) following adaptation, $t(19) = 2.23, p < .05$, one-tailed. Consistent with the orientation change, the lateral drift away from the adapted leg also increased, from 0.23 cm/s before adaptation to 1.17 cm/s after adaptation, $t(19) = 2.54, p < .01$, one-tailed. Overall forward drift also increased, from 10.6 cm/s to 13.1 cm/s, $t(19) = 2.23, p < .05$, one-tailed.

Evidently, a leg-specific change in calibration affects running in place as well as hopping. This is consistent with the suggestion by Rieser et al. (1995) that locomotor aftereffects are not gait-specific. They found that recalibration of forward walking generalized to side-stepping tasks. It has also been reported that differential limb calibration produces veering while walking following adaptation to walking on a rotary treadmill (Earhart et al., 2001).

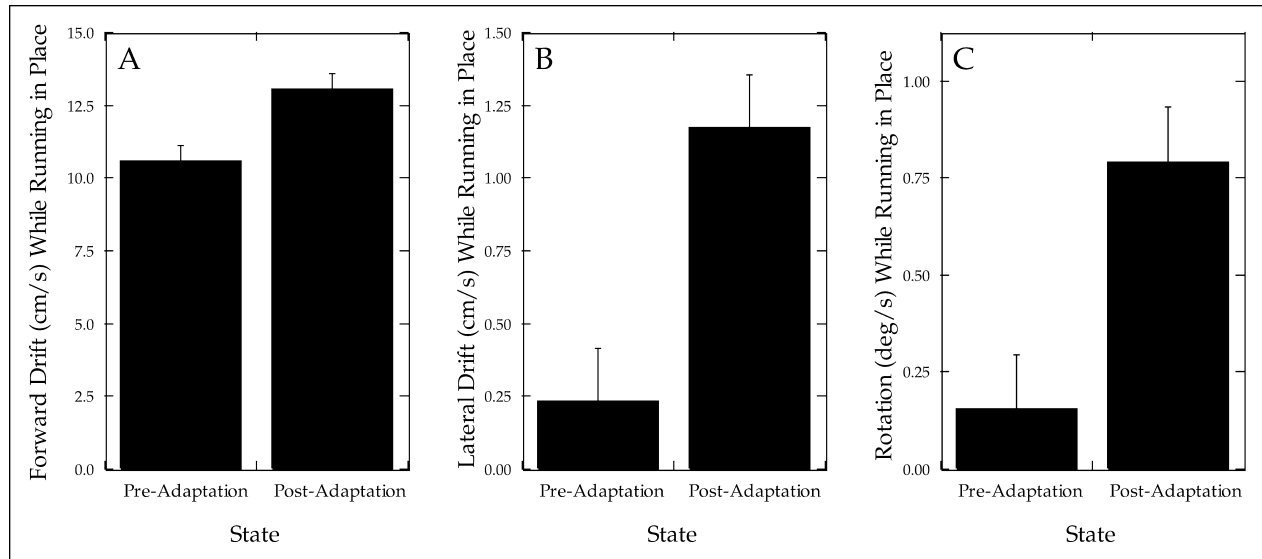


Fig. 3. Results of Experiment 3: Forward drift (a), lateral drift (b), and average rotation away from the hopped-on leg (c) while running in place with eyes closed before and after hopping with eyes open on a moving treadmill. Lateral drift was coded as distance drifted away from the side of the hopped-on leg.

GENERAL DISCUSSION

In the normal course of life, locomotor activity produces highly predictable perceptual feedback concerning self-motion. Calibration processes are ubiquitous in perception and must be tuned in to the relationships between action and perception, so that planned actions can have predictable perceptual consequences.

In this report, we have explored several locomotor aftereffects. The adaptation conditions, test conditions, and findings are summarized in Table 1. Consistent with the suggestions of Durgin and Pelah (1999; Durgin et al., 1998), these aftereffects appear to result from sensory-cue conflict, even though they are limb-specific.

Calibration processes should respond to cue conflict. In the case of locomotor recalibration, the hypothesized common cause of the after-effects investigated here is misperception of self-motion following cue conflict between locomotor activity and self-motion perception. A misperception of self-velocity after adaptation to a cue-conflict situation could produce both the drift seen for hopping in place and the overshoot seen in hopping to a target. It could also explain the turning found in Experiment 3. Presumably, such misperception arises because the normal relationship between locomotor activity and perceptual feedback has been altered by adaptation.

Although we were not expecting perceived self-motion to produce cue conflict for the nonadapted leg, the results of Experiment 1 are

Table 1. Summary of results

Experiment and condition	Adaptation	Information available			Finding	
		Specifying motion	Specifying stasis	Assessment (without vision)	Adapted leg	Other leg
Experiment 1 Conflict	Hop on track					
	Forward hopping, eyes closed	Motor (AL), vestibular	Absence of optic flow	Hopping in place	Increased drift	No change
Control	Forward hopping, eyes open	Motor, visual, vestibular	None	Hopping in place	No change	Decreased drift
Experiment 2 Conflict	Hop on treadmill					
	Moving treadmill, eyes open	Motor (AL)	Visual, vestibular	Hopping to target	Overshoot	No change
Control	Stopped treadmill, eyes open	None	Motor, visual, vestibular	Hopping to target	No change	No change
Experiment 3 Conflict	Hop on treadmill Moving treadmill, eyes open	Motor (AL)	Visual, vestibular	Running in place	Turning away from AL (both legs tested together)	

Note. AL = Adapted leg. Note that the leg not hopped on during adaptation arguably has a motor signal specifying stasis in all experiments.

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consistent with such a possibility. This other leg was not entirely inactive during hopping, because it was used as a self-stabilizing weight. Because it was not directly responsible for the perceived self-motion, it need not have shown an aftereffect. However, it is consistent with the cue-conflict account that the separate calibration of the limbs might not entail assessment of which limb is causally responsible for sensory feedback specifying self-motion. All that is required is that the current activity of a limb be compared with sensory feedback received and that changes in calibration result from any perceived mismatches.

We believe that our findings also bear on another issue. Proffitt, Stefanucci, Banton, and Epstein (2003) have recently suggested that distance perception is modified by exposure to locomotor-cue conflict. In a replication of Durgin et al. (2000), they found that a walking-in-place drift after treadmill walking was reduced when appropriate visual flow was supplied using virtual reality (thus reducing cue conflict). They then demonstrated that perceived distance (as measured by verbal estimations) was similarly modulated by their two adaptation conditions (optic flow and no flow while treadmill walking). However, because their adaptation conditions differed in visual feedback alone, it is possible that the apparent change in visual distance perception was due to adaptation to some aspect of the visual feedback received in the virtual environment. Because distance perception may typically be distorted by virtual reality itself (Loomis & Knapp, in press), it is possible that purely visual cue conflict (e.g., adaptation to motion parallax information in virtual reality) was responsible for the change in distance perception that Proffitt et al. found. However, it also remains possible that verbal estimates of distance reflect an interaction of visual distance information and altered motor calibration.

If visual distance perception had itself been altered by the present hopping paradigms, then we would not expect the aftereffects of hopping-to-target to be leg-specific. That is, if visually perceived distances had been increased by the effort of hopping, then all conditions in Experiment 2 should have shown overshoot, but they did not (see Philbeck, Loomis, & Beall, 1997). It is possible that distance judgments vary as a function of intended task, such that our subjects actually evaluated distance differently depending on which leg they were about to hop on. However, the hopping-in-place task (which involves no distance estimation) and the hopping-to-target task (which does) show a common leg-specific underestimation of self-velocity. This strongly suggests that locomotor aftereffects such as these are expressed primarily through the recalibration of unconscious control systems concerned with predicting the consequences of motor activity on self-motion.

We have suggested that these control systems are smart enough to separately calibrate different legs, but may not be smart enough to appreciate that a given leg has nothing to do with the actual sensory feedback received during locomotor activity. It is unclear whether entirely passive vehicular transportation might also produce a reduction in forward drift during stationary hopping. However, the manipulations of Rieser et al. (1995, Experiments 3 and 7) seem to rule this out for a blindfolded walking-to-target task.

The conditions for generating and measuring the first two aftereffects reported here are somewhat symmetrical. In Experiment 1, cue conflict during forward hopping locomotion produced an aftereffect on attempts to hop in place. Our procedure allowed us to vary whether visual information specifying self-motion was provided during the forward hopping. In Experiment 2, we showed that adaptation to cue conflict while hopping in place on a treadmill produced an aftereffect on attempts to hop forward to a target. We were able to vary cue conflict by manipulating whether kinesthetic-motor information specifying self-motion was present or not, by conducting the adaptation on a moving or static treadmill. In all cases, sensory-cue conflict produced recalibration whereas mere motor activity without conflict did not.

Cue conflict in locomotor control may arise whenever normal perceptuo-motor interactions are disrupted as by treadmill locomotion or by extended locomotion without vision. We conclude that limb-specific locomotor aftereffects result from extended adaptation to sensory-cue conflict rather than unusual motor activity alone.

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