Proprioceptive Adaptation and Aftereffects

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1. INTRODUCTION

Until relatively direct interface with brain signals become widely available, users will have to play a physically active part in controlling the virtual environment (VE). This involves moving the head, eyes, limbs, or whole body. Control and perception of movement depends heavily on proprioception, which is traditionally defined as the sensation of limb and whole body position and movement derived from somatic mechanoreceptors. This chapter presents evidence that proprioception actually is computed from somatic (muscle, joint, tendon, skin, vestibular, visceral) sensory signals, motor command signals, vision, and audition. Experimental manipulation of these signals can alter the perceived spatial position and movement of a body part, attributions about the source and magnitude of forces applied to the body, representations of body dimensions and topography, and the localization of objects and support surfaces. The effortless and unified way these qualities are perceived in normal environments depends on multiple, interdependent adaptation mechanisms that continuously update internal models of the sensory and motor signals associated with the position, motion, and form of the body, the support surface, the force background, and properties of movable objects in relation to intended movements.

An understanding of these mechanisms is important to VE users because VEs will sometimes inadvertently and sometimes purposely expose active users to never before encountered combinations of sensory and motor signals and environmental constraints. In many cases, this will lead to perceptual and motor errors in the VE until internal adaptation has been updated. When a user who has adapted to a VE carries the new adaptive state back into the normal environment, he or she will experience aftereffects, usually in the form of mirror image errors to those initially made in the VE (see chap. 31, this volume). These can include deviated execution of limb and whole body movements, proprioceptive errors, misestimates of externally imposed forces, and visual and auditory mislocalizations.
This chapter will use concepts derived from laboratory studies as a basis for interpreting measurements of proprioceptive side effects and aftereffects in virtual environments. It discusses what VE conditions will alter the state of sensory and motor adaptation, what components of the movement and orientation control system will adapt, what side-effects and aftereffects will result from adaptive modification of these subsystems, and what concepts will evoke aftereffects. This survey emphasizes facets of proprioception relevant to VEs involving manual performance and whole body motion tasks. A balanced presentation is attempted of both the value and the limitations of laboratory-based conceptual distinctions for making the best predictions in practice.

2. PROPRIOCEPTION, MOTOR CONTROL, AND SPATIAL ORIENTATION

2.1 Musclesory and Motor Factors

In his analysis of sensation and motor control, Sherrington (1906) coined the term proprioception for the mechanoreceptors located inside body tissues that are primarily responsive to changes within the animal itself. Examples of these receptors are spindle organs in the muscles, Golgi tendon organs, unmyelinated Ruffini endings of the joints, and various sensory types in the viscera and cardiovascular system, which were thought to be inaccessible to external energy but well suited to body orientation, configuration, and movement. In conscious, systems whose sensors are located on the body surface and receive external stimuli were categorized as exteroceptive. The skin mechanoreceptors are located on the boundary of the environment and the body and have overlapping proprioceptive and exteroceptive roles. They are involved in discriminative functions, texture, pain, temperature, and other complex properties of the external world as well as body configuration, motion, and orientation (especially for the fingers, lips, and tongue).

Vision, audition, and olfaction are exteroceptive systems, but they can also be used to monitor motion and orientation of the limbs and the whole body. Sherrington noted that the vestibular labyrinth of the inner ear (semicircular canals and otolith organs) is developmentally derived from the exteroceptive system, but it acts in concert with the proprioceptive system because it is stimulated by pressure changes and shear forces in the sensory end organs usually brought about by head and body motion and changes in orientation. His analysis acknowledges that proprioception is multisensory and overlaps with other experiential domains.

Proprioception is also directly related to motor control, internal signals corresponding to movement commands (the commanded not to move) have been posited as contributing to proprioception and spatial awareness. They have been called the desire (cristinum, 1978), the perceived effort of will (Helmholtz, 1925), "effence copy" (von Holst & Mittelstradt, 1950), or "corollary discharge" (Sperry, 1959). The idea that such effence copy signals are sufficient for conscious perception of movements or position lacks strong empirical support (see McCloy & Torga 1975, for a review). For example, when humans are subjected to local isometric nerve block or systemic neuromuscular block and attempts to move one of their paralyzed limbs they do not perceive any illusory movement, but instead have a sense of great heaviness (Lasle, 1963; Melzack & Bromage, 1973). However, motor signals seem to interact with effence signals in visual perception and eulomotor control. For example, faultless attempts to move a paralyzed eye are accompanied by a great sense of effort and apparent motion and displacement of visual targets (Main et al., 1972). It is not clear whether sensory signals brought about by self-initiated movements...
and "efferent" signals evoked by external events. One way for this to happen would be for an efference copy signal to cancel only the reafferent portion of the total afferent signal. This requires an internal calibration in which the afferent and efferent signals are represented in comparable units and in the appropriate proportions.

2.2 Sensorimotor Calibration

The correlations between afferent and efferent signals, however, are very complex. For example, there is no unique pattern of motor command and sensory feedback signals associated with even a simple single-joint arm movement. Raising the forearm 45 degrees vertically or flexing it 45 degrees in a horizontal plane involve very different efferent commands to and sensory feedback from the biceps brachii and brachialis muscles because the gravity torques are so different. The muscle command and feedback signals also differ when weights are wielded or machines are manipulated, even for the same movement amplitude and orientation of the arm. A constant efferent command will not produce the same force in fatigued and rested muscle. Self-locomotion or vehicular transport can generate accelerative loads requiring unique muscle forces for accomplishing an arm movement, relative to when the body is stationary. To complicate matters further, body acceleration activates vestibular afferent discharge, which through vestibulospinal pathways innervates skeletal muscles and modulates muscle spindle sensitivity (cf. Wilson & McVicar-Jones, 1976). In order for the central nervous system to use an efference copy signal to cancel just the reafferent portion of the total afferent signal, it must first parse the sensory signals into components due to intended movement and anticipated external loads and the efferent signals into voluntary and involuntary components.

In other words, calibration of perception and motor performance involves internalization of the relationship between combinations of sensory and motor signals in relation to body movement and orientation, external loads, environmental constraints, and internal conditions. Recalibration is required when conditions change. For example, alterations in body dimensions, strength and sensory capacity throughout the life span, loss or distortion of motor or sensory function due to illness or injury, migration to a novel environmental medium (land to water) all require adaptive accommodations. There is ample evidence that given sufficient time humans can adapt to a wide range of stable sensory–motor rearrangements produced in the laboratory or in applied technological environments such as aerospace flight, traditional simulators, teleoperation, and VE (Held & Outlad, 1981; Kennedy, Fowkes & Lillienhal, 1995; Lackner, 1976, 1981; Rock, 1966; Wallach, 1976; Welch, 1978; chap. 31, this volume). Adaptation is often accompanied by aftereffects that degrade performance on return to the normal environment. Such aftereffects raise questions that must be addressed by VE system designers (see Table 34.1).

2.3 Muscle Spindles

Muscle spindle organs provide signals correlated with the full natural range of muscle length (limb position) and velocity (Harvey & Matthews, 1961). Spindles are connected in parallel with the muscle body so that they can be unloaded when the muscle contracts on receiving input from alpha motor neurons and loaded when the muscle lengthens. Stretch receptors embedded in each spindle’s visco-elastic central region project two types of sensory fibers signaling both the spindle’s length and rate of change of length (primary fibers) or only its length (secondary fibers). The polar regions of each spindle are composed of cocontractile fibers innervated by gamma motor neurons that provide independent central regulation of their afferent sensitivity (see Fig. 38.1). Heightened gamma innervation shortens the polar regions and thereby stretches
TABLE 38.1
Questions Concerning the Nature of Short-term Effects of VE Exposure

- What conditions will trigger adaptation?
- How do the internal calibration change?
- Can multiple states of calibration be maintained?
- In what contexts will different calibration states dominate?

These theoretical questions translate into practical uses for the VE context:
- Which VEs will elicit adaptation of proprioception, motor control, and perceived orientation?
- What kinds of attention will be expressed, and under what conditions?

![Diagram](image)

**FIG. 38.1.** Muscle spindles reside in parallel with extrinsic muscle fibers, which are excited by α-motor neurons and provide the contractile force for movements. In this simplified diagram, the primary (α) and secondary (β) afferent fibers are shown with sensory endings on the central elastic portion (gray area) of a single spindle, but in reality, type α and β fibers innervate different types of spindles. Primary fibers discharge in proportion to muscle length and are of change in length, and secondary fibers discharge in addition to length. Afferent discharge can be modulated by α afferent activity innervating intramuscular contractile fibers (striped area) located at the poles of each spindle, which leads or unleads the central region containing the sensory α-fibers but does not contribute to overall muscle force.

The central region and produces a greater afferent discharge rate, for the same overall muscle length. In contrast, quiescent gamma afferent activity relaxes the spindle poles, unloads the central region, and decreases the afferent activity while muscle length remains constant.

Until relatively recently, muscle spindle organs were thought to be important in reflexive motor control but not to influence the conscious awareness of limb position. Position sense was thought to arise from receptors in the joint capsules, but this view was weakened by evidence from humans with artificial hips. Although capsular receptors are absent in artificial joints, patients post-surgery were found nevertheless to have normal position sense accuracy of their hip (reviewed by Burgess & Wei, 1982). Muscle spindle activity is still present and is implicated in the hip position sensitivity.

In relaxed mammals, the muscle spindle firing rate is very low, about 0 to 4 impulses/sec. Higbath and Ekland (1966) found that low amplitude mechanical vibration applied to the skin over a muscle causes reflexive contraction of that muscle by entraining spindle afferent discharge to the vibration frequency and activating the stretch reflex. This phenomenon is
known as the tonic vibration reflex (TVR). The vibration technique was extended by Goodwin, McCreery, and Manley (1972) to demonstrate plus spindle afferent signals influence conscious sense of limb position and motion. In these experiments, the biceps brachii was vibrated and the participant's unseen forearm was restrained so that reflexive contraction would not shorten the muscle and unload the spindles. All participants reported feeling an increase in the elbow joint angle. The illusion could be quantified by having participants match the perceived angle of the elbow of their vibration arm with the other arm and measuring the discrepancy in forearm positions (see Fig. 28.2A). Similarly, triceps vibration elicited an illusory flexion of the forearm. Thus, an abnormally high discharge rate in the vibrated muscle is interpreted as lengthening of the vibrated muscle and this "lengthening" is referred to the joint) controlled by the muscle. If the same arm vibration experiment is done in 0 G, weightless conditions, the magnitude of the illusion is smaller than in normal 1 G conditions, and in an increased gravitational force background the illusion is larger (Lackner, DiZio, & Fisk, 1992). (Note: Gravitational force is the resultant of gravitational and inertial acceleration on a mass. 1 G equals the force due to acceleration due to gravity at sea level.) The novel force background affects the otolithic organs, which influence muscle tone by activating gamma motor neurons in the spinal cord, heightening the spindle afferent signal in high-force backgrounds, and decreasing it in 0 G. This mechanism is part of the vestibulospinal regulation of the antagonistic musculature of the body. Clearly, muscle spindle afferent and efferent signals influence proprioception and motor control.

2.4 The Role of Body Schema and Spatial Orientation

Vibration of the proper muscles can produce apparent displacement and motion of the head, arm, leg, and trunk (Lackner, 1988) in a dim room. The character of these vibratory myesthestic illusions demonstrates that perceptual interpretation of the afferent signal takes into account the anatomy and dimensions of the body. For example, a vibration-induced increase in biceps brachii spindle afferent discharge; (1) affects the perceived angle of the elbow joint, which is spawned by the biceps brachii; (2) alters it in a direction (extension) that agrees with the biceps' role as a flexor; and (3) evokes apparent spatial hand motion in an arm consistent with the elbow joint's hinge-like motion and the length of the forearm. Some participants experience anatomically impossible hyperextension of the forearm during biceps vibration whereas others after reaching the normal limits of extension perceive a paradoxical illusion of continuous motion without further displacement (Craske, 1977). Even nonmuscle appendages can undergo apparent distortion. For example, Lackner (1988) showed that if the participant holds the tip of the nose while the biceps brachii is vibrated, he or she will perceive the nose to grow in length as the forearm extends away from the face, as illustrated in Fig. 28.2B. The relatively stable, but modifiable, cortical representation of the body schema (topography and dimensions of the body) interacts with the moment-to-moment representation of body configuration based on peripheral muscle spindle and tactile signals. This conclusion is consistent with phantom limb experiences (Henderson & Smyth, 1948).

Achilles tendon vibration gives rise to a whole body movement backward relative to the support surface because of the TVR activation of the calf muscles (Ekholm, 1972). When the Achilles tendons of participants restrained in a standing position are vibrated they perceive forward body pitch, sometimes in full 360-degree circles, and even though they are physically stationary, they also show nystagmoid eye movements similar to what would be evoked by vestibulo-ocular reflexes during real body tumbling. Tactile cues from environmental surfaces can modify postural vibratory myesthestic illusions. Achilles tendon vibration normally leads to apparent rotation about the ankles, but if the participant bites a rigid dental mold then it may become the pivot point (Lackner & Levine, 1979). If a head-fixed target light is present during such illusions, it will be perceived as moving spatially relative to the current axis of rotation,
either the feet or the mouth. Thus, limb position, body orientation, and object localization are overlapping, interdependent representations, each derived from different combinations of muscle spindle information about a particular appendage and cutaneous and vestibular signals about spatial orientation. Exposure to VEs will generally not alter muscle spindle signals directly, but often will affect the user’s spatial orientation, which will influence the central interpretation of proprioceptive signals, resulting in perceptual and motor errors until adaptation occurs.

2.5 Bidirectional Interactions of Visual and Muscle Spindle Influences

Most VEs will have treacous visual displays, so research on the registration of seen versus felt body position and orientation is very relevant. Lackner and Tushilov (1986) assessed this in experiments where they made either the whole head or a single finger visible in a dark room by application of phosphorescent paint. When the biceps brachii was vibrated, participants felt the unseen forearm move and saw their finger or hand move as well but through a smaller distance (see Fig. 38.2C). The magnitude of felt motion of the forearm was less with the finger visible than in complete darkness, and it was least with the hand visible. In other words, “visual capture” (Hay, Pick, & Ikeda, 1961) was incomplete because the physically stationary visual finger did not prevent participants from seeing and feeling motion of their finger. Proprioceptive capture was substantial, the finger was seen to move nearly as much as the forearm was felt to displace.
If participants attempted to fixate their unseen hand as it underwent illusory downward motion their eyes moved down. However, when they fixated on a visible finger that they perceived as moving down during vibration their gaze remained spatially constant. The character and magnitude of vibration illusions changed in normal illumination conditions where participants could see their hand or finger in relation to the contours of the room, with the remainder of their arm being hidden below a screen. In this case, when the biceps brachii was vibrated, participants felt their unseen forearm move down but did not see the unoccluded finger or hand move. Felt motion of the arm was about 30% of what it had been in the dark room. These results indicate that multiple, interdependent, body-centered and spatially centered representations of hand and arm position exist, which are influenced by the visual and muscular spindle inputs. Seen and felt hand position are dissociable from each other and from motor responses. The strength of the bidirectional visual-proprioceptive influence relates to the amount of the limb that is represented. In VEs, the spatial correspondence of visual and real body positions, the level of detailed visual representation of the body and of the remainder of the virtual visual context will determine the magnitude and nature of proprioceptive and sensor errors.

2.6 The Role of Tactile Cues in Unifying Muscle Spindle and Other Sensory Influences

When the fingertip is portrayed only by a single point of light or a punctate sound source, there are still bidirecional influences and the role of tactile contact cues is paramount. For example, if in darkness a small target light is taped to the index finger of a participant's spatially fixed arm, the stationary light will appear to displace when the biceps brachii is vibrated, but the felt motion of the arm will be less than if no target were present (Levine & Lackner, 1979). If the two forearms are restrained in a horizontal plane and vibration is applied to the right and left biceps brachii, then the apparent distance between the fingertips will increase. If target lights are attached to the opposing index fingers, participants will see them get farther apart as they feel their fingers move apart (Giaco, Lackner, & Latham, 1993). During vibration, if physical contact of a target light and finger is broken by moving the tight a millimeter or more away from the finger, then the illusory visual target movement and displacement will be abolished and the illusory felt movement of the unseen limb augmented (see Fig. 38.2D). In this case, the lights seem to represent external objects instead of the tips of the fingers. During vibration eliciting apparent forearm extension or flexion, a participant will hear a sound source attached to their hand move and change spatial position in keeping with the change in apparent hand position. Breathing tactile contact with the axillary target abolishes illusory movement during vibration. Taken together with the experiments in which various amounts of the hand were visible, it is clear that the strength of interaction among multimodal representations of self and target position depends on tactile contact cues, visual configural cues, and visual context cues.

These results have important implications for whether VEs should represent body parts with simple visual icons, high-fidelity visual representations, or haptic interfaces. In the natural world, perception and motor control are unified and accurate because there are adequate contextual cues defining how to group multisensory representations and adequate internal calibrations of how these signals should be combined. By contrast, VEs create alternate physical worlds that may require novel combinational rules. For example, if adequate visual form cues and tactile contact cues are present for the visual image to be perceptually grouped with the muscle spindle representation of hand position, then the visual and felt locations will influence each other. If either the visual or proprioceptive signal is inaccurate, then both perceptual representations will be biased. However, if only a visual icon is present and there isn't a contact cue with the body, then the visual object will likely be perceived as an external target rather than a representation of the hand, and the spatial perception of each may be independent.
3. PROPRIORCEPTIVE ADAPTATION OF THE ARM TO VISUAL DISPLACEMENT

3.1 Sensory Rearrangement

Visual distortion is a likely scenario in VEIs involving manual tasks, and exposures will likely be prolonged and require users to be active. The reinal image may be degraded or augmented by many VE features such as the computer model of environmental objects, the technique for tracking the user's visual perspective, the graphical rendering system, and the optics of the display system. Retinal image rearrangement may be caused by inadvertent technological limitations or deliberate augmentation of reality. A typical unplanned distortion is where the visually displayed virtual position of an object does not correspond to its tactile or auditory virtual position because one or more of the display device is inaccurate. Improper initial alignment and random slippage of a head-mounted display's (HMD's) focal axis relative to the user's optic axis are sources of such unintentional visual inaccuracy (see chap. 3, this volume). A system latency in rendering a user's moving hand in an HMD that occludes the real hand results in a dynamic spatial dissociation of the seen and real hand positions (Ellis, Young, Adelstei, Ehrlich, 1999; Held & Duric, 1991). A deliberate distortion is introduced for example, when the visual image is magnified, as in the case of virtual microsurgery systems (Hunter et al., 1994). The laboratory studies reviewed below will illustrate that the type of rearrangement, activities performed, and opportunity for refferent and esfferent sensory stimulation govern the nature, internal form and specificity of adaptation that occurs with exposure to visual rearrangements. Measuring and understanding the side effects and intereffects of sensory-motion adaptation requires observing baseline performance before the rearrangement is introduced, the initial and subsequent performance during exposure, and the initial postexposure performance when normal conditions are restored (cf. Held, 1965).

Lateral displacement of the visual world by wedge prisms is an experimental analog of a possible visual rearrangement in a virtual environment. The vast literature on this topic (cf. Howard, 1966; Rock, 1966; Welch, 1978, for reviews; originates from Helmholtz's (1925) demonstration that small azimuthal displacements by prisms of the visual field can be adapted to in a matter of minutes. If a participant looks through base-left wedge prisms without sight of the hand, any object chosen as the target for a reaching movement will appear to the right of its true position, and a movement will be directed accordingly to the right. The prisms will make the hand as it comes into view look like it is moving more to the right than intended, away from the target, and typically participants will steer the hand nearer to the target in midcourse, but the movement endpoint will tend to be right of the target. Participants will see this gap and may also describe with surprise not seeing their arms where they feel it. It takes only 10 to 20 reaches to the same target under these conditions for participants to hit it and to move straight again, but when the prisms are removed they will reach too far to the left initially. Fig. 38.3A illustrates typical reaching paths before, during, and after exposure to wedge prisms. Improvement of performance while the world is viewed through prisms and the aftereffect when they are removed are measures of adaptation. Similar improvements and aftereffects are seen when lateral displacements are purposely introduced in a virtual environment (Goss & Werblin, 1998).

3.2 The Internal Form of Adaptation

Harris (1965) argued that when one can see only his or her arm and external targets in a featureless background, adaptation is achieved by an internally modified position sense of the arm. The participant eventually feels the arm where he or she sees it. For example, after
FIG. 38.3. The panels on the left are schematics of different auxiliary-motor rearrangements that evoke reaching errors, and with continued exposure different forms of adaptation. The panels on the right are stereoscopic (top view) of finger-trajectory before the rearrangement (solid line), during the initial reach attempted in the presence of the rearrangement (open symbols), and during the trivial reach attempted on return to normal conditions (filled symbols). A. When prisms that shift a visual target to the right cause the initial reach to deviate to the right and to curve slightly due to compensatory movements made when the hand comes into view. With many attempts, participants learn to make straighter accurate reaches (not shown) by modifying their internal representation of left arm position (see text). Persistence of the adaptation when the prisms are removed causes leftward end-point and curvature errors, neither symmetric to the initial reaches made during prism exposure. B. When participants are unaware they are rotating, they do not compensate for the Coriolis force (\(F_{\text{Coriolis}}\)) in their movements (\(v\)) generated and initially make reaching errors in the direction of the Coriolis force (open symbols). With practice they modify their motor programs as necessary to restore their baseline trajectory. C. When rotation ceases and they again try stationary, they make leftward end-point and curvature errors (filled symbols). The par and preeffect reaching errors are the same in A and B, although the internal form of adaptation differs. C. Stationary participants feel like they are rotating when viewing a moving virtual scene presented in a head mounted visual display (HMD). Their reaching movements deviate in the direction opposite to the Coriolis force, which would be present if they were actually rotating (open symbols). With practice they regain straighter accurate movement paths by learning not to compensate for anticipated Coriolis forces. This motor adaptation is specific to the self-rotation context simulated by the HMD and does not carry over to a normal stationary context; consequently, there are no aftereffects when the HMD scene is again stationary (filled symbols).
adaptation to base-right prisms the participant will reach to the target’s true position but see and feel the arm to the right of that position. The felt arm position then does not correspond to the real position, but visual and proprioceptive perception are unified and reacting movements are directed accurately to the target.

Harris recognized but rejected other possible forms of adaptation under these conditions. For example, he rejected the possibility that the adaptation is simply a conscious process of reaching to the left of where the target appears because when the prisms were removed his participants showed negative aftereffects instead of inverting to their baseline performance. Second, the adaptation is not an internal change in visual perception. Such a change would mean that a midline target optically shifted right would be in the course of adaptation come to be perceived as straight ahead, and when the prisms are removed it would be registered to the left of its true position and any movement aimed at it should deviate to the left. Contrary to this, Harris found that when prisms were removed an adapted participant pointed accurately with the unadapted hand, there was no intermanual transfer. Participants positioned their adapted hand to the left of the unadapted one when asked to align the two hands in azimuth in default. Also contradicting a visual shift was the finding that after the prisms were removed participants made comparable errors pointing to a visual target or to an unseen sound source. An alternate explanation to Harris’s is motor adaptation. Participants could, for example, change the direction in which they reach to targets without a concurrent change in the felt sense of limb position. Motor adaptation will be discussed in section 4.

The internal form of adaptation is influenced by activities performed and feedback obtained while wearing prisms and how much of one’s body and the world is visible. An interesting case is walking around but keeping the arm out of sight while wearing rightward displacing prisms (Hold & Bousher, 1981). At first, participants bump into things but are soon able to get around. When the prisms are removed the participants initially point incorrectly, leftward, with both arms to visual targets. They also adapt a resting head posture that is deviated in the direction of the optical displacement. These facts have been interpreted as meaning that adaptation in this context is achieved by an internal recalibration of perceived head position on the torso (Harris, 1965). In the paradigm where participants just sat and reached with one arm, only the arm had to be remapped to compensate. This illustrates that the nervous system tends to adapt in the way most specific to the conditions encountered during exposure to rearrangement. More extensive reviews on this topic are available (Dolezal, 1983; Lacksner, 1981).

In the two cases presented above, the sensory rearrangement is the same but the resulting form of internal adaptive shift differs. There can be an arm-torso recalibration when the participant just sits and points to a single target in a featureless field and a head-torso recalibration when the participant walks about in the normal world. This means that detecting and understanding VE side effects and aftereffects must take into account the physical distortions introduced by the VE, the nature of the visual field, and the tasks required of the user. There is enough evidence to indicate that the form of adaptation to a sensorimotor rearrangement depends on fine details of task characteristics, but not enough to make accurate predictions for every case imaginable in practical virtual environments. Several examples not explicitly covered by the reviewed studies are VEs where the visual position of the user’s hand and the whole visual scene are displaced, VEs where the virtual visual objects have real or virtual counterparts, and VEs where the hand is represented as a symbolic visual icon instead of realistically.

3.3 Conditions Necessary for Adaptation to Occur
Understanding what factors are necessary for adaptation to take place is important for predicting proprioceptive side effects and aftereffects from VE exposure. Held and colleagues (Held, 1985;
Held & Bosson, 1961) showed that active reaching or locomotor movements during visual rearrangement could elicit adaptation, but a laterally displaced view of one’s passively moved arm or sight of the world during passive transport did not generate adaptation. This led to the idea that effrence copy signals are required for adaptation. Held developed a model in which effrence copy signals were stored along with their correlated reafferent sensory signals so that any active movement would call up the normally associated visual reafferent signal for comparison with the actual one. In the reaching and locomotion paradigms, discrepancies between the reactivated and current reafferent visual patterns were thought necessary for adaptation to occur. A practical implication is that greater activity within a VE should speed up adaptation.

An alternative point of view is that active movements are only superior because they enhance proprioception (Paillard & Brouillon, 1968). Consistent with the idea that active movement is not necessary, Wallach, Kwantz, and Lindauer (1963) demonstrated that partial adaptation of reaching movements to visually displaced targets occurs if an immobile observer simply views the rest of his body through displacing prisms for ten minutes. Lackner (1974) went further, showing that a discrepancy between actual visual feedback and the visual feedback associated with voluntary movement is not sufficient for adaptation to occur, but a visual-proprioceptive discrepancy is necessary and sufficient for eliciting adaptation to laterally displacing prisms. When participants reached without sight of their arm to visually displaced dowels and contacted them with vertically aligned, similarly shaped extensions of these targets there was no visual feedback about the arm to compare with the visual feedback normally associated with the executed movement. Adaptation still occurred in this condition because there was a discrepancy between the visual and felt target position. Adaptation did not occur if the visual-proprioceptive discrepancy was eliminated by having participants point to the same array of prism-displaced dowels whose hidden lower halves were laterally offset to match the optical displacement. The results emphasize the importance for adaptation of sensory discrepancies as well as active control. They also demonstrate that adaptation is enhanced by establishing through fingertip contact an association between the unseen arm and visual targets. In VE systems, finger contact can contribute to the fidelity of the synthetic experience if vision and haptic interfaces are in register, or create side effects and aftereffects if they are discrepant.

3.4 Retention and Specificity of Adaptation

To assess retention of adaptation of reaching errors caused by laterally displacing prisms, Lackner and Lobovitz (1977) had participants participate in two adaptation sessions 24 hours apart. Each session had pre- and postexposure periods of reaching to virtual visual targets without sight of the arm and a prism exposure period in which participants reached to the same loci with their arm in view. A surprising finding was that in the preexposure period of the second session, reaches were deviated in the direction of the aftereffects from the previous day, although none of the participants reported any difficulty with visuo-motor control between sessions outside the laboratory. This demonstrated a long-term aftereffect and raised the possibility that it was a context-specific aftereffect. To further evaluate retention and context specificity, Yacubel and Lackner (1977) gave participants six adaptation sessions over a 4-week period. The sessions were similar in that participants pointed to visual targets with their arm under a screen before and after exposure to visual displacement in which they reached with sight of their arm. Tests were conducted in two different sets of apparatus requiring different arm movements. Retention of adaptation from session to session was seen in the form of preexposure baseline shifts across the first five sessions, which were spaced two or three days apart. The size of the long-term aftereffect did not depend on what apparatus the participant was tested in. Aftereffects appeared when the participants were tested without being able to see their
4. ADAPTATION TO ALTERED FORCE BACKGROUNDs

The notion of motor adaptation introduced in section 3.2 is crucial for understanding side effects and aftereffects in real and virtual environments involving novel force backgrounds. Motion-coupled VEs rearrange the external force environment. For example, in VEs involving real body motion or visual portrayal of body motion, the background gravitational forces on the body are different from the forces that would be present if the body were physically moving in the experienced fashion. This is a situation where motor adaptation occurs and individuals need to reprogram their limb movements to achieve accurate control for the current force background. This can produce aftereffects when the individual leaves the virtual environment. The situation is very different when a novel real or virtual tool or machine is introduced. In this case, individuals make errors until they learn the properties of the manipulated device. Such tasks do not lead to aftereffects outside the specific context of that device.

4.1 Motor Adaptation to Coriolis Force Perturbations in a Rotating Room

Traditional vehicle motion simulators often have motion bases to try to mimic features of the gravitational force backgrounds of moving vehicles. For example, a rotating room generates centrifugal acceleration that stimulates artificial gravity, but it also generates a Coriolis force on any object moving nonparallel to the spin axis of the room. The Coriolis force is only present when an object is moving in relation to the rotating room and acts perpendicular to the direction of object motion, according to the cross-product rule: \[ \text{F}_{\text{corr}} = 2m(\omega \times v) \], where \( m \) and \( v \) are the mass and linear velocity, respectively, of the object and \( \omega \) is the angular velocity of the room. When an occupant of a room rotating counterclockwise travels forward, a rightward Coriolis force is generated on the arm deviating to the left. Both the movement’s start and endpoint are displaced relative to the prerotation path of straight movements directly to the target. Subsequent reaches during rotation return quasi-exponentially within 10 to 20 trials, to prerotation straightness and accuracy. A new set of motor commands is being issued in order to move the hand straight to the target. When rotation stops and Coriolis forces are absent, reaching movements show curvature and endpoint deviations in the direction opposite those of the initial perturbed movements (LaChat & DiZio, 1994).

This pattern of pre-, per-, and postrotation movements resembles the pre-, per-, and postexposure phases of a photon displacement experiment (compare Figs. 38.3A and 38.3B), but there are important differences. Adaptation to rotation involves motor remapping instead of the proprioceptive shifts that underlie some forms of adaptation to prism spectral. Adaptation to rightward photon displacements can make movements that go straight ahead to a midline target feel like they are going rightward, and it may cause participants to make errors aligning the adapted hand with the undistorted one if it is hidden. By contrast, the true trajectory of the arm is experienced throughout the pre-, per-, and postexposure phases of adaptation to rotation.
Participants who adapt to reaching with one arm during rotation also can accurately align their left and right fingers.

4.2 Motor Adaptation and Force Perception

Another special feature of motor adaptation to rotation is the attenuation of force perception that accompanies it. Participants report their first movements during rotation as being deviated by a magnetic-like pull in the direction of the Coriolis force, whereas no unusual force is perceived during movements whose visual paths are perturbed by prisms. When participants adopt fully to rotation, they no longer can feel the Coriolis forces that are still present during their movement, even if their attention is called to them. They report that whatever had initially perturbed their arm is now gone and they can produce the desired movement with the same effort as before the perturbation. When rotation stops and there are no Coriolis forces during movements, participants report feeling a force on their arm that is the mirror image of the Coriolis force they had adapted to. The relationship of actual to perceived force is modified during adaptation because of an internal calibration mechanism that integrates force feedback signals and velocity with motor commands. Externally observations clearly show that adaptation to rotation alters the feed and control of objects and surfaces that are handled following return to a normal stationary environment. Virtual environments that alter the force environment or that involve visual stimulus of body accelerations without the normal consensual gravito-inertial forces will cause illusions in the feel of tools and affect the manual control of a vehicle or other machines.

4.3 Context-specific Motor Adaptation and Aftereffects in Different Force Environments

Participants who sit quietly in an enclosed rotating room turning at a constant velocity feel after about 30 seconds like they are in a completely normal, stationary environment. This is because the angular velocity sensitive semicircular canals have had time to return to their resting discharge level after acceleration to constant velocity, and the room is fully enclosed so there are no visual flow cues about rotation. Thus, participants who adapt their reaching movements to this situation learn to associate making Coriolis force compensations and receiving Coriolis force feedback with an internally registered nonrotating context. These recalibrations are carried over the post-rotation period, which also is internally registered as being a normal stationary environment, and cause aftereffects. If after adaptation to rotation, the rotating room instead of being stopped is accelerated to twice the initial speed, then after a minute the participants will again feel stationary and when reaching for the first time will make more end-effort errors with the eyes and cancel errors of the same magnitude and in the same direction as the first movements at the previous speed (Lackner & DZ, 1993). The Coriolis forces are greater at the new speed, but the motion mapping from the lower speed is carried over because the internally registered nonrotating stage is the same.

Understanding whether adaptation to one rotation speed will carry over to a different speed requires the converse of the conditions provided by the rotating room where participants are rotating but feel stationary. Participants who are actually stationary can experience virtual rotation by viewing a moving visual scene in a head-mounted display. The first reaches of participants experiencing constant velocity commands clockwise rotation and displacement will be deviated leftward in path and end point (see Fig. 3B, Cohn, DZ, & Lackner, 2000). The magnitude of the reaching errors is proportional to the perceived speed of self-rotation. If the participants had actually been rotating counterclockwise there would have been a rightward Coriolis force when they reached. Their leftward errors show that they had anticipated and
generated muscle forces to resist the expected but absent Coriolis forces. These participants also report feeling a phantom leftward force on their arm, which has the characteristic bell-shaped profile of a Coriolis force. When repeated reaches are made during virtual rotation, the reaches become straighter and progressively more accurate, and the "force" perceived to be deviating the arm vanishes. When the visual scene is again stationary and participants feel stationary, their first postexposure reaches feel normal and go straight to a target. That is, there is no aftereffect.

These results show that the motor plays for a forthcoming reaching movement compensates for the Coriolis forces normally generated at the currently registered speed of self-rotation. In other words, we normally maintain multiple motor adaptation states that are context-specific for egocentric/body motion. Experimental alteration of the relationship between Coriolis forces and registered bodily speed alters the motor compensation only for the body rotation speed at which movement are practiced and is not carried over to other speeds. Thus motor adaptation is specific to the registered context of body motion where aberrant forces were experienced. No enough is known to allow prediction of how faithfully a moving base training simulator must reproduce the operational environment in order for training to transfer. Virtual training environments that simulate bodily motion with just a dynamic visual scene are unlikely to cause motor aftereffects is everyday life, but they may well produce adaptation in which participants cease to compensate or anti-compensate in terms of postural and movement control for inertial forces that will actually be present in the operational moving environment. That is, they could maladapt participants to the operational context.

4.4 Motor Adaptation to Environments Versus Local Contexts

The rotating room and virtual rotation provide environmental contexts in which individuals carry out all their actions. Real and virtual tools and machines create force-reflected feedback or force fields that are local contexts a user may interact with in a unified fashion. For example, humans can use a planar robotic linkage to control a video screen in the presence of external forces generated by torque motors on the handle. Shahin et al. (1993) created a force field that resembles the Coriolis force field in a rotating room, such that the manipulandum pushed the hand perpendicular to its current velocity. Their participants movements were initially perturbed, but after many hundreds of trials straight paths ending at the target characteristic of movements with a null force field were regained. This contrasts sharply with the complete adaptation participants achieve in 10 to 20 movements to Coriolis force perturbations of their reaching movements in a rotating room. Thus, learning an internal model of an electromechanical device takes much longer than recalibrating one's own under-
tended movement. The nature of force perception also differs sharply during self-calibration versus internalization of a machine's force properties. As described above, perturbing Coriolis forces become perceptually transparent when motor adaptation of free reaching movements to rotation is complete. However, participants interacting with a manipulandum can still detect and describe the force; it applies even after they have learned to resist them and to move their arm in the desired path to the target. The implication of this is that learning a local force field by interacting with a real or virtual machine will not cause aftereffects in any context outside the confines of the machine. By contrast, learning to move one's arm will affect perception and performance in any local context embedded in an environment that provides the same stimuli about self-motion as the environment in which adaptation was acquired.

4.5 The Role of Touch Cues in Motor and Proprioceptive Adaptation

Cutaneous contact cues during a movement and at the summit of the movement contribute to perception and adaptation of limb position and force. Continuous cutaneous contact cues throughout movements are prominent differences between Coriolis force perturbations in the
rotating room and force field perturbations produced by a manipulandum. When a manipulandum perturbs a movement the muscle spindles, Golgi tendon organs, and vision can signal that the movement deviated from the intended path, and the cutaneous mechanoreceptors of the hand signal the continuous presence of a local external force. There is a systematic correlation of the cutaneous force profile and the compensatory muscular forces that need to be learned. The nervous system, following the principle of making the most parsimonous change possible, can simply lean the dynamics of the perturbing object. In adaptation to Coriolis force perturbations, there is no local cutaneous stimulation because the Coriolis force is a noncontacting inertial force applied to every moving particle of the limb. In the absence of an external agent contacting the limb, the most specific form of adaptation is an alteration in motor control of the exposed limb. This is because the central nervous system recognizes a situation requiring motor recalibration when it detects an error in movement path without an external obstruction while the movement is in progress.

The transient cutaneous stimuli occurring when the finger lands on a surface at the end of a reaching movement also influence proprioception and motor adaptation in real and virtual environments. Coriolis force induced end-point and curvature deviations of visually open-loop reaching movements in a rotating room are eliminated by adaptation within 10 to 15 movements if the reaches end on a smooth surface. However, only 50% of the initial end point error is eliminated before performance reaches a steady asymptote if the reaches end with the finger in the air. In other words, if terminal contact is denied participants will not fully adapt. This pattern shows that information obtained from finger touchdown provides information about limb position errors, which is critical for adaptation to rotation. The source of this information is the direction of shear forces generated in the first 38 ms after a reaching movement contacts a smooth surface. These shear forces are systematically mapped to the location of the finger and could where the finger is relative to the body (D'Zio, Landman, & Lackner, 2009). These shear forces are about 1 N in magnitude. When participants reach in the air to objects on a virtual instrument panel their end-point variability is greater than when reaching to a similar real panel (D'Zio & Lackner, forthcoming). The variability is greatest if the virtual panel is presented only in the virtual mode and the reaches end in mid-air. It is greatly reduced by the addition of a real textured surface in the same spatial plane as the visual virtual panel (see Fig. 38.4). Thus, minimalaptic cues, just a flat surface in the proper plane, can improve proprioception, reduce movement errors and enhance the visibility of VE-visual interfaces.

**FIG. 38.4.** Plot of endpoint error of repeated reaches made without sight of the arm to a single target on a real or virtual horizontal work surface. Variability is least in the set of movements, where the target is a light-emitting diode (LED) embedded in a smooth sheet of Plexiglas with no distinguishing marks indicating the target location. Variability is greater in the second set of movements, which are aimed at a virtual target on a virtual surface programmed to coincide with the spatial location of a real Plexiglas work surface which the participant contacts at the end of each movement. The same virtual target and surface are presented without the real surface in the last set of reaches, and the variability increases markedly in the absence of physical contact. Reintroducing the real surface (not shown) restores low variability immediately.
5. PERCEPTION OF LIMB AND BODY MOTION DURING POSTURE AND LOCOMOTION

Control of posture and movement are highly integrative, multimodal processes, requiring sensitivity to complex environmental constraints. Touch cues play a major role in control and perception of whole body movement, the apparent stability of the environment, and attributions of causality.

5.1 Touch Stabilization of Posture

Finger-tip contact with environmental surfaces has a stabilizing influence on standing posture. If participants standing on one foot or heel-to-toe in darkness hold their index finger on a stable surface with a force of about 0.4 N (about 41 grams), their body sway amplitude is cut in half relative to not touching (Holden, Ventura, & Lackner, 1994; Jeka & Lackner, 1994). This level of force is too low to provide mechanical stabilization, but it corresponds to the maximum sensitivity range of finger-tip sensory receptors (Westling & Johansson, 1987). The horizontal and vertical forces at the finger-tip fluctuate with a correlation of 0.6 to both body sway and ankle EMG activity, but lead EMG by about 150 ms and body sway by 250 to 300 ms. Light touch even attenuates body sway when the eyes are open. The stabilizing influence of touch is lost if sensory-motor control of the arm is disrupted by vibration of brachial muscles, but with the arm functioning normally touch can stabilize the body even when excessive sway is induced by ankle muscle vibration (Lackner, Rabin, & DiZio, 2000). Patients with no vestibular function who cannot stand in darkness for more than a few seconds can maintain stance for as long as desired and are as stable as control participants with eyes closed if allowed light touch of the finger (Lackner et al., 1999). These findings indicate that the finger-arm system functions as an active proprioceptive probe providing sensory information about body position and velocity. This stabilization system works with nested sensory-motor loops. A finger to brachial sensory-motor loop stabilizes the finger relative to the surface and minimizes the force changes at the finger-tip. These residual finger-tip force fluctuations activate the leg muscle to stabilize posture better than is possible with ankle proprioception, vision, or vestibular signals alone.

Light contact cues with a simple surface are an effective way to stabilize body sway in VEs where participants are free standing. An HMD and head-tracking system that introduces temporal distortions of visual feedback when head movements are made induces severe postural instability, and light touch suppresses this side effect (DiZio & Lackner, 1997). Postural aftereffects also occur upon return to a normal environment resulting in further postural disruption. Light touch stabilizes posture and suppresses aftereffects in such situations.

5.2 Touch and Locomotion

A seated individual holding his or her hands or feet in contact with a rotating floor or railing will experience self-motion in the opposite direction (Brandt, Buchel, & Arnold, 1977; Lackner & DiZio, 1984). As a result, pedaling the free wheeling floor while seated or running the railing with a hand-over-hand motion makes the experience very powerful. Pedaling movements made without surface contact do not elicit any experience of self-motion. These demonstrations illustrate that in normal bipedal locomotion contact with the floor is very important.

The pattern of ground reaction forces during locomotion is not related to body motion through space in a univariant way. For example, walking down a hill, one is progressing forward but pushing backward. An experimental situation used by Lackner and DiZio (1993) to assess the interactions among surface contact, leg movements, and whole body motion is illustrated.
in Fig. 38.5. It is basically a VE in which the visual display and the substrate of support can be independently manipulated. A participant holding onto the world-fixed handlebar and walking in place on the backward rotating floor experiences forward motion through space. The experience is compelling and immediate if the chamber walls also are revolved backward, but it occurs in darkness (Bles & Kapteyn, 1977) and even if the stationary walls are in plain view. In the latter case, the motor and somatosensory signals from walking in place capture the visual scene, which will appear to be dragged along (Lackner & DiZio, 1993).

If the visual scene is moved backward twice as fast as the floor, a participant who is walking in place will feel the handlebar pulling him forward and sense an increase in body velocity through space. Some participants report an illusory elongation of each leg at the toe-off phase of the step cycle, and others sense that the floor has become rubbery and bounces them forward. If the visual scene motion is reversed, participants stepping forward in place will report either that they are moving backward through space and making backward stepping movements or the steps, which usually propel them forward are now propelling them backward. These effects powerfully demonstrate that afferent signals about limb movements, the body schema representation, internal calibration of body motion, and apparent environmental stability are all interrelated.

5.3 Proprioceptive Recalibration of Locomotion

These relationships can be recalibrated by walking in place on a circular treadmill for an extended period. After doing so for an hour in a visually normal environment, participants walk in a curved arc when trying to maintain a straight line on solid ground in darkness (Gordon, Fletcher, Melville-Jones, & Block, 1995). When passively pushed in a wheelchair, eyes closed, they can differentiate straight and curved paths as well as they can before the treadmill exposure.
indicating vestibular function is not changed. These investigators concluded that the afferents
are due to adaptive recalibration of a "pokokinetic system," which through ground contact, 
leg proprioception, and motor copy signals provides a representation of trunk rotation relative 
to the stance foot. When forced not to turn by guide rails after prolonged stepping around in 
place, participants feel they are turning in the other direction, and they exhibit nystagmoid 
eye movements consistent with their perceived direction and rate of turning, not their actual 
body motion (Weber, Fletcher, Melville-Jones, & Block, 1997). Allowed visual feedback, the 
participants can walk in their desired path with no ocular nystagmus. This is an example where potentially dangerous aftereffects due to internal recalibration of proprioception in 
the exposure environment can be masked by the appropriate sensory information.

6. CONCLUSIONS

Many Vs will intentionally or inadvertently introduce users to sensorimotor rearrangements 
that will result in side effects, followed by adaptation, and aftereffects or maladaptive transfer on 
return to a normal environment. Proprioceptive adaptation is one form of adaptation associated 
with potential VE side effects and aftereffects. Two important facets of proprioception that can 
dergo adaptive modification are the sense of position and orientation and the sense of force or 
effort. Predicting and measuring the manifestation and underlying form of adaptation require 
understanding that it is not a unitary phenomenon. Proprioception involves the interplay of 
afferent and efferent signals about limb and body position and motion, internal representations 
of the body schema, and spatial orientation and representations of environmental constraints. 
All of these variables are labile and can undergo long-term adaptive changes in relation to the 
others. Reaching errors in a VE that look similar on the surface can have different causes that 
lead to diverse forms of adaptation and aftereffects. For example, the visual visual displacements, 
mis-matches of the virtual gravito-inertial force environment, and novel contact force fields cause 
adaptation of proprioception, of motor control, and of internal models of objects, respectively. 
Understanding the cause and form of adaptation in a specific VE context will help predict 
ways of enhancing adaptation, for example, when more user activity versus sharpening the 
sensory discordance will help. Principles governing the specificity of adaptation are key for 
understanding what aftereffects will occur when a user leaves the VE and either goes about 
daily life or engages in the real-world operational task that was simulated. Such principles are 
scarcely but one important factor is feedback from contact cues during movement. Continuous 
and terminal cutaneous signals contribute to neural computations that partition the net force 
environment into functionally relevant components. For example, in adaptation of reaching 
movements, cutaneous signals are critical for determining whether the motor system will 
recalibrate or the representation of a tool's properties will be updated. Motor adaptation in a 
VE will carry over to any task performed with the exposed limb, but learning an internal 
model of a device will not deleteriously affect performance on dissimilar devices. Touch cues 
and visual cues can also mask potentially dangerous long-term aftereffects that appear in 
impoverished conditions or specific contexts.

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