

Motor Illusions: What Do They Reveal About Proprioception?

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Five illusions involving distortions in the perception of limb position, movement, and weight are described in the context of their contribution to understanding the sensory processes involved in proprioception. In particular, these illusions demonstrate that the position sense representation of the body and the awareness of limb movement result from the cross-calibration of visual and proprioceptive signals. Studies of the vibration illusion and phantom-limb phenomenon indicate that the perception of limb movement and position are encoded independently and can be dissociated. Postural aftereffects and the illusions of movement induced by vibration highlight the remarkable lability of this sense of limb position, which is a necessary feature for congruence between the spatial senses. Finally, I discuss the role of corollary discharges in the central processing of afferent information with respect to the size-weight and vibration illusions.

The study of visual illusions has provided many valuable clues about the operation of the visual system (Coren & Girgus, 1978), to the extent that visual aftereffects have been described as the psychologist's microelectrode (Frisby, 1979). With the notable exception of the size-weight illusion, which was first described in the late nineteenth century (Charpentier, 1891), illusions involving the motor system have received much less attention. However, recent reports of illusory movements induced by mechanical vibration of the muscle tendon (Goodwin, McCloskey, & Matthews, 1972; Roll & Vedel, 1982; Vedel & Roll, 1983) have led to a revival of interest in kinesthetic illusions (Feldman & Latash, 1982a; Goodwin, 1976; Granit, 1972; Matthews, 1982). As with the classical visual illusions, these phenomena offer valuable insights into the perceptual mechanisms involved in proprioception and must be explained in terms of normal physiological mechanisms. I discuss disturbances in the perception of limb position and movement and of force and weight in this review in the context of their contribution to understanding perceptual processing in the sensorimotor system.

Vibration-Induced Illusions

Illusions of Movement

In 1972, two publications describing the effects of vibration on the perception of limb position and movement independently showed that vibration of a muscle tendon at 100 Hz induces illusory movements of the limb about which the vibrated

muscle acts (Eklund, 1972; Goodwin et al., 1972). Using blindfolded subjects who were required to track the position of their vibrated arm with the unperturbed arm, Goodwin et al. investigated the effects of percutaneous muscle-tendon vibration on position sense at the elbow. They found that vibration of the biceps tendon in an immobilized arm consistently produced the illusion that the elbow was moving into extension, as if the vibrated muscle were being stretched. Conversely, the elbow was perceived to be flexing when the triceps brachii tendon was vibrated. The illusion was primarily one of movement rather than altered position and was present only if the reflex-induced movement of the vibrated arm (i.e., tonic vibration reflex, Hagbarth & Eklund, 1966) was prevented from occurring. Associated with the illusory movement was an error in the sense of position; that is, the joint was perceived to be in the position it would occupy if the vibrated muscle was stretched (Goodwin et al., 1972).

The illusions induced by vibration have been evoked in postural, facial, and axial muscles and, in each case, create illusory changes in body motion and posture provided that visual information about body orientation is absent (Lackner & Levine, 1979). The direction of the illusory movement corresponds to that of a real joint movement stretching the vibrated muscle. Table 1 is a summary of a number of experiments investigating the kinesthetic effects of vibration. With regard to the visual system, these apparent motions are interpreted as if they are real movements of the body (Lackner & Levine, 1979). For example, during vibration of the biceps muscle, subjects show a lowered direction of gaze when attempting to fixate the position of their unseen index finger (Lackner & Taublieb, 1984), and if a target light is attached to the restrained hand, subjects experience motion of their unseen, stationary arm and see the target light move in the direction of perceived arm motion, even though they have continued to fixate on the stationary target (Lackner & Levine, 1978; Levine & Lackner, 1979). Both the apparent displacement and the apparent velocity of forearm

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Table 1
Influence of Conditions of Stimulation on Vibration-Induced Movement Illusions

Author	Variable	Result
Goodwin, McCloskey, & Matthews (1972)	Influence of cutaneous and articular sensory signals and of the contractile state of the muscle on vibratory illusions	Vibration of joint has no effect on position sense, and matching is also possible when hand is anoxic. Illusion persists when muscle is mildly contracted but is abolished during strong contractions.
McCloskey (1973)	Effect of loading and fatiguing the muscle on vibration-induced movement and position illusions	Loading or fatiguing the muscle causes illusory movements to be slowed but increases (loading) or has no effect (fatigue) on the position error.
Craske (1977)	Position sense of the limb when the muscle is passively stretched during vibration	Stretching the muscle makes it more sensitive to vibration; perceived position of the limb can be beyond its anatomical limit.
Lackner & Levine (1979)	Vibration of different postural and axial muscles	Illusion of displacement and motion can be elicited in virtually any direction by vibrating the appropriate muscle.
Clark, Matthews, & Muir (1979)	Amplitude of vibration at constant frequency	Velocity of illusory movement decreases as amplitude of vibration diminishes.
Capaday & Cooke (1981, 1983)	Effect of vibration on the accuracy of voluntary arm movements	Vibration of muscle antagonistic to the movement being performed results in undershooting the required target position. Vibration of agonist muscle has no effect.
Roll & Vedel (1982)	Effect of vibration frequency on velocity of the illusory movement	Frequency of vibration modulates the illusory movement quantitatively. Perceived velocity reaches a maximum value at between 60 and 80 Hz and diminishes at other frequencies.
Feldman & Latash (1982b)	Influence of attention on illusory movements	Direction of the illusory movement changes during auditory stimulation.
Lackner & Taublieb (1983)	Effects of spatial information from nonvibrated arm on perceived position of vibrated arm	If arm is grasped during vibration, illusory motion is abolished; but if arm is in position prior to onset of vibration, both arms are felt to move.
Lackner (1984)	Influence of vibration of one arm on the accuracy of movements made by the other arm	Movements made by the nonvibrated arm are less accurate when the contralateral arm is vibrated.
Lackner & Taublieb (1984)	Effect of vision of part of the limb when it is vibrated in darkness and in normal light	Apparent velocity of the illusory movement diminishes when part of the limb is seen and in normal light. The illusion occurs even when eye-movement records indicate that subjects are fixating the stationary limb.
Rogers, Bendrups, & Lewis (1985)	Limb position matching during postvibration period	There is a disturbance in the perceived position of a vibrated limb for up to 4 min after vibration has ceased. The muscle is perceived to be shorter than it actually is.
Gilhodes, Roll, & Tardy-Gervet (1986)	Effects of simultaneous vibration of agonist and antagonist muscles at different frequencies	Movement sensation is in the direction of lengthening of the muscle vibrated at the higher frequency. If both muscles are vibrated at the same frequency, no illusions occur.

motion are diminished, however, when part of the limb can be seen, and when the muscle has been vibrated under these conditions, subjects have reported a dissociation between the visual and felt locations of a limb and between the location of adjacent limb segments (e.g., finger and hand), such that they are no

longer spatially contiguous (Lackner & Taublieb, 1984). But when the visual cues are concordant with the illusory movement (by moving the visible background beneath the arm at a constant velocity), then the illusion is enhanced (Tardy-Gervet, Gilhodes, & Roll, 1986). In contrast, if the whole limb is visible,

no movement illusions occur (Lackner & Levine, 1979; Roll, Gilhodes, & Tardy-Gervet, 1980).

The illusory motion of a vibrated arm is also affected by the activity of the contralateral limb and can be attenuated or eliminated if the vibrated arm is grasped by the other hand. If the grasping arm is in position prior to the onset of vibration, compelling illusory movements of both arms are evoked, although the apparent velocity of the movement is less than that reported under the usual stimulation conditions (Lackner & Taublieb, 1983). These results suggest that even very simple perceptions, such as the awareness of limb position, result from the cross-referencing of a number of sensory inputs.

Vibration of the elbow joint does not produce any illusions of movement, and subjects can quite accurately track passively imposed movements during vibration of only the joint (Goodwin et al., 1972). Furthermore, even when the muscle tendon is located some distance from the joint about which it acts (e.g., the wrist flexor tendon in the region of the elbow), vibration of the tendon produces position errors referred to the relevant joint (i.e., the wrist), while the perceived position of the adjacent joint (i.e., the elbow) remains unchanged (Craske, 1977). These results, together with the finding that illusory movements can be induced in patients with joint prostheses (Pouget, Gilhodes, & Roll, 1983), indicate that articular receptors are not necessary for the occurrence of the illusions. Local anesthesia of the skin overlying the tendon does not reduce the effects of the vibratory stimulus (Hagbarth & Eklund, 1966), and anoxic anesthesia of the hand does not affect the illusory movements induced by vibration of the long flexor or extensor muscles of the thumb (Goodwin et al., 1972). Thus, the kinesthetic illusions do not depend on the excitation of Pacinian corpuscles or other cutaneous mechanoreceptors normally activated by vibration (Freeman & Johnson, 1982; Talbot, Darian-Smith, Kornhuber, & Mountcastle, 1968).

On the basis of these observations, Goodwin et al. (1972) concluded that the illusions of movement induced by muscle-tendon vibration arise from the activation of muscle receptors and that sensory signals originating in the muscle spindle can therefore contribute to the perception of limb position and movement. They attributed the illusion of extension of the vibrated and contracting muscle to the intense firing rates of spindle receptors, which are interpreted by the central nervous system as indicating that the muscle is being stretched. Because movement illusions do not occur when spindle receptors discharge during the course of normal voluntary motor activities, Goodwin et al. further postulated that only those spindle discharges that are inappropriate for the level of muscle activation are perceived. Support for this proposition came from the observation that the movement illusion that usually occurred during vibration could be reduced or eliminated if the vibrator was applied while the muscle was contracting isometrically to generate a large force (Goodwin et al., 1972). The velocity of the illusory movement decreases even further if the muscle is fatigued (McCloskey, 1973). The discharge rates of spindle receptors increase during sustained isometric contractions (Vallbo, 1970) and when the amplitude of the force generated by a muscle increases (Vallbo, 1971), which means that in the two situations

described, vibration would have had very little effect on spindle firing rates if they were already near their saturation point.

This explanation of the illusory movements was supported by microneurographic recordings from sensory nerves innervating human muscles. Primary spindle receptors were found to be extremely sensitive to high-frequency vibration and were able to be driven in an harmonic or subharmonic manner (Burke, Hagbarth, Löfstedt, & Wallin, 1976; Roll & Vedel, 1982; Vedel & Roll, 1983). Burke et al. (1976) found that the discharge rates of spindle receptors recorded during percutaneous-tendon vibration of human muscles were, however, lower than those reported in animal experiments in which the vibrator was applied directly to the exposed muscle tendon (Brown, Engberg, & Matthews, 1967).

Vibration Frequency and Movement Velocity

The velocity of the illusory movement evoked by vibration depends on both the frequency (Roll & Vedel, 1982) and the amplitude (Clark, Matthews, & Muir, 1979) of the mechanical stimulation. Roll and Vedel (1982) examined the influence of the parameters of vibration on movement illusions by using the matching procedure (McCloskey, 1973), in which subjects track the illusory movements of a restrained, vibrated forearm by moving the nonvibrated contralateral arm. They reported that changing the frequency of vibration from 10 to 70 Hz during stimulation of the biceps tendon increased the perceived velocity of the illusory extension movement of the elbow to approximately 5.5° per second. A further increase in frequency from 80 to 120 Hz generally resulted in a decrease in the perceived velocity (see Figure 1). Vibration trains of the same frequency and duration applied alternately to the distal tendons of the brachial biceps and triceps muscles induced an illusion of alternating extension and flexion of the forearm. The amplitude and velocity of the movements reproduced by the tracking arm increased when the frequency of the vibration was changed from 20 to 70 Hz and again diminished as the stimulation frequency rose above 80 Hz, although under these conditions, the velocity of the illusory movement was three times greater (16° per second) than the value obtained during vibration of a single muscle (Roll & Vedel, 1982). However, if the two antagonistic muscles are now vibrated simultaneously at the same frequency, there is no sensation of movement, but if the stimulation frequencies differ, the illusory movement is always in the direction of stretching the muscle vibrated at the higher frequency (Gilhodes, Roll, & Tardy-Gervet, 1986). The findings from these three experiments are summarized in Figure 1.

The existence of a vibratory-frequency range within which the velocity of illusory movements is maximized could reflect an optimal range for stimulating muscle receptors or saturation in sensory processing systems at higher frequencies. The covariation between the frequency of the vibratory-stimulus train and the velocity of the illusory movement reported by Roll and Vedel (1982) suggests that muscle receptors are able to code this movement parameter. The receptor most responsive to velocity is the primary spindle ending with its marked dynamic sensitivity (Matthews, 1981).

Juta, van Beekum, and Denier van der Gon (1979) disputed

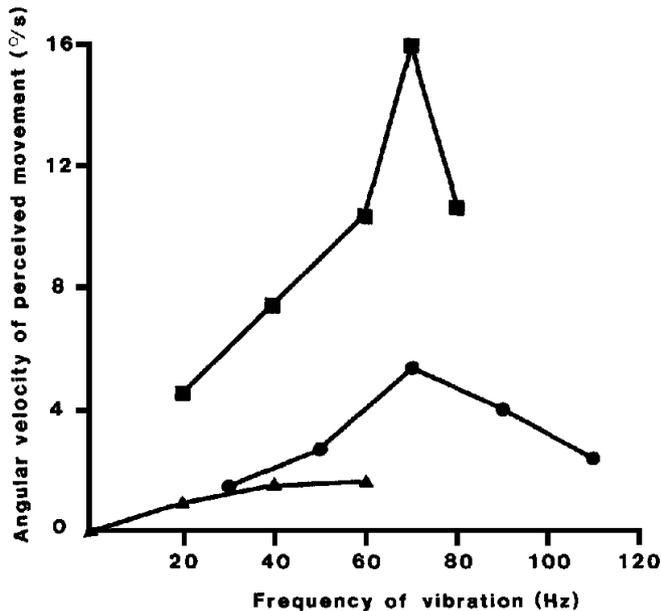


Figure 1. Mean angular velocity of illusory movements of the forearm perceived by subjects during (a) vibration of the left biceps tendon at different frequencies (circles, Roll & Vedel, 1982), (b) simultaneous vibration of the left biceps and triceps tendons at different frequencies (the abscissa is the difference between the frequencies of vibration applied to the biceps and triceps tendons; triangles, Gilhodes, Roll, & Tardy-Gervet, 1986), and (c) alternate vibration of the left biceps and triceps tendons at different frequencies (squares, Roll & Vedel, 1982). In each experiment, the perceived movements were reproduced by the right arm and were recorded by using a linear potentiometer.

this relation between stimulation frequency and the velocity of the illusory movement and claimed that only the direction of the illusory movement is coded and not its velocity. They reported on an experiment in which subjects had to track the position of a visual target by moving their forearm. When visual feedback of the limb's position was switched off, vibration was applied to the biceps tendon, and the target began to move at a constant velocity in the direction of arm extension. Jutta et al. found that the tracking limb remained stationary despite changes in the velocity of the visual target and that the vibration frequency, which could vary by means of a negative feedback system, remained constant for each subject. Unlike Roll and Vedel's (1982) experiment, this study required that subjects match the velocity of movement of a visual target by actively moving a limb that was already perceived to be involuntarily mobile. The perceptual difficulty of this task may have contributed to the insensitivity of the subjects to velocity cues.

Errors in Perceived Position

The error in matching the position of the limbs during vibration of one limb is usually between 5.5° and 8° (Goodwin et al., 1972), but it increases considerably (i.e., by a factor of three) if the muscle is stretched during vibration of the tendon. Craske (1977) found that when subjects indicated the position of the

forearm and hand (by making a mark on a solid plastic sheet adjacent to the arm) during active stretching of the vibrated elbow or wrist flexor muscles, they often indicated that the limb was in an anatomically impossible position; that is, they perceived the hand to be bent back toward the dorsal surface of the forearm. Other investigators have reported similar findings (Gandevia, 1985; Lackner & Taublieb, 1983). This suggests that the cortical sensory centers extrapolate beyond previous experience to produce this perception and that the sensory limits of the sense of position are not set by the anatomical constraints of joint excursion (Craske, 1977). Recordings from spindle afferent fibers in human muscles indicate that increasing the length of a muscle, thereby elongating the muscle spindles, enhances the responses of all sensory endings to vibration (Burke et al., 1976). This finding is consistent with the increase in position errors induced by stretching a vibrated muscle.

The size of the position error does not increase with the duration of the vibration (McCloskey, 1973), and procedures that diminish or eliminate the illusory movement do not necessarily affect the magnitude of the position illusion. For example, the error in matching the positions of the limbs during vibration increases when the muscle is loaded (Eklund, 1972; McCloskey, 1973), whereas fatigue has no effect on error amplitude (McCloskey, 1973). McCloskey (1973) also reported that errors of position can occur when the muscle is vibrated at such low frequencies (i.e., 2–48 Hz) that no illusory movements are apparent. These errors in the perceived position of limbs do not appear to result from the central integration of discharges signaling movement, because they can be induced in the absence of illusory movements and can be increased by stimuli (e.g., loading) that diminish the magnitude of the movement illusion.

McCloskey (1973) argued on the basis of these findings that position and movement information could be signaled separately in the afferent discharges arising peripherally. In several experiments, subjects have reported a dissociation between the velocity of the apparent motion and the extent of limb displacement (Goodwin et al., 1972; Lackner & Levine, 1979), which is consistent with this hypothesis. Microneurographic recordings from human spindle afferent fibers have shown that secondary spindle receptors respond to vibratory stimuli (Burke, Hagbarth, Wallin, & Löfstedt, 1980). Given their sensitivity to changes in muscle length (Stein, 1980), these receptors are the most likely candidates for position information. If this is the case, then they presumably play a role in disturbing the sense of position during vibration.

Summary

These studies on the effects of vibration yielded a number of findings that altered the traditional view of proprioception. First, they demonstrated that signals arising from muscle spindle receptors could contribute to the perception of joint position and movement (Goodwin et al., 1972; Roll & Vedel, 1982), a conclusion representing a complete reversal of the classic viewpoint, which considered the perception of movement to be mediated by joint afferent activity (Merton, 1972; Mountcastle & Powell, 1959; Skoglund, 1973). Muscle receptors were thought to be reserved solely for the purpose of servo-control-

ling movement (Merton, 1953, 1964). As a consequence of the results from the vibration studies, the experimental evidence purportedly demonstrating that muscle receptors could not be involved in proprioception was reexamined. In each case, replication of the experiment, generally with improved testing procedures, produced different findings that were consistent with the hypothesis that muscle receptors contribute to the perception of limb position and movement (McCloskey, 1978).

Second, the relation observed between the frequency and amplitude of vibration and the velocity of the illusory movement (Clark et al., 1979; Roll & Vedel, 1982) is consistent with the notion that primary spindle receptors code this movement parameter. Furthermore, the perceived direction of the limb movement is clearly determined by the relative level of afferent activity in two antagonistic muscles, because it can change, depending on which of the two muscles is being vibrated at the higher frequency (Gilhodes et al., 1986).

Third, the finding that errors in the perception of limb position occur independently of movement illusions (McCloskey, 1973) supports the idea that position information is also derived from muscle receptor discharges and that the senses of limb position and movement can be dissociated (Clark, Burgess, Chapin, & Lipscomb, 1985; Horch, Clark, & Burgess, 1975). Clark et al. (1985) demonstrated the ability of human subjects to make independent judgments of the static positions and movements of limbs in another experimental paradigm in which extremely slow joint rotations were applied to a limb. They reported that subjects could detect changes in the position of the knee and finger in the absence of any awareness that the limb had moved.

Finally, the dissociations evident during vibration, such as the perceived spatial separation of adjacent limb segments (Lackner & Taublieb, 1984) and the perception that the limb is in an anatomically impossible position (Craske, 1977; Lackner & Taublieb, 1984), suggest that the internal scale for limb position is not constrained by the anatomical limits of joint excursion. Under these experimental conditions, the sensory centers in the brain extrapolate from the previously calibrated position domain to derive new information. These results also indicate that the sense of limb position is not coded solely in terms of the activity of single modality-specific topographic maps. Rather, there are complex interactions between the sensory representations of different body parts (as shown by the influence of the location of one arm on the perceived position of the other [Lackner & Taublieb, 1983]), which are in turn cross-referenced with information from other afferent domains, such as vision (Lackner & Taublieb, 1984). In all these computations of limb position, priority appears to be given to changing rather than static patterns of afferent activity (Lackner & Taublieb, 1983).

Phantom-Limb Illusions

After amputation of a limb, patients almost invariably experience phantom limbs, that is, the illusion that the amputated limb still exists and can change its position in space (Bors, 1951; Mitchell, 1872; Sunderland, 1978). During the latter part of the 19th century, the phantom-limb illusion was used as evidence

that the innervation of the motor tracts in voluntary action produced sensations within the brain (Boring, 1942; Helmholtz, 1866/1925). This notion of centrally originating sensations of movement gradually lost ground to the concept of a peripherally derived sense of position and movement (Sherrington, 1900), and Goldscheider's (1889) demonstration of a well-developed sensory capacity for detecting movements passively imposed on the limbs indicated that this aspect of kinesthesia could not be attributed to centrally generated motor signals. Nevertheless, signals produced within the central nervous system as corollaries of motor commands (i.e., corollary discharges) have continued to be ascribed various roles in the control of movement and in the processing of sensory information (Evarts, 1971; Holst & Mittelstaedt, 1950/1980; McCloskey, 1981; Sperry, 1950).

Phantom-limb illusions are relevant to studies of kinesthesia in that on initial inspection, they suggest that an awareness of limb position can be experienced in the absence of any sensory input from a muscle and that sensations of movement can result from a centrally generated motor command (Merton, 1964). A phantom limb can be perceived to move in two ways: First, when the body part bearing the stump of the limb is moved, the phantom may appear to move with it, although it does not alter its position relative to the other limb segments. Second, the phantom limb may move in response to a motor command, and the relative positions of the imaginary parts may change. In the first situation, the phantom limb is perceived to be maintaining its position with respect to the stump, so there is no change in its neural representation, and there are no new sensory signals related to its position. The ability to alter the position of parts of a phantom limb appears, however, to be consistent with the idea that corollary discharges have perceptual consequences, because this is the only way that the sensory centers could be informed of the intention to move the limb.

Henderson and Smyth (1948) undertook one of the most comprehensive studies of the phantom-limb illusion, using 300 amputees in prisoner-of-war camps during World War II. They found that 98% of the upper- and lower-limb amputees whom they studied experienced a phantom limb that manifested itself as a pleasant, tingling sensation that was not painful. Although phantom limbs are almost inevitable after the traumatic loss of a limb, occurring in approximately 95% of amputees (Mitchell, 1872; Sunderland, 1978), they are much less common in patients who have slowly developing limb losses (e.g., a frozen limb [Gallinek, 1939; Gerstmann, 1942]). Phantom limbs also occur less frequently when the limb loss is within the first decade of life, but the percentage of children reporting phantom-limb sensations increases as a function of the age at which the limb is amputated (Simmel, 1962). It is surprising that phantom limbs have even been described in children who are congenital amputees (Weinstein & Sersen, 1961). The less frequent appearance of phantoms in young children is probably related to the limited extent of the sensory and motor experiences with the affected limb prior to its loss and to the period of time required for consolidation of the body image.

The incidence of phantom limbs does not depend on either the level of the amputation or on the limb amputated, and the experience usually occurs immediately or very soon after the

operation. In general, the phantom limb is aligned with the stump and fits in with the normal posture of the limb (Sunderland, 1978). The more distal parts of the limb, such as the hand or foot (and especially the digits), are more strongly perceived than the proximal segments, and with respect to the hand, the thumb and index finger are clearly perceived (Riddoch, 1941). These differences in the intensity of sensory awareness of different parts of the body are consistent with the more extensive somatosensory representation of certain areas of the body in the cerebral cortex (Penfield & Boldrey, 1937). The phantom limb is therefore composed of parts of the missing limb, and although amputees are aware of the gaps in the representation of the phantom, they are able to estimate where the various parts of the limb would be in space, and they report that they can orient the different segments with respect to each other. This loss of proportionality in the phantom limb suggests that it is not primarily derived from a visual impression of the body.

The perception of the phantom limb changes over time, with the more weakly perceived parts fading from awareness; this gradual shrinkage results in a telescoping of the limb (Riddoch, 1941), such that the digits come to be perceived as being attached to the stump. The period of time over which these changes occur does not depend on whether the amputation is proximal or distal and ranges from 1 month to several years after the operation (Henderson & Smyth, 1948). However, these changes in the representation of the limb do occur more rapidly in lower-limb than in upper-limb amputees (i.e., 18 months and 30 months, respectively). This difference is probably related to the relative weakness of lower-limb phantoms and again reflects the extent of cerebral representation of the different body parts. Although awareness of the phantom limb diminishes with time, for some patients with major amputations the limb is still felt, on occasion, after 10 to 20 years. Once a prosthesis is worn, the form of the phantom limb changes, with the telescoping effect being lost, presumably because the phantom and the prosthetic device are now integrated. In this situation, the amputee often reports that the limb has regained its original length (Sunderland, 1978).

One of the more bizarre properties of the phantom limbs described by Henderson and Smyth (1948) was their ability to pass through solid structures without arousing any awareness of an obstruction or painful sensation. For example, if an amputee is asked to place or move the stump near a wall, the phantom fingers seem to enter the wall, and it is not until the stump touches the solid surface that the fingers are perceived to be displaced either sideways or inside the lower end of the stump. On retracting the stump, the fingers return to their normal positions. These unusual perceptions occur independently of whether or not the patient is watching the limb, indicating that in this situation, the cutaneous input from the stump takes precedence over other sensory signals.

Voluntary Movements of Phantom Limbs

Most of the amputees in the Henderson and Smyth (1948) study reported that they were able to move certain parts of the phantom, especially the digits, although the range of movement was always restricted, and the ability to move a particular joint

depended on the extensiveness of its sensory representation. Movement of the phantom limb becomes more difficult with time, and a stage is often reached after 12 to 18 months in which the ability to move the digits is lost, although the limb is still perceived to exist (Sunderland, 1978). Phantom-limb movements are always consciously made and do not occur spontaneously, which suggests that sensations of movement can result from the voluntarily generated motor command. Henderson and Smyth noted, however, that every voluntary movement of a phantom limb was accompanied by a contraction of the appropriate muscles in the stump and that if the remaining muscles in the stump were denervated, thereby eliminating the contractions, the ability to move the phantom was lost.

Melzack and Bromage (1973) reported a similar finding in a more recent study of patients with experimentally induced phantom limbs. They found that whenever patients experienced voluntary movements of a phantom limb after blocking the brachial plexus with local anesthetic, there was concomitant electromyographic (EMG) activity in the forearm muscles. Moreover, the impression of voluntary movements of the phantom persisted only as long as EMG activity could be recorded.

The question of whether corollaries of a descending motor command can produce a conscious awareness of movement in the absence of peripheral sensory feedback has been investigated by using other experimental paradigms. In each case, the results are consistent with those from studies of the phantom-limb illusion in demonstrating that sensations of movement do not arise from central efferent signals.

Goodwin et al. (1972) found that during anoxic paralysis of the hand, subjects consistently underestimated the extent of movements made by the index finger. Moreover, movements made just prior to total paralysis were not perceived at all, as Laszlo (1966) had reported. These results indicate that a voluntarily generated motor command cannot signal the occurrence of a movement, because this would produce the awareness of movement in the absence of any change in the position of the anoxic finger. Laszlo attributed the underestimation of the extent of movements to a reduction in feedback from muscle receptors in the intrinsic muscles of the hand and presumed that the inability to perceive movements made just prior to complete paralysis was due to a time difference in the rate at which afferent and efferent fibers were affected by the procedure. In contrast to the results of Goodwin et al. (1972), Kelso (1977) reported that when movements made by an anoxic finger were impeded at their onset, they were still perceived to have occurred as planned. This finding does not, however, necessarily suggest that sensations of movement arise from corollary discharges, because the unexpected obstruction of the movement would have led to an increase in the discharge rates of both muscle spindle and tendon organ receptors (Kelso, 1977).

Further evidence indicating that efferent signals are not in themselves sufficient to produce sensations of movement has been obtained under conditions in which the peripheral afferent fibers have remained intact. Using a neuromuscular blocking agent to induce paralysis in the forearm muscles, McCloskey and Torda (1975) found that subjects (with vision excluded) were aware that they were unable to move their paralyzed but unanesthetized fingers, and no sensations of movement accom-

panied their attempts to move. In contrast, the subjects accurately perceived passive movements and movements made by paretic but not paralyzed muscle groups. These findings, together with those from studies of the phantom-limb illusion, demonstrate the importance of muscular afferent feedback in the perception of limb movement.

Summary

The perception of voluntary movements of a phantom limb has been shown to depend on the presence of innervated muscle in the stump (Henderson & Smyth, 1948; Sunderland, 1978). In contrast, the existence of the phantom limb and its static position does not depend on peripheral sensory input, because they can persist after denervation of the stump. Phantom limbs therefore seem to arise from neural activity originating in the sensorimotor cortex; this is reflected in the close correspondence between the distribution and intensity of sensory tingling in the phantom and the extent of cortical representation of different parts of the limb. Lesions in the somatosensory cortex, in particular in the postcentral area, have been found to eliminate the perception of a phantom limb (Head & Holmes, 1911; Stone, 1950). These observations suggest that a sense of position can be generated by neural activity that is internal to the central nervous system (Goodwin, 1976), although peripheral sensory inputs continue to influence this representation (McCloskey, 1981).

The phenomenon of telescoping is probably related to the changes that occur in the somatosensory cortex after amputation. A number of investigators have presented evidence showing that after amputation of a digit in monkeys (Kaas, Merzenich, & Killackey, 1983) and in raccoons (Kelahan, Ray, Carson, Massey, & Doetsch, 1981; Rasmusson, 1982), there is considerable reorganization in these cortical areas. Part of the cortex deprived of peripheral sensory input is activated by input from new skin surfaces, which results in the somatotopic expansion of previously existing representations of body parts and the development of new sensory maps (Kaas et al., 1983). Some of these changes occur immediately, whereas others take place over several months (Kelahan & Doetsch, 1981). Anatomical boundaries seem to determine the limits of this somatosensory reorganization (Merzenich et al., 1983), however, so one must be cautious in extrapolating from single-finger amputations to surgical removal of the upper or lower limb.

Force–Movement Illusions

The perception of static limb position has recently been shown to be influenced by the forces generated as the limb moves from one location to another, although this movement illusion is apparent only under dynamic conditions (Matthews, 1982; Roland & Ladegaard-Pedersen, 1977; Rymer & D'Almeida, 1980; Watson, Colebatch, & McCloskey, 1984; Worringham & Stelmach, 1985). In most situations, the positions of two limbs can be accurately aligned even when the reference limb is passively moved or moves against a constant force. A movement imposed on the reference limb while it is maintaining a constant force can also be precisely reproduced by the contralateral

limb (Rymer & D'Almeida, 1980). If a subject is now required to generate a changing isometric force against a device flexing the limb, then considerable errors in the perception of position occur, with the limb perceived to be more flexed than it actually is. The magnitude of these errors is proportional to the amplitude of the quasi-isometric forces being produced at the end of the imposed movement, and errors occur independently of whether the forces produced by the subject are increasing or decreasing in magnitude (Rymer & D'Almeida, 1980).

The subjects' task in the above experiment is difficult in that they are required to track a target force with one finger and then reproduce its final position with the other index finger. Feldman and Latash (1982a) argued that in this difficult situation, subjects probably simplified the task by sending equivalent motor commands to both index fingers, with the result that the distance moved by the unimpeded matching finger exceeded that of the restrained reference finger. This proposition is supported by the linear relation found between the amplitude of the target forces being produced by the reference finger and the overestimation of the extent of movement, as indicated by the contralateral hand.

Rymer and D'Almeida (1980) claimed that these force-related errors in perceived position are contrary to what would be expected on the basis of the vibration illusion, in which an increase in the spindle receptor discharge rate is interpreted as indicating extension of a limb (Goodwin et al., 1972). They proposed that their illusion of muscle shortening arises because of a mismatch between (a) the force and length signals originating in the muscle and (b) the sensory input expected on the basis of the voluntary motor command. In human subjects, both muscle spindle and tendon organ receptors increase their firing rates during isometric contractions, and these receptors' sensitivity to limb movement and contractile force (Burke et al., 1976; Vallbo, 1971) makes them a very plausible source of the force-related errors. Discharges arising from the motor command may also play a role in the illusion, because the critical condition for its occurrence is a changing voluntary force in the presence of an involuntary limb movement. Although judgments of position were made in this experiment after both position and force had stabilized, Rymer and D'Almeida's results indicate that the conditions under which a limb moves from one position to another are extremely important in determining its perceived location.

Given the body of evidence implicating muscle spindle receptors in the perception of limb movement and position (Goodwin, 1976; McCloskey, 1978), it is possible that the force–movement illusion results from a marked change in the discharge rates of spindle receptors when the finger is flexed. This diminution in firing rates could be interpreted centrally as indicating that the finger is more flexed than it actually is. When a muscle voluntarily shortens under normal conditions, there is compensatory adjustment in the activity of the fusimotor system, which maintains the sensitivity of the spindle receptors (Matthews, 1981; Vallbo, 1971). In the absence of this adjustment, the signals arising from the spindle receptors are presumably ambiguous with respect to the actual length of the muscle. Other peripheral receptors, such as joint capsular afferents, may play a role in this illusion: They have been shown to increase their

discharge rates during contraction of adjacent muscles (Grigg & Greenspan, 1977), although the number of articular receptors firing in the midrange of joint movement probably does not change with muscle contraction (Clark & Burgess, 1975). Interpretation of the force-related errors in perceived position in terms of an absence of fusimotor coactivation is not entirely satisfactory, however, because a similar illusion has been described under conditions in which both the force and the extent of limb displacement are under voluntary control.

Roland and Ladegaard-Pedersen (1977) reported that when subjects matched the extent of compression of two springs with different coefficients of stiffness, errors in the perceived amplitude of the reference movement occurred. They found that the stiffness of the springs and, hence, the external force that the subjects had to work against influenced the perception of the distance compressed. The stiffer the reference spring, the further subjects felt it was compressed, as indicated by the extent of compression of the more compliant spring held in the other hand (Roland & Ladegaard-Pedersen, 1977). Roland (1978) found that the error in matching the amplitudes of the movements was proportional to the difference in the coefficients of stiffness of the two springs.

The influence of force on the perceived position of a limb has been demonstrated in a slightly different experimental paradigm, in which the effects of externally imposed elastic loads on the perception of limb position have been examined (Watson et al., 1984; Worringham & Stelmach, 1985). Watson et al. reported that when subjects moved one arm against an elastic load to align it with the other, stationary arm, the magnitude of the load influenced the accuracy of matching. The larger the force the subject had to flex or extend the arm against, the greater the error in matching the position of the two limbs. If subjects were instructed to match a target force, however, they were able to do this more accurately than when matching the position. The influence of external forces on the perception of limb position reported by Roland (1978) and Watson et al. (1984) occurs under conditions very similar to those described by Rymer and D'Almeida (1980). In each experiment, the forces produced during the course of a movement were changing, with the result that the amplitude of the movement was overestimated. The magnitude of the error was found to be related to the forces generated at the time that the movement was terminated.

The final situation in which a force-movement illusion has been described was first documented early in this century, when Hollingworth (1909) observed that errors in the perception of movement occur following the unexpected obstruction of a voluntary limb movement. When subjects are asked to reproduce the extent of an arm movement that has been unexpectedly and momentarily impeded by an obstacle during its course, the matching movements made by the contralateral arm are consistently greater than the reference movement (Hollingworth, 1909). The displacement of the impeded movement is perceived to be up to 2½ times its actual distance, and this occurs independently of whether the movement is preselected (i.e., the distance is determined by the subject) or constrained (i.e., the endpoint of the movement is defined by the experimenter). The illusion is not attenuated with practice, but if subjects are given feed-

back of the extent of their errors, they can learn to adjust the amplitude of the matching movement so that it is equivalent to the reference movement (Hollingworth, 1909).

Two factors influence the magnitude of this force-movement illusion: first, the force of impact and, second, the time at which the impact occurs during the course of the movement (Granit, 1972). Hollingworth (1909) noted that the perceived amplitude of the movement increased with the force of impact, which is consistent with the findings of Roland (1978) and Rymer and D'Almeida (1980) described previously. He also observed that there was an inverse relation between the point at which the impact was encountered and the extent of overestimation of the movement amplitude. This latter result suggests that spindle receptors play an important role in these illusions, because they are the main muscular receptor whose discharge rates would diminish the later an obstruction was encountered in a limb movement (Granit, 1972).

Summary

The forces generated during the course of a movement have been shown to influence the perception of limb position and movement in three situations. In each case, the amplitude of a movement and, hence, the final position of a limb are overestimated if the forces produced during the movement change. The error in perceiving the extent of the movement occurs independently of whether the forces change gradually (Roland & Ladegaard-Pedersen, 1977; Rymer & D'Almeida, 1980) or suddenly (Hollingworth, 1909), but in each situation, the extent of overestimation is directly related to the force generated at the end of the movement (Roland, 1978; Rymer & D'Almeida, 1980). Subjects are not aware of their errors, and practice has no effect on error magnitude (Hollingworth, 1909).

These force-movement perceptual illusions argue against considering the proprioceptive system solely in terms of changes in force, limb movement, and joint angle and indicate the complex nature of the interactions arising between sensory signals conveying force, movement, and position information. It is hardly surprising to find that force cues play an important role in the perception of limb position (Watson et al., 1984), because the external forces acting on a limb must be taken into account during limb movements (Worringham & Stelmach, 1985). These force-movement illusions also demonstrate that the conditions under which a limb moves from one position to another play an important role in determining its perceived final location and that in calculating the position of a limb, the proprioceptive system gives priority to dynamic over static sensory input, as was shown for the vibration illusion.

Postural Aftereffects

The perception of limb position is influenced not only by the forces generated during limb movements but also by previously held positions and movements. These postural aftereffects have been demonstrated in a variety of situations, ranging from inaccuracies in judging the position of a limb when it is moved to a new location after being held immobile for a brief period of time (Craske & Crawshaw, 1974) to errors in realigning the po-

sitions of the arms after one arm is held 45° above or below the other (Jackson, 1954). These results suggest that the perceived position of a stationary limb changes with time and that when the limb is subsequently moved to a new position, errors in localization occur because of adaptation when the limb was immobile. Paillard and Brouchon (1968) showed that the perceived position of a stationary limb changes steadily, with the drift in the direction of underestimating the limb's position. These findings are consistent with the nature and sign of postural aftereffects, which are typically in the direction of the horizontal or vertical midline of the body (Howard & Anstis, 1974).

The lability of the sense of position demonstrated by these postural aftereffects seems surprising in view of the results from studies of kinesthetic memory, which have indicated that human subjects can remember positions of their limbs quite accurately (Horch et al., 1975) and for long periods of time (i.e., up to 24 hr [Clark & Horch, 1986]). The encoding and retrieval from memory of limb positions relies, however, on central processes different from those involved in signaling limb position.

Summary

Postural and movement aftereffects demonstrate that perceptual adaptation occurs in the proprioceptive system and that these adaptive changes influence subsequent judgments of limb position. The occurrence of these effects emphasizes their generality across different sensory modalities and indicates that within short periods of time, one's sense of limb position can become unreliable. In this situation, vision presumably plays an important role in recalibrating position sense. Studies of kinesthesia during parabolic flight maneuvers support this proposition, in that they indicate that free-floating subjects who cannot see their limbs experience a degradation in their sense of limb position (Lackner, 1985).

Size-Weight Illusions

The *size-weight illusion* (Charpentier, 1891) refers to the observation that the perceived heaviness of an object depends on both its weight and volume. I discuss the nature of this illusion briefly; a more detailed account is given in Jones's (1986) article. Flournoy (1894) systematically investigated the influence of volume on the perception of weight in the late 19th century. He confirmed Charpentier's finding that the larger of two objects of equal mass is perceived as lighter than the smaller one. More recent studies of the size-weight illusion show that when the volume of an object remains constant, its heaviness increases as a power function of weight (Harper & Stevens, 1948) but that at different constant volumes, a family of power functions is required to describe the relation between weight and heaviness (Cross & Rotkin, 1975; Stevens & Rubin, 1970). Various mathematical expressions, ranging from logarithmic (Stevens & Rubin, 1970) to exponential decay functions (Rule & Curtis, 1977), have been proposed to describe the relation between heaviness and volume as a function of weight. These studies of the size-weight illusion are consistent in showing that the magnitude of the illusion increases with an increase in the relative volume of the object lifted (Cross & Rotkin, 1975), but the

potency of the illusion diminishes as the absolute weights of the objects increase (Ross, 1969; Stevens & Rubin, 1970).

The illusion is not dependent on any particular class of sensory receptor, because it persists when cutaneous receptors in the hand supporting the weight are blocked (using a pressure cuff, Ross, 1966) but can also occur when only these receptors are providing cues about the weight of the object (McCloskey, 1974; Usnadze, 1931). This suggests that afferent signals arising in the muscle are not crucial for the occurrence of the illusion. Many explanations of the size-weight illusion have emphasized the role of previous experience in judgments of weight, in particular the expectation that larger objects are heavier than smaller ones (Koseleff, 1957; Ross & Gregory, 1970). This expectation leads to a greater efferent command's being transmitted to the muscles involved in lifting the larger object, which is reflected in the amplitude of the EMG signals recorded from these muscles (Davis & Brickett, 1977), and this in turn results in a greater initial acceleration of the limb (Davis & Roberts, 1976). The rapid adjustment in the force exerted by the limb as the object is lifted at an unexpectedly fast rate has been hypothesized to lead to the perception that this object weighs less than a smaller one of identical mass (Davis & Roberts, 1976; Koseleff, 1957).

This proposition derives indirect support from Bower's (1976) research on weight conservation in young children. He found that when a ball of clay is placed in a child's hand and is then removed, rolled into an elongated sausage, and replaced in the hand, the new shape completely changes the pattern of muscle activation generated to lift the object. The child now expects the object to be much heavier, with the result that the arm flexes forcefully when the second object is lifted. The opposite result occurs when the clay is returned to its original, spherical shape, indicating that in each situation, the motor command sent to the muscles involved in lifting the object has been determined by the child's visual appraisal of the object's weight (Bower, 1976). In children, the potency of the illusion depends on their ability to discriminate weights. The more accurate the child's judgments of relative weight, the less frequent the tendency to manifest the illusion (Robinson, 1964).

Under conditions in which subjects have no visual or tactile cues about the size of an object being lifted, the perception of weight has been shown to be mediated by means of centrifugal feedback pathways and is probably derived from corollaries of the centrally generated motor command (Jones, 1986; McCloskey, 1981). If muscular afferent signals are involved in scaling these corollaries (McCloskey, Gandevia, Potter, & Colebatch, 1983) and in signaling the success of an intended movement (Gandevia & McCloskey, 1978), then the size-weight illusion could result from the discrepancy between the sensory signals expected on the basis of the efferent command and the actual afferent input from the periphery. Under most conditions, these two sets of signals are appropriately matched for the weight of the object, so no adjustment in the corollary discharges is required. When there is a mismatch between the predicted and actual afferent signals, then this difference could be enhanced at the expense of information about the absolute weight of the stimulus.

Summary

The size-weight illusion demonstrates that the perception of weight cannot be considered simply in terms of the processing of sensory signals arising as a direct result of activation of a muscle. The physical properties of an object (e.g., volume and density) can have a very potent influence on its perceived heaviness (Harshfield & DeHardt, 1970; Ross, 1969) and on the manner in which the object is lifted (Davis & Brickett, 1977; Davis & Roberts, 1976). By virtue of the association between size and weight, visual cues come to play a role in weight estimation (Robinson, 1964), and the final percept of heaviness is then derived from both visual and kinesthetic inputs (Sjöberg, 1969). The way in which information from the visual system is integrated with that from other sensory modalities to yield a judgment of weight awaits further investigation. On other perceptual tasks, it has been shown that when visual and kinesthetic cues are in conflict, visual information dominates proprioceptive signals (Laszlo & Broderick, 1985; Pick, Warren, & Hay, 1969; Posner, Nissen, & Klein, 1976; Warren & Cleaves, 1971).

Conclusions

It has been argued that illusions do not represent a breakdown in the normal processes of perception but, rather, result from the operation of perceptual mechanisms working to produce a percept that is different from physical reality (Coren & Girgus, 1978). Support for this proposition comes from experiments that demonstrate that illusions occur when specific and often unusual patterns of neural activity (e.g., the extremely high firing rates of muscle spindle receptors induced by vibration) are processed by the perceptual system in the same manner as other sensory inputs. In some instances, such as the phantom-limb and vibration illusions, the system has to extrapolate beyond previous experience to produce the percept, but the modes of processing these sensory configurations appear to be invariant. Because these illusions are consistent with current descriptions of the processes involved in the perception of limb position and movement, researchers have presumed that they can be accounted for in terms of the perceptual mechanisms that mediate kinesthesia under normal circumstances. Nevertheless, the conditions under which these illusions occur have been instructive in elucidating further the nature of sensory processing in the proprioceptive system.

First, these illusions indicate that the awareness of limb position, movement, and force results from cross-referencing the inputs from a number of sensory modalities. In particular, the assignment of visual direction, the position sense representation of various body parts, and the coordination of hand and eye movements are consequences of the complex interplay of visual and proprioceptive factors. Second, these illusions attest to the importance of central processing of afferent information and to the role of corollary discharges in proprioception. Finally, a number of these motor illusions provide support for the idea that the perception of limb movement and limb position are independent aspects of proprioception. I now discuss each point in detail.

Intersensory Calibration

Cross-calibration of sensory signals from different modalities has been considered in the context of the size-weight illusion, in which it has been demonstrated that visual and tactile cues can influence the properties of the movement generated to lift an object and, possibly, the processing of incoming sensory information. The former influence has featured in explanations of the size-weight illusion, in which the underestimation of weight with increasing volume has been hypothesized to result from a discrepancy between the sensory input anticipated on the basis of the efferent signal and the actual input from the periphery (Davis & Roberts, 1976; Ross, 1969). If this explanation is correct, then the size-weight illusion should be regarded primarily as a proprioceptive illusion that arises as a consequence of an inappropriate motor command. This hypothesis could be tested by examining weight perception under conditions in which the subject receives visual or tactile cues about the size of the object only after it has been lifted.

For the vibration illusion, there also appears to be cross-referencing between proprioceptive and visual signals, with the result that the potency of this illusion is markedly diminished when there is visual information about the position of the limb (Levine & Lackner, 1979). The illusion is subservient to vision, because it is absent when the whole limb is visible (Lackner & Levine, 1979) but occurs when only part of the limb can be seen (Lackner & Taublieb, 1984), indicating that the visual specification of limb position predominates over the proprioceptive only when the visual representation of the limb is complete. If the visual input is reduced, then visual localization can be influenced by the apparent position of the limb, or there will be a dissociation between the seen and felt positions. In the absence of any visual impression of a limb, such as in the case of the phantom limb of an amputee, the perception of the limb and its loss of proportionality must result from cortical sensory processes. If, however, at some point the visual representation of the limb becomes complete, which occurs when a prosthesis is worn, the distorted form of the phantom limb is lost (Sunderland, 1978) as the phantom and the prosthetic device are integrated.

The interaction between the proprioceptive and visual systems is reciprocal, because positional information about limb orientation can influence the assignment of visual direction, as indicated by the change in the position of a stationary target light when illusory movements are induced by vibration (Lackner & Levine, 1978). The apparent movement of the target light attached to the stationary limb always coincides temporally with the illusory limb motion. In this context, it is interesting to note that illusory movements of a limb can also be evoked by manipulating the visual environment in which the limb is perceived. If the visual background against which the arm is viewed is artificially displaced at a constant velocity, there is an illusory sense of arm movement in the opposite direction (Tardy-Gervet, Gilhodes, & Roll, 1984, 1986).

On initial analysis, the force-movement illusions seem to arise from interactions between force and position signals, with the result that the perception of static limb position is influenced by the forces generated during limb movements (Rymer

& D'Almeida, 1980; Watson et al., 1984). The size of the error in perceived position is directly related to the force exerted at the end of the movement and not to the directionality of the force change during the movement. This finding supports the idea that subjects can judge changes in limb position on the basis of the sensory information arising at the onset and termination of a movement. In the situation in which the forces generated by the limb vary during the course of the movement, the final sensory signals will reflect not only changes in position but also variations in force. Secondary spindle receptors have been shown to alter their firing rates in response to changes in both muscle length and force (Vallbo, 1971), which makes them a likely contributor to this illusion. Because muscular receptors respond to changes in both muscle force and length, there seems to be considerable scope for other interactions similar to those documented here. It appears, however, that positional cues have much less influence on the perception of force than force cues have on perceived limb position (Watson et al., 1984). This result is consistent with centrally mediated theories of force perception, which assume that sensory signals arising in the muscle play a relatively minor role in the perception of force (Jones, 1986; McCloskey, 1981).

The force-movement illusions can also be explained in terms of the influence of changes in limb stiffness or viscosity on the perception of position, because both of these variables increase with the force of contraction (Hunter & Kearney, 1982). The sensitivity of the human sensory system to changes in these mechanical variables has not been systematically investigated, so the influence of a change in stiffness or viscosity on the perceived position of a limb is unknown. It may prove appropriate in the future to incorporate these variables, in addition to force and displacement, in descriptions of the proprioceptive system.

Central Processing

The concept of internal neural correlates of the motor signal (i.e., corollary discharges) has featured in explanations of several of the motor illusions described, in which they have been ascribed various roles in the processing of proprioceptive information. Goodwin et al. (1972) and McCloskey (1973) reported that the potency of the movement illusion during vibration depended on the contractile state and level of fatigue of the muscle. These findings suggest that the sensory centers in the brain can distinguish between inputs that are a consequence of internally generated motor activity and inputs that result from an external stimulus. Feldman and Latash (1982a) and Matthews (1982) hypothesized that this is done on the basis of information conveyed by corollary discharges from motor to sensory centers. The kinesthetic illusions produced by vibration are consistent with this type of mechanism, because no movement illusions occur during normal voluntary contractions despite the high level of fusimotor-induced spindle activity (Vallbo, 1971). In the absence of corollary discharges, the use of spindle afferent signals to perceive a change in limb position seems impossible, because a change in spindle receptor firing may result from an increase in fusimotor activity, a change in muscle length, or both. For example, Vallbo, Hulliger, and Nordh (1981) found that when subjects actively maintain a steady limb

position, the level of fusimotor activity can be adjusted to maintain spindle receptor firing at an approximately constant rate at different muscle lengths. Although the manner in which corollary discharges assist in decoding spindle activity is not known, they appear to be used within the central nervous system to distinguish the spindle receptor firing that is appropriate for the level of motor activity (e.g., during normal voluntary contractions) from that which is inappropriate and therefore of potential kinesthetic importance, such as the discharges arising during vibration.

Corollary discharges do not, however, produce an experience of movement in the absence of peripheral afferent activity. Henderson and Smyth (1948) reported that movements of phantom limbs are made consciously and do not occur spontaneously, but they also noted that these movements are inevitably accompanied by contractions of the appropriate muscles in the stump. The ability to move the phantom limb is lost if the muscles are denervated (Sunderland, 1978). In contrast to these findings on the perception of movement, the continued presence of a phantom limb after denervation demonstrates that an internal schema of one's body can exist independently of sensory input. Peripheral afferent activity appears to be required to establish this central representation (Simmel, 1962) and to update the body image, because the perceived intensity of a phantom limb diminishes with the passage of time (Henderson & Smyth, 1948).

The role of corollary discharges in the perception of force has been subject to considerable debate and experimentation (Jones, 1986; McCloskey, 1981). Nevertheless, the results from a number of experiments suggest that sensations of force are centrally mediated by means of corollaries of the voluntarily generated motor command. This has been demonstrated most convincingly in experiments examining the effects of fatigue and partial curarization on the perception of force and weight, in which subjects have been found to overestimate the perceived magnitude of forces generated by fatigued or paretic muscles (Gandevia & McCloskey, 1977; Jones & Hunter, 1983). McCloskey et al. (1983) hypothesized that the roles of muscular afferent signals in the perception of force are to signal the success or failure of the motor command for the task being performed and to scale the internal correlate of the efferent command. The size-weight illusion does not appear to be consistent with this theory of weight perception, which would predict that the greater the motor command transmitted to the muscles involved in lifting an object, the larger its perceived heaviness. If, however, peripheral afferent signals are involved in scaling corollary discharges, presumably by means of a mechanism that automatically compares the expected and actual afferent inputs, then the size-weight illusion can still be accommodated by this theory. For this, one must assume that afferent discharges arising from muscles influence the processing of central sensory signals only when there is a discrepancy between the afference anticipated on the basis of the motor command and the actual input from the periphery. As was the case for the vibration illusion, incongruent information assumes major importance in kinesthetic processing.

Perception of Limb Position and Movement

Over the past decade, a distinction has been made between the perception of force that is centrally mediated and the per-

ception of limb position and movement that is derived from peripheral afferent activity (Matthews, 1982; McCloskey, 1978). It now appears that a further distinction should be made between the senses of position and movement. The evidence for this division comes from the illusory phenomena presented here and from studies in which subjects have been able to make independent judgments of the static positions and movements of limbs (Clark et al., 1985; Clark & Horch, 1986; Horch et al., 1975). Under certain conditions (e.g., very-low-frequency vibratory stimulation), it has been shown that changes in the perceived position of a limb can occur in the absence of any awareness of limb movement (McCloskey, 1973). Similarly, variables that influence the magnitude of the illusory movement induced by vibration do not necessarily affect the size of the position error (McCloskey, 1973). These results suggest that movement and position are encoded independently and that movement sensations may result from the activation of a more rapidly adapting receptor population. Clear delineation of the receptors involved in these two aspects of proprioception has not been possible, although neurophysiological evidence indicates that muscle spindle afferents are capable of encoding muscle length and, hence, could contribute to the awareness of limb position and movement.

One finding that has emerged from these studies of motor illusions is the remarkable lability of the sense of position. This is evident in the perception of anatomically impossible limb positions during vibration (Craske, 1977), the reports of postural aftereffects (Craske & Crawshaw, 1974), the fluctuations in the awareness and form of a phantom limb, and its modification when a prosthesis is worn (Henderson & Smyth, 1948). Experiments with displacing prisms have also demonstrated that limb position sense is labile and can be rapidly modified when visual and kinesthetic signals are in conflict (Kornheiser, 1976), but this adaptation affects only joints that are seen moving and does not transfer to other parts of the limb (Putterman, Robert, & Bregman, 1969). The process by which these systems undergo adaptation is not known, but Craske, Kenny, and Keith (1984) suggested that this discordance-driven adjustment and recalibration of the spatial senses are efficient means of ensuring intersensory congruence, which is necessary for accurate sensorimotor coordination. In addition, the capacity to modify one's body image to represent objects, such as tools, as extensions of one's body is an important consequence of this proprioceptive lability (Clark & Horch, 1986).

In summary, these illusions provide valuable cues about the operation of the proprioceptive system and attest to the importance of considering both central and peripheral feedback systems in descriptions of kinesthesia. They also indicate that the compartmentalization of kinesthetic sensibility into the three categories of movement, position, and force (McCloskey, 1978) is somewhat artificial in the context of normal motor performance.

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Cutting Appointed Editor of *JEP: Human Perception and Performance*, 1989-1994

The Publications and Communications Board of the American Psychological Association announces the appointment of James E. Cutting, Cornell University, as editor of the *Journal of Experimental Psychology: Human Perception and Performance* for a 6-year term beginning in 1989. The current editor, William Epstein, will be receiving submissions through September 30, 1987. At that point, the 1988 volume will have been filled, and all submissions after that should be sent to James Cutting. Therefore, as of October 1, 1987, manuscripts should be directed to

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