Chapter 2
Motor Control and Position Sense: Action-Perception Coupling

Anatol G. Feldman, Nabil Ilmane, Samir Sangani and Helli Raptis

2.1 Introduction

This chapter focuses on the relationship between motor control and position sense (PS) defined as the ability of humans to recognize the position of body segments under different conditions. Studies showed that afferent signals from proprioceptive and cutaneous and, to a lesser degree, articular receptors satisfactorily reflect passive changes in the position of body segments (Matthews 1972; Edin and Johansson 1995). In contrast, afferent signals deliver ambiguous positional information during intentional motor actions. For example, the activity of a major contributor to PS—muscle spindle afferents—increases with increasing isometric muscle torque (Vallbo 1974) whereas the arm position at which the torque is produced is perceived as unchanged. During slow intentional finger motion in isotonic conditions, discharges of spindle afferents virtually remain constant (Hulliger et al. 1982) and thus do not reflect the perceived changes in the finger position. These and other examples, justified the conclusion that afferent signals are somehow integrated with central control signals underlying motor actions to form PS (von Holst 1954; McCloskey 1981; Feldman and Latash 1982a; Proske and Gandevia 2012). The nature of this integration in PS remains unclear. This situation results, in particular, from controversies in the understanding of how motor actions are controlled.

A. G. Feldman (✉) · N. Ilmane · H. Raptis
Department of Neuroscience, University of Montreal,
6300, Darlington, Montreal, QC H3S 2J4, Canada
Tel.: +(514) 340-2111
e-mail: feldman@med.umontreal.ca

Center for Interdisciplinary Research in Rehabilitation (CRIR), Institut de readaptation
Gingras-Lindsay de Montreal, Montreal, QC, Canada

S. Sangani
Center for Interdisciplinary Research in Rehabilitation (CRIR),
Jewish Rehabilitation Hospital, Laval, QC, Canada

M. F. Levin (ed.), *Progress in Motor Control,* Advances in Experimental Medicine
and Biology 826, DOI 10.1007/978-1-4939-1338-1_2

This chapter reviews major hypotheses on how motor actions are controlled and the respective views on how PS is formed. Data will be described that permit choosing between alternative hypotheses of motor control. This approach may help advance the understanding of how control signals underlying motor actions contribute to PS in different conditions as well as of kinesthetic illusions, including the phantom limb phenomenon—the feeling that the amputated limb is present.

2.2 Alternative Views of Motor Control

Historically, a departure point in thinking about neural control of actions was based on the fact that motor actions obey and therefore are described in terms of the laws of mechanics. Many outstanding scholars in the field of action and perception, including von Holst (1954) combined this fact with the unconditional assumption that control levels of the nervous system are directly involved in the specification of variables characterizing the motor outcome in terms of movement kinematics, muscle forces and electromyogram (EMG) activity commonly called motor commands. One problem associated with this assumption was recognized by Von Holst (1954). He noticed that direct specification of motor commands to muscles to make intentional motion from a stable posture would be met with the resistance of posture-stabilizing reflexes (the posture-movement problem). To solve the problem, he suggested that neural control centers use a copy of pre-programmed motor commands—efference copy (EC)—to suppress movement-related afferent signals (reafference) and thus prevent resistance of postural reflexes to movement. The EC concept introduced by von Holst (1954) replaced similar concepts expressed under different names since the nineteenth century (Bridgeman 2007). Except for some researchers (e.g. Gibson 1968), the solution for the posture-movement problem and the EC concept has been accepted by the majority of researchers in the field without any critical analysis. It became a key concept in theories of motor control, including those that postulated the use of internal neural models for computations and specification of the motor outcome (e.g. Bays and Wolpert 2007).

A recent analysis (Feldman and Latash 2005; Feldman 2009, 2011) has revealed some drawbacks of the solution of the posture-movement problem offered by von Holst (1954). Physically, by suppressing reafference or, in modern terminology, position- and velocity-dependent feedback, would make the initial position unstable. This proposal does not explain how stability of the final posture is regained. Before the motion, postural mechanisms were tuned to stabilize the initial posture and, once restored at the final posture, would react to the accumulated deviation from the initial posture and drive the arm back to it. This prediction of von Holst's proposal conflicts with consistent findings that arm motion ends at a stable posture without any tendency to return to the initial posture. His proposal also conflicts with physiological data that postural reflexes are not suppressed but are reset to a new position when self-initiated motion is made, thus transferring stability to the final posture (Asatryan and Feldman 1965; Adamovich et al. 1997; Feldman 2011).

The resetting mechanism represents an empirically based solution to the posture-movement problem that does not rely on the idea of preprogramming of motor commands to muscles and the EC concept (Feldman 2011). When postural reflexes are reset (re-addressed) to a new posture, the initial posture becomes deviated from the new posture, and the same posture-stabilizing mechanisms that would resist self-initiated motion, now drive the body segments to the new position to which stability is transferred. In other words, by shifting the threshold position at which posture-stabilizing mechanisms are centered, the nervous system converts postural reflexes from a movement-resisting to a movement-producing mechanism.

EC-based theories of motor control have further been questioned by recent findings that descending systems in humans, particularly the corticospinal system, do not carry information about motor commands (EMG, forces) to muscles (Raptis et al. 2010; Sangani et al. 2011; Ilmane et al. 2013). Instead, these systems specify spatial thresholds at which neuromuscular structures (including reflexes and intrinsic muscle properties) begin to act, thus confirming the hypotheses that motor control is not based on preprogramming of the motor outcome and EC. These thresholds define a certain position, *R,* of body segments at which the activity of muscles is minimized. Thereby, any deviation from this position is opposed by reflexes. The *R* is also called the *referent position* since it plays the role of the origin of the spatial frame of reference in which the muscles and reflexes are constrained to work (Feldman 2011). These studies confirmed the earlier demonstration that central shifts in the referent position of body segments underlie intentional arm movements in humans (Asatryan and Feldman 1965), an empirical finding underlying the equilibrium-point hypothesis (for recent review see Feldman 2011).

2.2.1 Alternative Views on the Role of Central Control Processes Underlying Motor Actions in Position Sense

The alternative theories of motor control motivated different answers to the question of how PS is formed. One answer is based on the dominant view that the brain is directly involved in preprogramming of the desired motor output, including EMG patterns and muscle forces. It suggests that a copy of motor commands, i.e., EC, is somehow integrated with afferent signals to form PS (Proske and Gandevia 2012). It has also been assumed that EC underlies the sense of effort and therefore this sense and PS are interrelated. Evaluations of PS before and after ischemic deafferentation of the arm have been considered as supporting evidence of a contribution of sense of effort to PS (Proske and Gandevia 2012). This proposal, however, conflicts with results of the study by Allen et al. (2007) showing that under normal conditions, PS is load- and effort-independent.

Threshold position control is an alternative to the EC-based view not only about how motor actions are controlled but also about how they are perceived. Specifically, as the threshold position for muscle activation, the *R* carries essential positional information and as such, it can be used to form PS. The PS rule based on the *R* concept was previously proposed by Feldman and Latash (1982a) and recently updated (Feldman 2009, 2011; Feldman et al. 2013). Specifically, to determine the actual position, Q, of body segments, the nervous system can use already available information about the referent position, R, and combine it with sensory information related to the *deviation*, P, of the actual position of body segments from the referent position:

$$Q = R + P \tag{2.1}$$

This formula describes a natural, physical relationship between variables Q, R, and P, as illustrated in Fig. 2.1a for a single joint interacting with a load. To clarify, suppose that a referent position R, is centrally set, say, for wrist flexor muscles. A load counteracting these muscles will stretch them beyond the threshold, R. The muscle activity and torque will increase until muscle and load torques become balanced at some actual position, Q. To perceive this position, it is sufficient to know its deviation, P, from R, as defined by formula 1.

By applying this formula to PS, we need to assume that proprioceptive, cutaneous, and articular afferents do not convey direct information about the actual position, Q, of body segments but instead signal the deviation, P, of the actual position of the body segments from the referent position. In other words, it is assumed that PS has central (R) and afferent (P) components that are integrated at some level of the brain to perceive the actual position of body segments. The R is the control variable underlying motor actions and the P is the afferent outcome conveyed by ascending pathways to the brain. The PS rule thus represents *an explicit expression of action–perception coupling in kinesthesia* (see also Ostry et al. 2010).

2.2.2 Explanations of Position Sense Based on the PS Rule

The PS rule provides an explanation of PS in different motor tasks as well as of kinesthetic illusions and the phantom limb phenomenon (Feldman 2009; Feldman et al. 2013)—the sense that the amputated limb is still present. In particular, the PS rule suggests that passive changes in position that do not involve changing in the central PS component are perceived from changes in afferent signals, P, from muscle spindles and cutaneous receptors. In contrast, all active (self-initiated) changes in position are associated with changes in the central component, R, and PS will result from combined changes in both PS components. The relative contribution of these components to PS may be different depending on the motor task. Consider several examples.

Figure 2.1 shows not only how the PS rule is derived (A) but also how it works under different conditions. The thick solid curve in each panel is the muscle-reflex characteristic (torque versus joint angle) for a given R. The thin solid curve is the characteristic following a shift in the R. Dashed lines are load (L) characteristics. Subscripts i and f refer to initial and final values of variables, respectively, and filled dots are the initial and open dots are final equilibrium points of the system.

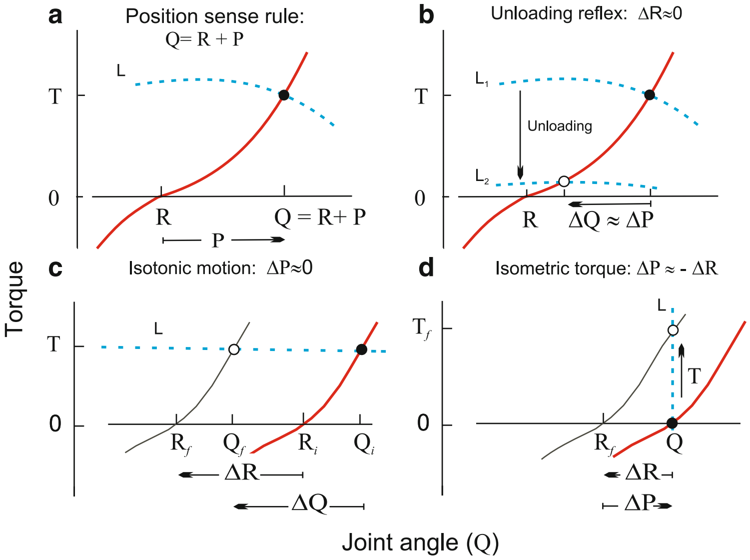

Fig. 2.1 The position sense rule: its derivation and application to different motor tasks. **a** PS rule for a single joint interacting with a load. When a referent joint angle (R) is set by descending systems, the activity of muscles and the net joint torque (T) increases with deviation of the joint angle from the R position (*solid curve*). The load (L) stretches the muscles (flexors in this example) until the system reaches an equilibrium point (*filled circle; point of intersection of the two curves*), i.e., the combination of the joint angle and muscle torque that balances the load (*dashed curve*) at some position, Q. To identify this position, it is sufficient to know the deviation, P, of the joint from its referent position: $Q = R + P$. It is assumed that this deviation is transmitted by ascending afferent pathways and converges with the referent joint angle at some central level where position sense is formed. **b–d** PS in different motor tasks. **b** during the unloading reflex elicited by a sudden change in the load, the same R is maintained. Changes in the joint angle, ΔQ, are perceived from changes in the *afferent* PS component, $\Delta Q \approx \Delta P$. **c** During slow isotonic motion, changes in the joint angle are predominantly perceived from changes in the *central* PS component, $\Delta Q \approx \Delta R$. **d** During isometric torque production, changes in the two PS components are equal but opposite, such that the joint angle is perceived as unchanged, $\Delta Q = 0$. Thick solid curve in each panel is the muscle-reflex characteristic (torque versus joint angle) for a given R; *thin solid curve* is the characteristic following a shift in the R; *dashed lines* are load (L) characteristics; subscripts i and f refer to initial and final values of variables, respectively; *filled dots* are the initial and *open dots* are the final equilibrium points of the system. (Reproduced with permission from Feldman et al. 2013)

During the unloading reflex (B) elicited by a sudden change in the load of say, preloaded elbow flexors, the same R is maintained (see Ilmane et al. 2013) and the arm moves to another position at which the residual load and muscle torques are balanced. According to the PS rule, changes in the joint angle, ΔQ, in the unloading reflex are perceived from changes in the *afferent* PS component alone, $\Delta Q \approx \Delta P$, since in this case, $\Delta R \approx 0$.

In contrast, during slow isotonic motion (Fig. 2.1c), the afferent PS component remains virtually constant, which is consistent with data by Hulliger et al. (1982) on the absence of position-related changes in muscle spindle afferents during isotonic finger motion. Thus, in isotonic conditions, changes in the joint angle are predominantly perceived from changes in the *central* PS component, $\Delta Q \approx \Delta R$.

During isometric torque production, the position (Q) of the joint remains unchanged but the deviation of this position increases when the threshold position, R, decreases (Fig. 2.1d). As a result, the activity of muscles and isometric torque increases. This process is associated with increasing proprioceptive signals (Vallbo 1974). The changes in the two PS components are equal but opposite such that the joint angle is perceived as unchanged, $\Delta Q = 0$.

The alternative, EC-based PS hypothesis is not sufficiently specific to explain all these cases. In particular, EC and sense of effort are virtually the same at different positions under isotonic conditions (Fig. 2.1c) and hardly contribute to PS. It is unclear how afferent signals can be used to identify the changes in position in isotonic conditions. Muscle spindle afferents in this condition do not signal changes in position (Hulliger et al. 1982). However, the contribution of cutaneous afferents to PS in isotonic conditions cannot be rule out. To our knowledge, positional sensitivity of these afferents has been demonstrated during *passive changes* of different joint angles (e.g., Edin and Johansson 1995). Cutaneous and proprioceptive afferent influences usually converge on common interneurons (Jankowska 1992; Hultborn 2006) and it is likely that during *active isotonic movements,* cutaneous, like spindle afferents, convey ambiguous positional information.

The unloading reflex and isometric torque production are associated with changes in effort. The EC or effort-based hypotheses are also not specific enough to explain why the sense of effort can contribute to the sensation of changes in position during the unloading reflex and to the sensation of the absence of changes in position during isometric torque generation. The sense of effort is primarily associated with muscle torques and the EC- or effort-based hypotheses do not provide clues as to how it can affect PS that is formed in the positional domain.

2.3 Testing Alternative Hypotheses on PS

The prediction of the effort-based hypothesis of PS was tested by asking subjects to produce changes in elbow position against different isotonic loads. According to the Weber–Fechner law (Weber 1834; Fechner 1860), the sense of effort and the error in identification of the changes in the load are scaled with the magnitude of the load. Therefore, if dependent on the sense of effort, PS would reflect such properties of the law. It appeared that PS is load-independent (Feldman et al. 2013; Fig. 2.2), confirming previous findings by Allen et al. (2007). These findings conflict with the effort-based PS hypothesis, but are consistent with the PS rule that is based on experimental findings that control signals underlying motor actions do not carry information about motor commands or sense of effort.

In the unloading reflex (Figs. 2.1b, 2.3), the changes in the wrist position were correlated with the amount of unloading and thus with the sense of effort. However, the precision with which subjects reproduced the positional changes for different

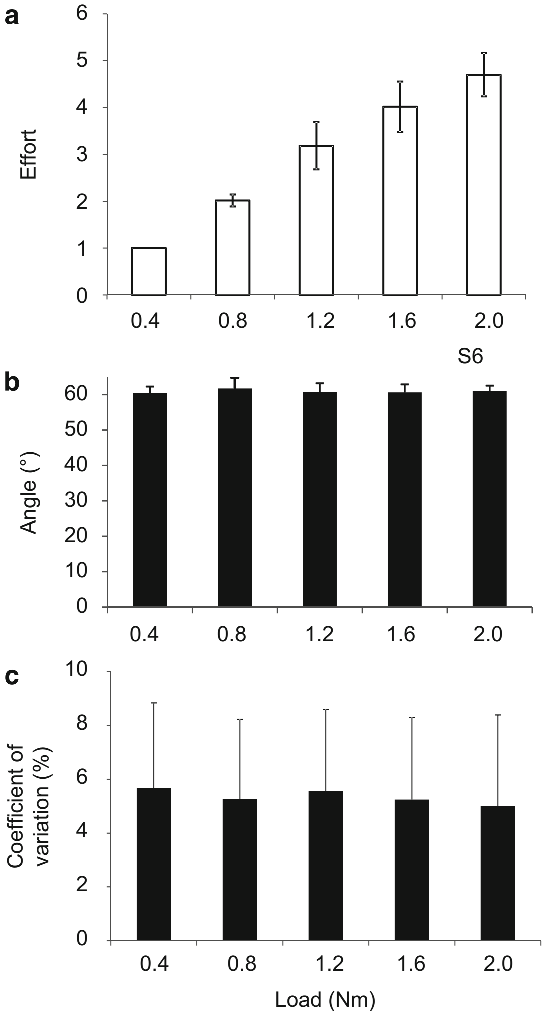

Fig. 2.2 The sense of position is independent of the sense of effort. **a** Different loads counteracting elbow flexor muscles were associated with different efforts identified with numbers 1–5 (group data). **b** With eyes closed, the subject (*S6*) reproduced the same elbow angle regardless of the load. **c** The precision of the reproduction (coefficient of variation) was also load-independent in this and other 11 subjects. (Reproduced with permission from Feldman et al. 2013)

amounts of unloading was load-independent (Feldman et al. 2013). This finding also conflicts with the assumption that PS depends on the sense of effort since if the PS were effort-dependent, the precision of the perceived changes in the wrist position would be scaled with the load according to the Weber–Fechner law (Weber 1834; Fechner 1860).

Consider findings that have been regarded as evidence that PS depends on the sense of effort (Gandevia et al. 2006; Smith et al. 2009; Walsh et al. 2010). In these studies, PS at the wrist was measured before and after the arm was paralyzed by an anesthetic or by ischemia produced by a blood pressure cuff. Before paralysis, subjects accurately detected the position of the wrist when it was passively rotated. After paralysis, subjects were unable to indicate the position of the hand at rest.

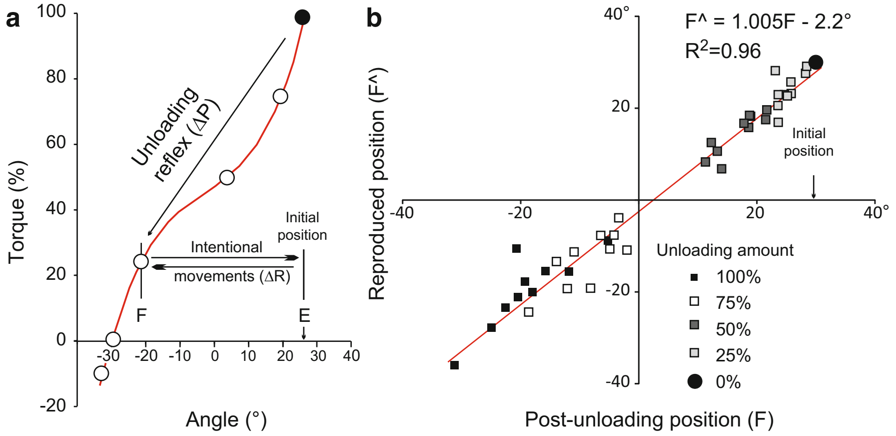

Fig. 2.3 Converting changes in the afferent component of position sense into intentional motion. **a** The mean initial (*filled circle*) and final (*open circles*) wrist equilibrium points resulting from different levels of unloading of wrist flexors from an initial position (E) in a representative subject, in the absence of vision. After unloading, the subject intentionally moved the wrist from the post-unloading position (F) to the initial, pre-unloading position and back to the memorized post-unloading position ($F^\wedge$). According to previous analysis (Ilmane et al. 2013), motion resulting from unloading was predominantly perceived from changes (ΔP) in the afferent component of position sense whereas intentional movements from position F to the pre-unloading and back to the post-unloading position, $F^\wedge$, required respective changes ($\Delta \mathrm{R} \approx \Delta \mathrm{P}$) in the referent position. The test was made for a different amount of unloading (100, 75, 50, and 25 % of the initial load; 0 % is for trials in which unloading was not produced). **b** A plot of position $F^\wedge$ versus F for different amounts of unloading. The slope of the regression line between positions $F^\wedge$ and F was close to 1 in this and other 9 subjects. (Reproduced with permission from Feldman et al. (2013))

Efforts to move the hand during paralysis produced large illusions of hand motion. From these observations, the authors suggested that PS depends on the sense of effort.

Alternatively, these observations can be explained in terms of the PS rule. During passive movements or relaxation, the R is shifted outside of the biomechanical range of the joint (Levin and Feldman 1994). As a result, PS during muscle relaxation is mainly based on changes in the afferent PS component. Naturally, when afferent feedback is blocked, subjects are unable to perceive the changes in wrist position, as observed by Gandevia et al. (2006). Based on the PS rule, the illusion of motion of the hand during paralysis can be explained in the following way. In the absence of afferent feedback, the position of body segments can still be sensed based on the central PS component, R. In experiments by Walsh et al. (2010), subjects learned to produce different efforts before paralysis. They thus learned to scale the R shifts with effort (cf. Fig. 2.1d). Indeed, when subjects reproduced these R shifts during paralysis, they perceived illusory movements correlated with the sense of effort. Since correlation between the two senses was preconditioned by the experimental protocol, results of the above studies cannot be considered as evidence for a dependency of PS on the sense of effort. This conclusion is also supported by the obvious dissociation between the two senses in isotonic, isometric, and reflex unloading conditions (Fig. 2.1b–2.1d).

Experiments were also conducted to test specific predictions of PS rule. According to the PS rule, the central and afferent components are equally important to position sense. The relative contribution of the two components to PS depends on the condition. In particular, it has been shown that descending influences on motoneurons of wrist muscles and thus the referent position, *R,* are similar at the pre- and post-unloading positions (Ilmane et al. 2013; Fig. 2.3). This means that changes in position elicited by unloading are predominantly perceived from a change in the afferent PS component, *P:* $\Delta Q = \Delta P$. In contrast, descending influences are modified when the wrist is intentionally moved to another position, suggesting that intentional changes in position in isotonic conditions are predominantly perceived from the change in the referent position, *R*. We tested the hypothesis that the nervous system is able to transform afferent information about changes in the wrist position resulting from unloading into the *R* command to make *intentional* isotonic movement of the same extent as that resulting from unloading (Fig. 2.3). Preloaded wrist flexors were fully or partially unloaded, and subjects were required to reproduce the involuntary wrist excursions by intentionally moving the wrist, in the absence of vision. Subjects had no difficulty in performing the required transformation of the *P* into the *R* component of PS. Indeed, such a sensorimotor transformation was facilitated by the parity in the dimensions of the two PS components as well as by the fact that the central PS component also underlies intentional motor actions. The finding of a strong correlation between voluntary and involuntary changes in the wrist position (Fig. 2.3) seems obvious, but only in the context of the PS rule. The initial and final positions in the unloading reflex were associated with different tonic EMG levels (or ECs), different senses of effort and different afferent feedback whereas these aspects, including afferent feedback (Hulliger et al. 1982), were hardly distinguishable at wrist positions established before and after intentional motion in isotonic conditions. In other words, the effort- or EC-based PS theory is not helpful in the explanation of PS. Indeed, intuitively, we take for granted that our sense of position is adequate regardless of what we do, but the PS rule shows that this intuition is physiologically justified in the context of the PS rule, rather than in the context of effort- or EC-based theory.

2.4 Kinesthetic Illusions

Usually, vibration of a muscle tendon elicits the illusion of muscle lengthening (extension of the elbow joint if vibration is applied to elbow flexors; Matthews 1972) in the absence of physical motion. If vibration is prolonged, the illusion can be reversed (Roll et al. 1989, 1980; Feldman and Latash 1982b). In terms of the PS rule, these illusions result from influences of vibration predominantly on the afferent and central PS components, respectively.

Physical changes in position are apparently coupled with appropriate awareness about these changes. The integration of the two components may just be a first step in the formation of PS and it does not address the challenging question of how subjects become consciously aware of physical or illusory changes in position. Normally, subjects are well aware of the position of body segments but this awareness may become inadequate during artificial stimulation (e.g. tendon vibration or electrical stimulation of the brain). The illusion of motion elicited by tendon vibration is an example of such inadequacy. Another example was observed in a patient undergoing brain surgery (Desmurget et al. 2009). Electrical stimulation of inferior parietal areas (Brodmann areas 39 and 40), elicited the sensation of arm movement although no movement was made. The authors concluded that activation of these areas reflected the intention to move even in the absence of motion. One can add that under normal conditions, activation of these areas might be combined with opening of pathways that transform the intention to move into changes in the referent position of the appropriate body segments. The resulting motor action (a movement or, if movement is prevented, isometric torque generation) is recognized by combining afferent feedback with the referent command, as implied by the PS rule.

No motion illusions have been observed in two studies (Desmurget et al. 2009; Feldman et al. 2013). In one, electrical stimulation of the premotor area (the dorsal sector of Brodmann area 6) in patients undergoing brain surgery triggered limb movements but patients denied that they had moved (Desmurget et al. 2009). One can suggest that the physical motion was elicited by changes in the *R* command without simultaneous influence of this command on the PS. In the other study (Feldman et al. 2013), no motion illusion has been observed during long-term tonic vibrations of elbow flexors in the absence of vision when subjects were unaware of any physical motion of the arm elicited by the vibration (Fig. 2.4).

It appeared that the no-motion illusion elicited by vibration is preserved when the arm moves against different isotonic loads. The critical angle at which subjects start perceiving physical motion does not depend on the magnitude of the load, further confirming that PS does not depend on the sense of effort.

2.5 Phantom Limb Phenomenon

The phantom limb phenomenon was considered as supporting the assumption that PS depends on the sense of effort (Proske and Gandevia 2012). However, a phantom limb can be sensed in the absence of any physical or mental effort. The phantom limb phenomenon can be explained without the assumption that it relies on the sense of effort. According to the PS rule, when afferent sensitivity is deficient or absent, the amputated limb can still be sensed as being present based on the central PS component, *R*. Because of the absence or deficiency of the afferent PS component, however, the shape of the phantom limb can be abnormal (e.g., twisted phantom elbow or knee joint) and associated with pain or other abnormal sensations.

Although *R* may be controlled independently of the current position, the transformation (“re-calibration”) of electrochemical descending influences into a spatial (positional) variable *R* would be impossible in the absence of position-dependent afferent feedback to α-motoneurons (for details see Fig. 2.4 in Feldman 2009). Therefore, in the absence of such feedback, the association of descending influences with

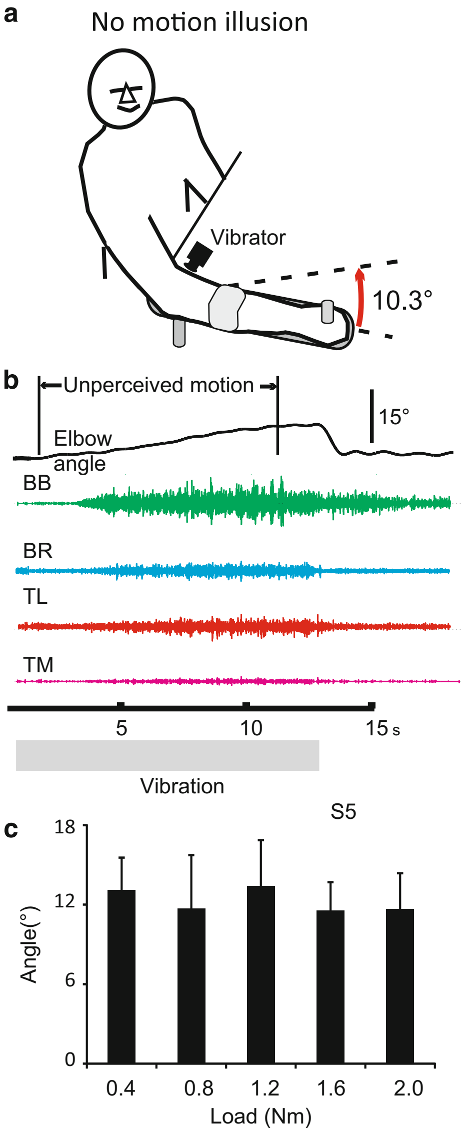

Fig. 2.4 No-motion illusion and its independency of the sense of effort. **a** Experimental setup. **b** Tonic vibration of the biceps tendon (frequency 100 Hz, amplitude 3 mm) elicited activation of elbow flexors (*BB, BR*) and extensors (*TL, TM*), resulting in elbow flexion. This subject (and other 9 subjects) was not aware of this motion (no-motion illusion) until the change in the joint angle began to exceed 10.3°. **c** The mean (± SD) change in the elbow joint angle after which the subject began to feel the motion, for different loads counterbalanced by elbow flexor muscles. (Reproduced with permission from Feldman et al. 2013)

spatial variables, like the *R*, gradually decays. This explains why phantom limb sensation in amputees eventually disappears and why chronically deafferented subjects do not have phantom limb sensations (Paillard 1991). The absence of referent control in deafferented humans may result in the loss of the body scheme and other sensorimotor deficits (Paillard 1991).

2.6 Further Implications and Future Directions

The notion that somatosensory feedback conveys information about deviation of the actual position of body segments from a centrally specified referent position may be applicable to ascending somatosensory pathways as well as to neurons of dorsal and ventral spinocerebellar tracts and propriospinal neurons having recurrent projections to the cerebellum (Arshavsky et al. 1972, 1978; Alstermark et al. 2007). According to the PS rule, this would be helpful in continuously monitoring changes in the actual position of body segments to decide whether it is necessary to correct the ongoing movement or switch to another pattern of referent shift in response to destabilizing external perturbations, environmental events, or internal intentions. Indeed, this is not the only function of ascending pathways. In particular, together with other proprioceptive afferents, tendon organ afferents may transmit information about muscle forces to form the sense of effort associated with the ongoing action.

Another implication of the present results is that they constrain the choice between different theories of action–perception coupling. Previous studies (Raptis et al. 2010; Sangani et al. 2011; Ilmane et al. 2013) have questioned the long held assumption (von Holst 1954) that the brain preprograms motor commands to muscles or efference copy (EC). Descending systems, particularly the corticospinal system, have been shown to not be involved in direct specification of motor commands to muscles. The same conclusion refers to theories of motor control based on the idea of internal models in which EC is a core concept (e.g., Bays and Wolpert 2007). Results obtained in our recent studies have also shown that PS is independent of motor commands and the sense of effort, thus rejecting EC- or effort-based theories of PS.

Some emerging theories of action and perception have not integrated the notion of referent position control. The sensory prediction theory (SPT) suggests that the brain predicts the proprioceptive consequences of the intended movement and that these predictions are delivered to motoneurons via descending pathways (Adams et al. 2013). Motoneurons are activated or not depending on the difference ("predictive error") between the predicted and the actual proprioceptive feedback. The SPT is reminiscent of a similar theory proposed several decades ago by Powers (1973) with the complementary assumption that the predictive error is eliminated by the neuromuscular system that works as a linear closed-loop servo-controller. To be functional, such a controller would have to have a physiologically unrealistic high gain, like in the servo-control hypothesis by Merton (Merton 1953; see also criticisms of the Powers' theory by Fowler and Turvey 1978). In any case, by assuming that the nervous system preprograms the sensory consequences of the motor outcome, SPTs do not help explain how PS is formed since these sensory consequences carry ambiguous information about positions of body segments (see Introduction). In addition, SPT seems to misrepresent how motor actions are controlled. Consider, for example, isometric torque production. In terms of SPTs, this is achieved by preprogramming of the sensory signals ("afference copy") associated with the required torque resulting from activation of motoneurons that function depending on the error in prediction of these signals. After several trials, the sensory signals associated with the required torque could be identified correctly and reproduced with a minimal error. Then, paradoxically, motoneurons that function depending on this error would barely be activated to generate the required torque. Therefore, not only PS but also motor control is inexplicable in the framework of SPTs.

Previous studies (Raptis et al. 2010; Ilmane et al. 2013) have shown that isotonic wrist movements are accomplished by shifting the referent wrist position, R. Results of these studies were interpreted based on the assumption that changes in the afferent PS component in isotonic conditions were minimal and therefore the difference in the initial and final wrist angles in these conditions was predominantly perceived from the difference in the central PS component. Future experiments are necessary to test whether this conclusion can be generalized to isotonic positions at other joints, including the elbow joint. The contribution of cutaneous afferents to PS in isotonic conditions cannot be rule out. To our knowledge, positional sensitivity of these afferents was demonstrated during *passive changes* of different joint angles (e.g., Edin and Johansson 1995). Cutaneous and proprioceptive afferent influences usually converge on common interneurons (Jankowska 1992) and it is likely that during *active movements,* cutaneous, like spindle afferents, convey ambiguous position information, which can also be tested in future studies.

The nature of information conveyed by ascending pathways to the cerebellum and other brain areas remains unclear. Based on our present findings, future studies can address the question of whether these pathways carry information about the deviation of the actual position of body segments from their referent position, rather than information about efference copy, as usually assumed.

2.7 Conclusions

There are several demonstrations that the corticospinal and other descending systems specify the referent position, R, of body segments at which motor commands can emerge without preprogramming. It is assumed that the referent position not only underlies motor actions but also represents a component of position sense. In other words, motor actions and position sense are controlled jointly, by setting and resetting of the referent position of body segments. Thereby, feedback from proprioceptive, cutaneous, and articular afferents delivers information about the deviation (P) of the body segments from the referent position. Taken together, the central and afferent components of position sense provide adequate information about the actual position (Q) of body segments, as defined by the PS rule: $Q = R + P$. This rule is helpful in the explanation of PS in many motor tasks as well as of kinesthetic illusions, including the phantom limb phenomenon. Three suggestions derived from the PS rule were confirmed by showing that: (1) changes in the afferent PS component resulting from unloading can be converted to changes in the referent position to produce intentional motor actions, (2) PS is independent of motor commands or sense of effort, (3) subjects may be unaware of arm motion elicited by continuous tendon vibration (no-motion illusion). Several theories of action and perception are rejected based on the present results and previous findings of how motor actions are controlled and perceived. Such are theories that assume direct preprogramming of the motor or/and sensory outcome by the brain based on internal models. Our study thus advances the understanding of how motor actions are controlled and perceived.

Acknowledgments Supported by Natural Sciences and Engineering Research Council (NSERC) to AGF, Fonds de la recherché en santé du Québec (FRSQ) (Canada) and postdoctoral fellowship for NI from team grant l'Équipe de Recherche en Réadaptation Sensori-Motrice, CIHR (Canada). We thank Mindy Levin for the valuable commentaries on the paper and Gevorg Chilingaryan for the statistical consultation.

References

Adamovich SV, Levin MF, Feldman AG. 1997. Central modifications of reflex parameters may underlie the fastest arm movements. J Neurophysiol 77:1460–1469.

Adams RA, Shipp S, Friston KJ. 2013. Predictions not commands: active inference in the motor system. Brain Structure Funct 218:611–643.

Allen TJ, Ansems GE, Proske U. 2007. Effects of muscle conditioning on position sense at the human forearm during loading or fatigue of elbow flexors and the role of the sense of effort. J Physiol 580:423–434.

Alstermark B, Isa T, Pettersson L-G, Sasaki S. 2007. The C3-C4 propriospinal system in the cat and monkey: a spinal pre-motoneuronal centre for voluntary motor control. Acta Physiol 189:123–140.

Arshavsky YI, Berkinblit MB, Fukson OI, Gelfand IM, Orlovsky GN. 1972. Origin of modulation in neurones of the ventral spinocerebellar tract during locomotion. Brain Res 43:276–279.

Arshavsky YI, Gelfand IM, Orlovsky GN, Pavlova GA. 1978. Messages conveyed by spinocerebellar pathways during scratching in the cat. II Activity of neurons of the ventral spinocerebellar tract. Brain Res 151:493–506.

Asatryan DG, Feldman AG. 1965. Functional tuning of the nervous system with control of movements or maintenance of a steady posture: I. Mechanographic analysis of the work of the joint on execution of a postural task. Biophysics 10:925–935.

Bays PM, Wolpert DM. 2007. Computational principles of sensorimotor control that minimize uncertainty and variability. J Physiol 578:387–396.

Bridgeman B. 2007. Efference copy and its limitations. Comp Biol Med 37:924–929.

Desmurget M, Reilly KT, Richard N, Szathmari A, Mottolese C, Sirigu A. 2009. Movement intention after parietal cortex stimulation in humans. Science 324:811–813.

Edin BB, Johansson N. 1995. Skin strain patterns provide kinesthetic information to the human central nervous system. J Physiol 487:243–251.

Fechner GT. 1860. Elemente der Psychophisik. 2 vols. Leipzig, Breitkopf und Härtel. Engl transl. (Vol. 1): Elements of Psychophysics. 1966. Adler HE, editor. NY: Holt, Rinehartand, Winston.

Feldman AG. 2009. New insights into action-perception coupling. Exp Brain Res 194:39–58.

Feldman AG. 2011. Space and time in the context of equilibrium-point theory. Wiley Interdisciplinary Reviews. Cog Sci 2:287–304.

Feldman AG, Latash ML. 1982a. Afferent and efferent components of joint position sense; interpretation of kinaesthetic illusion. Biol Cybern 42:205–214.

Feldman AG, Latash ML. 1982b. Inversions of vibration-induced senso-motor events caused by supraspinal influences in man. Neurosci Lett 31:147−151.

Feldman AG, Latash ML. 2005. Testing hypotheses and the advancement of science: recent attempts to falsify the equilibrium point hypothesis. Exp Brain Res 161:91–103.

Feldman AG, Ilmane N, Sangani S, Raptis H, Esmailzadeh N. 2013. Action-perception coupling: a new approach. Neuropsychologia 51:2590–2599.

Fowler CA, Turvey MT. 1978. Skill acquisition: An event approach with special reference to searching for the optimum of a function of several variables. In: Stelmach GE, editor. Information Processing In Motor Control and Learning. New York: Academic Press, pp. 2–38.

Gandevia SC, Smith JL, Crawford M, Proske U, Taylor JL. 2006. Motor commands contribute to human position sense. J Physiol 571:703–710.

Gibson JJ. 1968. The Senses Considered as Perceptual Systems. London: George Allen & Unwin Ltd.

Hulliger M, Nordh E, Vallbo AB. 1982. The absence of position response in spindle afferent units from human finger muscles during accurate position holding. J Physiol 322:167–179.

Hultborn H. 2006. Spinal reflexes, mechanisms and concepts: from Eccles to Lundberg and beyond. *Progress in Neurobiology*, 78, 215–232.

Ilmane N, Sangani S, Feldman AG. 2013. Corticospinal control strategies underlying voluntary and involuntary wrist movements. Behav Brain Res 236:350–358.

Jankowska E. 1992. Interneuronal relay in spinal pathways from proprioceptors. Prog Neurobiol 38:335–378.

Levin MF, Feldman AG. 1994. The role of stretch reflex threshold regulation in normal and impaired motor control. Brain Res 657(1–2): 23–30.

Matthews PB. 1972. Mammalian muscle receptors and their central actions. Arnold: London.

McCloskey DI. 1981. Corollary discharges: motor commands and perception. In: Brookhart JM, Mountcastle VB, editors. Handbook of Physiology: The Nervous System. Bethesda: American Physiol Soc. Vol. 2 (Pt 2), p 1415–1447.

Merton PA. 1953. Servo action in human voluntary movements. In: Malcolm J L, and Gray JAB, editors. The Spinal Cord. London: Churchill. p. 247.

Ostry DJ, Darainy M, Mattar AA, Wong J, Gribble PL. 2010. Somatosensory plasticity and motor learning. J Neurosci 30:5384–5393.

Paillard J (1991). Motor and representational framing of space. In: Paillard J, editor. Brain and Space. Chapter 10, Oxford: Oxford University Press. pp. 163–182.

Powers WT. 1973. Behavior: The Control of Perception. Chicago: Aldine.

Proske U, Gandevia SG. 2012. The proprioceptive senses: their role in signalling body shape, body position and movement, and muscle force. Physiol Rev 82:1651–1697.

Raptis H, Burtet L, Forget R, Feldman AG. 2010. Control of wrist position and muscle relaxation by shifting spatial frames of reference for motoneuronal recruitment: possible involvement of corticospinal pathways. J Physiol 588:1551–1570.

Roll JP, Gilhodes JC, Tardy-Gervet MF. 1980. Perceptive and motor effects of muscular vibrations in the normal human: demonstration of a response by opposing muscles. Arch Ital Biol 118:51–71.

Roll JP, Vedel JP, Ribot E. 1989. Alteration of proprioceptive messages induced by tendon vibration in man: a microneurographic study. Exp Brain Res 76:213–222.

Sangani SG, Raptis HA, Feldman AG. 2011. Subthreshold corticospinal control of anticipatory actions in humans. Behav Brain Res 224:145–154.

Smith JL, Crawford M, Proske U, Taylor JL, Gandevia SC. 2009. Signals of motor command bias joint position sense in the presence of feedback from proprioceptors. J App Physiol 106:950–958.

Vallbo AB. 1974. Human muscle spindle discharge during isometric voluntary contractions. Amplitude relations between spindle frequency and torque. Acta Physiol Scand 90:319–336.

von Holst H. 1954. Relations between the central nervous system and the peripheral organs. Br J Animal Beh 2:89–94.

Walsh LD, Gandevia SC, Taylor JL. 2010. Illusory movements of a phantom hand grade with the duration and magnitude of motor commands. J Physiol 588:1269–1280.

Weber EH. (1834). De pulsu, resorptione, auditu et tactu. Engl translat of chapters De Tactu and Der Tastsim, In: E.H. Weber's the sense of touch. 1978. Ross HE, Marray DJ, editors and translators. UK: Acad Press, Erlbaum, Taylor & Francis.