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Advanced Review

Space and time in the context of equilibrium-point theory

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Advances to the equilibrium-point (EP) theory and solutions to several classical problems of action and perception are suggested and discussed. Among them are (1) the posture–movement problem of how movements away from a stable posture can be made without evoking resistance of posture-stabilizing mechanisms resulting from intrinsic muscle and reflex properties; (2) the problem of kinesthesia or why our sense of limb position is fairly accurate despite ambiguous positional information delivered by proprioceptive and cutaneous signals; (3) the redundancy problems in the control of multiple muscles and degrees of freedom. Central to the EP hypothesis is the notion that there are specific neural structures that represent spatial frames of reference (FRs) selected by the brain in a task-specific way from a set of available FRs. The brain is also able to translate or/and rotate the selected FRs by modifying their major attributes—the origin, metrics, and orientation—and thus substantially influence, in a feed-forward manner, action and perception. The brain does not directly solve redundancy problems: it only limits the amount of redundancy by predetermining where, in spatial coordinates, a task-specific action should emerge and allows all motor elements, including the environment, to interact to deliver a unique action, thus solving the redundancy problem (natural selection of action). The EP theory predicts the existence of specific neurons associated with the control of different attributes of FRs and explains the role of mirror neurons in the inferior frontal gyrus and place cells in the hippocampus.

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INTRODUCTION

A clear definition of the purpose of scientific inquiry was offered by Einstein (Ref 1, p. 1):

> The object of all science, whether natural science or psychology, is to coordinate our experiences and bring them into a logical system.

The equilibrium-point (EP) theory is a logical system that coordinates a substantial bulk of data on motor actions. The present review focuses on fundamental principles of action and perception in the framework of the EP theory, summarizes empirical data underlying this framework, offers physiologically feasible solutions to a set of classical problems of action and perception that conventional theories have been unable to solve,[2] and formulates critical tests that can confirm or falsify the theory.

In the past, claims of rejection of the EP theory have been based on false premises that could have arisen because of differences in perceptions of how basic physiological mechanisms were viewed in the EP theory. These have been addressed[3,4] and are not considered further here. Limitations of alternative formulations of the EP theory[5] have been clarified in the past.[6] Motor learning in the EP context is also not considered here because of space limitations (see Refs 7–9).

THRESHOLD POSITION CONTROL UNDERLIES INTENTIONAL MOTOR ACTIONS

The EP theory originated from an experimental comparison of three motor actions at the elbow joint in humans—involuntary movement elicited by unloading of the preloaded arm (the unloading reflex),

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intentional change in the joint angle, and passive motion when a subject relaxed his/her arm muscles and another person moved the subject's arm.[6,10] The purpose of this comparison was to identify the neurophysiological variables that remained invariant or were modified to make these actions. The unloading reflex is usually demonstrated by asking a subject to hold a heavy book on the palm of the hand by flexing the elbow against gravity in the sagittal plane. When an assistant suddenly lifts the book, the arm involuntarily moves upward and stops at a more flexed position. No instruction is needed for such a response, but the response depends on the subject's ability to not intervene voluntarily in the sudden unloading.

Asatryan and Feldman[10] (see also Refs 6,11) analyzed the unloading behavior by placing the forearm on a horizontal manipulandum while counteracting an initial load. The elbow joint, load torque, and flexor and extensor electromyographic (EMG) activity were measured. The combination of the joint angle and the load torque at equilibrium is called the *equilibrium point* (EP) of the joint (Figure 1, filled circle *a*). Neither the equilibrium position nor the equilibrium torque alone comprises an EP: these are the *EP components*. In repeated trials, the initial EP was the same but the amount of unloading was varied from trial to trial, resulting in different final EPs (open circles). Together with the initial EP, *a*, these EPs described a smooth nonlinear torque-angle characteristic (upper left solid curve in Figure 1). Mathematically, such a characteristic represents a one-dimensional set of points, although a priori unloading responses could produce a two-dimensional set of EPs that covers some area of the torque-angle plane. The reduction in the dimensionality of this dataset implied that when reacting to unloading, the brain maintains some variable responsible for the second dimension invariant. Apparently, neither the arm position nor the muscle torque or force, nor stiffness (the slope) was invariant for different points of the torque-angle characteristic. The unloading behavior could easily be explained if the nervous system specified and maintained the same level of EMG activity, regardless of the applied load, thus relying on elastic properties of active muscles to react to unloading. It appeared, however, that the EMG activity level was not an invariant of the unloading behavior: the EMG activity simply scaled with the magnitude of the load (Figure 1, vertical segments near EPs), in accordance with the known EMG–force relationship.[12]

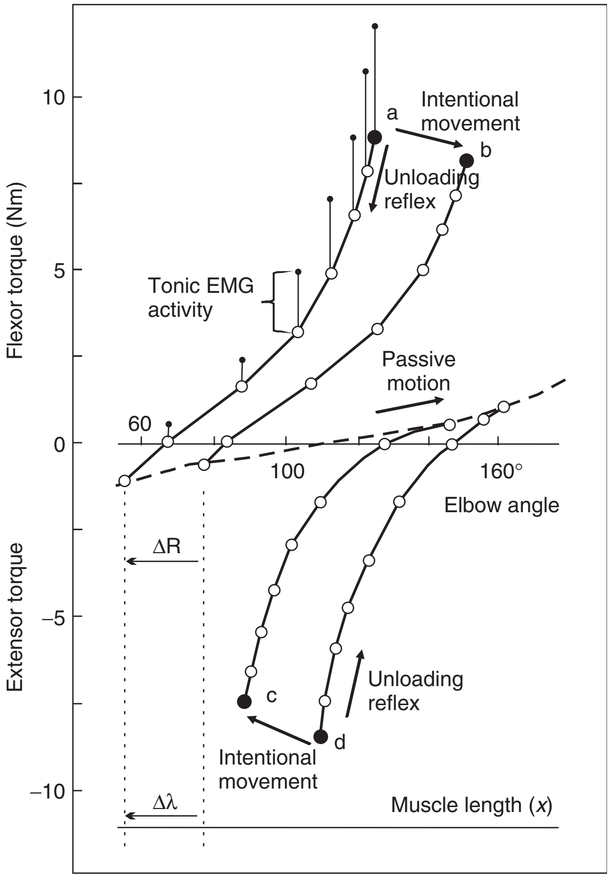

FIGURE 1 | Threshold position control underlies voluntary motor actions. A family of static torque-angle characteristics (solid curves) was obtained in unloading experiments. Each of the filled circles a–d shows the respective mean initial equilibrium point (EP), i.e., the combination of the elbow angle and torque established by the subject before unloading. Open circles show the final EPs established after different amounts of unloading. For each characteristic, the tonic EMG activity (vertical segments) decreased with the decreasing load. The dashed curve shows the passive torque-angle characteristic measured in a separate experiment by rotating the manipulandum with the forearm on it when the subject was instructed to completely relax his arm muscles. Note that each solid curve merges with the characteristic of passive muscles at a specific position—threshold joint angle (R). This threshold was different (ΔR) for different characteristics ($\Delta\lambda$ show the difference in terms of threshold muscle length). Thus the voluntary motor action responsible for the transition from one torque-angle characteristic to another was associated with a change in the threshold joint angle (Reprinted with permission from Ref 6. Copyright 1986 Heldref Publications).

The following assumption appeared helpful in finding the invariant of the unloading behavior: the invariant in question might be kept constant in the case of *involuntary* reactions to unloading, but it could be changed to produce *intentional* arm motion. To test this assumption, subjects were asked to *intentionally change* the starting position while compensating a load. The unloading procedure was then repeated but from a new EP (point b in Figure 1), resulting in another torque-angle characteristic (right upper curve). Subjects were also asked to produce another *intentional* action—to fully relax arm muscles. When this was done, the experimenter rotated the manipulandum to get a torque-angle characteristic of the subject's passive arm muscles (dashed curve in Figure 1). The two unloading characteristics (starting from points *a* and *b*) were similar: for each of them, the torque was nonlinearly related to the arm position, and EMG activity changed depending on the load. The characteristics were somewhat different in terms of shape but this could have resulted from differences in the mechanical properties of muscles in different parts of the angular range, rather than from a voluntary action. It appeared that each of the two unloading curves merged with the passive joint characteristic at a specific joint angle (R) at which muscles became silent and ceased to generate active torque. These threshold angles were different for different characteristics (Figure 1). It was concluded that: the threshold angle, R, at which muscles ceased to be active remained invariant for the unloading behavior; the R changed when intentional motion was made; to fully relax arm muscles, the R was shifted beyond the upper biomechanical limit of the elbow joint so that muscles remain silent in the entire biomechanical range of the elbow joint angle. These empirical results underlie the EP theory.

It is worth emphasizing that R is not an abstraction but an experimentally measurable variable. Anatomically, for each muscle, threshold R is achieved at a certain muscle length, λ. The question arises how, physiologically, the electrochemical synaptic signals descending from the brain to α-motoneurons are transformed into variables that refer to our body—threshold elbow angle R and threshold muscle length λ. These are *spatial variables*. Indeed, α-motoneurons that innervate muscles have thresholds but these thresholds are electrical and mostly constant (see subsequent text). In contrast, λ and R are broadly regulated and not electrical but spatial thresholds.

Figure 2 illustrates that variables λ and R characterize *integrative properties* of the neuromuscular system, rather than properties of its separate elements.[2,13] Figure 2(A) shows a minimal unit of such integration. It includes an α-motoneuron (MN) with the output to the muscle; facilitatory afferent feedback from muscle

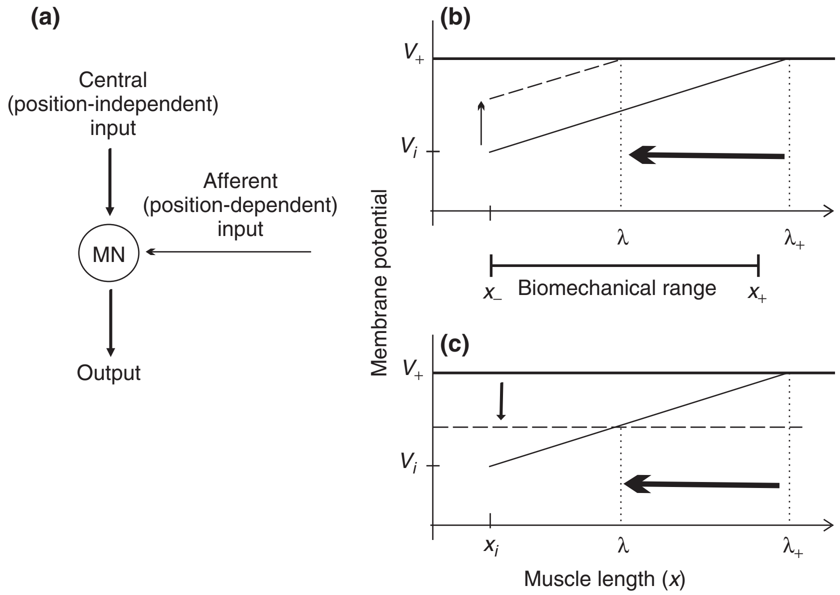

FIGURE 2 | Physiological origin of threshold position control. (A): Minimal integrative unit that produces threshold position control at the level of a single motoneuron (MN). The MN receives afferent influences that depend on the muscle length as well as central control influences that are independent of muscle length. The MN is recruited when the membrane potential exceeds the electrical threshold (V_+). (B) When the muscle innervated by the MN is stretched quasi-statically from the biomechanically minimal length (x_-) in the absence of independent control input, the motoneuronal membrane potential increases from its initial value (V_i) according to length-dependent feedback from the muscle (lower diagonal line). The electrical threshold (V_+) is reached at length λ_+ that is higher than the biomechanically maximal muscle length (x_+). When independent control facilitation is added (vertical arrow), the same stretch elicits motoneuronal recruitment at a shorter threshold length (λ). (C) Shifts in the spatial threshold (horizontal arrow) can also result from changes in the electrical threshold (vertical arrow). In both cases (B or C), shifts in the membrane potentials and respective changes in the threshold position are initiated prior to the onset of EMG activity and force generation (a feed-forward process). Thereby, the activity of motoneurons and muscle force emerge depending on the difference between the actual (x) and the threshold (λ) muscle length (Reprinted with permission from Ref 13. Copyright 2007 Springer).

receptors, some of which, called muscle spindles, send facilitatory *length-dependent* signals to the MN; and a central input from descending systems, that, in part, carries signals that, in certain limits, are *independent of muscle length* (but can depend on other sensory signals). When descending signals are minimal and the muscle is slowly stretched, the motoneuronal membrane potential increases (Figure 2(B), low diagonal line). The MN is recruited when its electrical threshold (V_+) is reached. This electrical threshold occurs at a certain muscle length, λ_+. In the situation in which descending facilitation is minimal, this threshold will be higher than the upper limit (x_+) of the biomechanical range [x_-, x_+] and the muscle will be relaxed within this range. If descending systems elicit a length-independent facilitation of the MN, then its membrane potential will increase (shifted upward; the upper diagonal line in Figure 2(B)), and the same muscle stretch will elicit motoneuronal recruitment at a shorter threshold length, λ. The discharge frequency of the MN will increase with increasing muscle length beyond threshold λ. Note that the threshold muscle length can be changed even if the electrical threshold remains constant. However, changes in electrical motoneuronal thresholds[14,15] may be an additional source of shifting the spatial threshold (Figure 2(C)).

The physiological explanation of the origin of spatial thresholds is helpful in the understanding of many other aspects of the EP theory. In particular, it implies that the motoneuronal membrane is the place where independent electrochemical signals descending from the brain are converted ('decoded') into spatial thresholds that associate our motor actions with the body. Also note that such decoding *would be impossible* in the absence of position-dependent feedback.

Studies in decerebrated cats have confirmed the existence of threshold position control, although unlike studies in humans cited earlier, they did not go far enough to demonstrate that this control underlies intentional motor actions, i.e., actions elicited by the organism itself, rather than external forces. Vestibulo-, reticulo-, rubro-, and corticospinal pathways influencing α-motoneurons directly (monosynaptically) or indirectly (pre- or postsynaptically via spinal interneurons or γ-motoneurons) can reset the threshold length of muscles spanning the ankle joint.[16–21] The motor cortex in humans is involved in threshold position resetting without any direct specification of motor commands.[22] The importance of threshold position control is emphasized by findings that brain injury in adults and children limits the range of threshold regulation, resulting in motor deficits such as abnormal muscle *coactivation*, weakness, spasticity, and impaired interjoint coordination.[23–25]

The threshold muscle length is velocity dependent,[6] which is important for stability of posture and movement.[26] It also depends on reflex reciprocal inhibition and other heterogenic reflexes.[17] To reflect these findings, symbol λ^* is used for the composite (net) threshold, whereas symbol λ is reserved for its central, independent component (Figure 3). It thus appears that the threshold muscle length is an important variable affected by many neural systems.

In earlier formulations of the EP theory, λ was interpreted as the threshold of the tonic stretch reflex. Actually, the torque-angle characteristics recorded by the unloading method are a direct demonstration of the presence of such a reflex in humans. Their nonlinear form is essential in increasing the stability margins with the increasing load (cf. Ref 27). However, λ and its dynamic extension λ^* are the thresholds for any source of muscle activation—reflex, central or combined. This point is consistent with the experimental finding that descending facilitation does not elicit motoneuronal recruitment unless the

Threshold control of muscle activation and force

Threshold muscle length:

$$\lambda^* = \lambda - \mu v + \rho + \varepsilon(t)$$

Muscle is active if the current muscle length (x) exceeds the threshold length, λ^*:

$$x - \lambda^* > 0$$

Muscle activation is proportional to

$$A = [x - \lambda^*]^+$$

Muscle force is a function of muscle activation, velocity and time:

$$F = f(A, v, t)$$

Motor action results from the tendency to diminish the gap between x and λ^* within the limits defined by the necessity to balance external forces

The range of λ regulation, $[\lambda_-, \lambda_+]$, is greater than the biomechanical range of changes in the muscle length, $[x_-, x_+]$.

FIGURE 3 | Basic rules describing threshold position control, EMG, and force regulation for a single muscle. Symbol λ^* is the composite (net) threshold; λ is its central component; μ is a temporal parameter related to the dynamic sensitivity of muscle spindle afferents; v is the velocity of change in the muscle length ($v = dx/dt$); ρ is the shift in the threshold resulting from the intermuscular interaction, in particular, reciprocal inhibition, and cutaneous stimuli (e.g., from pressure-sensitive receptors in the finger pads during grasping); $\varepsilon(t)$ represents temporal changes in the threshold resulting, in particular, from intrinsic properties of motoneurons; $[u]^+ = u$ if $u \geq 0$ and 0 otherwise. Note that muscle activation is a strongly nonlinear function of $x - \lambda^*$, implying that contrary to the servo-assistance hypothesis, muscle activation cannot be decomposed into two additive components, one resulting from central and the other from reflex influences on motoneurons.

length of the host muscle is bigger than the threshold length.[17]

Different Forms of Threshold Position Control

Figure 2 shows that changes in λ and thus intentional motor actions result from sub-threshold changes in the state of the neuromuscular system, occurring in advance of any changes in the motor output, implying that motor control is *feed-forward* in nature.[2] Also note that the diagram in Figure 2(B) can be applied not only to motoneurons but also to different neurons if we plot on the abscissa a gradual measure (e.g., intensity) of sensory signals received by these neurons. In that case, independent inputs to the same neurons (Figure 2(B), vertical arrow) can be identified as setting thresholds for recruitment of neurons by these sensory signals. When referring to a single neuron, the integrative scheme in Figure 2(A) can be considered as a *minimal cognitive unit*: When the sensory input matches the centrally established threshold, it signals to other neurons about this event. When generalized this way, different forms of threshold position control can be defined as shown in Figure 4.[7,11,28–31]

Suppose there is a group of neurons that receives visual signals about the location of the body in the environment (*body location neurons*). Then independent inputs to these neurons can be identified as producing changes in thresholds that shift the referent location (R_{l}) of the body in the environment. These neurons may or may not be activated depending on the gap between the actual location of the body (Q_{l}) in the environment and its referent location.[32] Suppose that the body location neurons control other neurons that, taken together, receive composite afferent signals about the actual configuration (Q_{c}) of the body (*body configuration neurons*) and project the same to motoneurons of all skeletal muscles of the body. Signals from body location neurons can be considered as independent of afferent signals delivered to the body configuration neurons. Then, according to Figure 4(B), these independent signals can be identified as changing the referent configuration (R_{c}) of the body. At this configuration, all skeletal muscles of the body, regardless of their biomechanical functions, reach their activation thresholds. Thereby, the activity of each skeletal muscle depends on the gap between the body's actual and referent configurations. By shifting the referent body location in the environment, the system can elicit changes in the referent body configuration, resulting in motor behavior such as gait.

Indeed, threshold positions can be defined for each or a combination of body segments (Figure 4). For example, one can define the *referent arm configuration* (R_{a}) and *referent hand shape* (R_{h}), characterized, in particular, by the degree of hand opening—*referent hand aperture* (R_{o}). Like λ*, other forms of threshold position control are likely velocity-dependent and an asterisk in symbols of these forms (e.g., R_{a}*) implies this dependency.

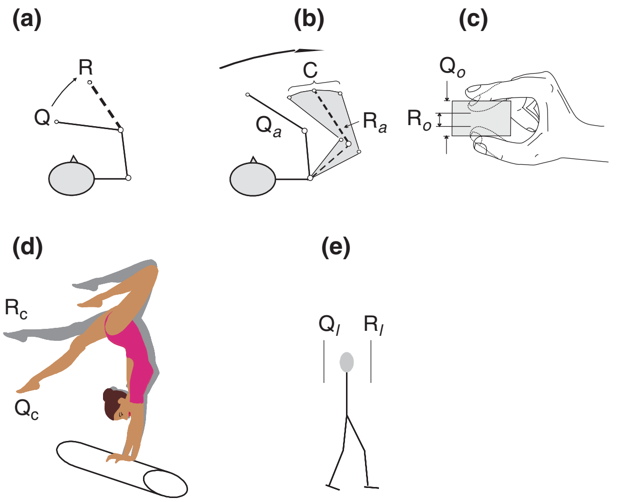

FIGURE 4 | Different forms of threshold position control. The specific form of threshold position control is chosen depending on the desired action. (A) In motor tasks involving a single joint, the system changes the referent joint angle R and the activity of muscles is generated depending on the difference between the actual joint angle (Q) and angle R. (B) In tasks involving the whole arm, the system changes the referent arm configuration (R_a) that defines a common threshold position for all arm muscles, except that the system may set thresholds for agonist and antagonist muscle groups differently such that these groups will be coactive at the R configuration and in the range, C, of adjacent configurations—referent range for muscle coactivation. (C) In precision grip force control, the system changes the referent hand opening (aperture), R_{o}, that defines a virtual distance between the index finger and the thumb. In the presence of the object, the actual hand aperture (Q_{o}) is constrained by the size of the object held between the fingers whereas, in the referent position, the fingers virtually penetrate the object. Deviated by the object from their thresholds of activation, hand muscles generate activity and grip forces in proportion to the gap between the Q_{o} and R_{o}. (D) In tasks involving skeletal muscles of the whole body, the system changes the referent body configuration (R_{c}). During the gymnastic exercise, the athlete presumably specifies an R_{c} configuration at which the net joint torques are zero and cannot compensate the weight torques of body segments. The body will move until the difference between Q_{c} and R_{c} become sufficient to elicit muscle activation and torques that balance the weight torques. (E) A single step or continuous walking is produced by a discrete or, respectively, continuous shifts in the referent location (R_{l}) of the whole body in space (Reprinted with permission from Ref 28,29. Copyright 2007 Elsevier).

The R_{c} postures underlying jumping, sit-to-stand movements, stepping in place and jeté movements in skilled ballet dancers have been identified experimentally.[30,31,33] The EP theory predicts the existence of specific neurons responsible for different forms of referent shifts such as R_a, R_c, and R_l.

Some data suggest that body location neurons actually exist. In the hippocampus, cells are activated when the body moves to specific areas of the animal's environment (place cells[34]). It is possible that these cells not only react to certain locations of the body in the environment but are also responsible for the referent shifts, R_l, bringing the body to these locations. Thus, these neurons could guide the central pattern generator (CPG) for locomotion by influencing locomotor areas discovered by Shik and Orlovsky.[35] Thereby, the CPG itself can likely be better understood as generating the motor output, depending on the difference between the actual and the velocity-dependent referent position (R_c*) of the body.

One can also suggest that by observing the body movements of others, subjects could mentally reproduce these movements by modulating neuronal activity responsible for changes in the referent body configuration (R_c), while movement execution is prevented. Therefore, it is possible that 'mirror neurons' that are activated in unison with observed actions[36] are related to R_c neurons.

Threshold Position Control and Equilibrium-Point Shifts

The EP is an important variable that characterizes the steady state ('attractor') that the nervous system may influence and tend to reach. However, the system cannot entirely predetermine the EP or its shifts, since external forces equally influence the EP. There is an advantage in this: by producing the same shifts, the system can elicit different motor actions. Thereby, the redundancy problem will be avoided since the interaction of the joint with the environment will result in a unique action. Depending on external conditions (loads), the same shift in R for muscles of a single joint may result in motion to another arm position (Figure 5(A)), in an isometric torque generation (b) or in a change in both position and torque (c). The EP theory is thus applicable not only to motor actions involving changes in position but also to actions in which the position remains the same, such as isometric torque production, muscle coactivation at the same joint position, squeezing a solid object[13] (Figure 4(C)), or pushing on a wall.[37]

Physiologically, shifts in threshold position R result from reciprocal influences on motoneurons of opposing muscle groups, say, from depolarization of flexor and hypo-polarization of extensor motoneurons

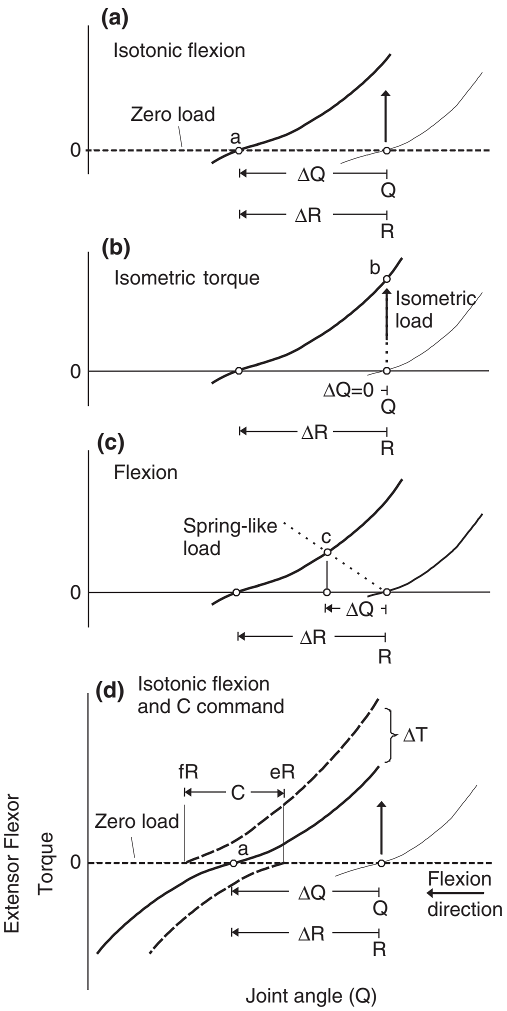

FIGURE 5 | Threshold position control of single-joint actions. By changing the threshold joint angle (ΔR) from its initial value (R), the system shifts the torque-angle characteristic of the joint in the flexion direction. The final characteristic (thick curve in each panel) represents a set of possible equilibrium points (EPs) that the system can reach. Each EP is the combination of the position and torque that can be established in the process of the interaction of the joint segment with the external forces (loads). A specific final EP (*a*, *b*, or *c*) of the redundant set of potential EPs is established depending on external condition (isotonic in A, isometric in B and intermediate in C, respectively). In D, shift in R can be combined with co-facilitation of flexors and extensors, resulting in a range (C) in which muscles are coactive. This process does not affect the final EP, *a*, but elicits additional torque (ΔT) at the initial position (Q) that helps to speed up the movement. Note that in all panels, the initial torque-angle characteristic (thin curve) determines the resistance of the posture-stabilizing mechanisms to deviations from the initial position (Q). Following the shift in the threshold position (in A), muscle activity and torque at the initial position begin to increase (vertical arrow), resulting in movement acceleration toward the final referent position in A, C, and D. In this way, the nervous system converts the posture-stabilizing to movement-producing mechanisms, thus solving the posture–movement problem. In B, movement is prevented and the shift in R results in an increase in isometric muscle torque (Reprinted with permission from Ref 22. Copyright 2010 John Wiley & Sons).

('reciprocal command'). Such influences shift the angular thresholds for activation of these groups in the same direction such that the common threshold angle for activation of all muscles is shifted from R to $R - \Delta R$ (Figure 5 (A)–(C)). In contrast, co-facilitation of motoneurons of these groups shifts their activation thresholds in the opposite directions, to R_f and R_e in Figure 5(D). In the angular range between these thresholds, C, all elbow muscles are co-activated ('coactivation command'). Outside the C range, only one of the two antagonistic groups is working. Depending on task demands, the system can increase or decrease the C range. The C area surrounds the R command. Therefore, the whole C range moves together with the R command (Figure 5(D) and thus the R command predetermines where, in the biomechanical range of the joint, muscles are coactivated. The hierarchy between the R and C commands is very important: without resetting the C range by the R command, muscles coactivated at the initial elbow position would squeeze the joint and resist movement to another position elicited by the R command (see the section *Posture–Movement Problem and its Empirical Solution*). In contrast, relocated by the R command, the C command is able to substantially accelerate and decelerate the elbow motion to the final position (Figure 5(D)). A bell-shaped velocity profile and the characteristic tri-burst EMG pattern of fast single-joint movements can be considered as *straightforward effects* of the cooperative action between R and C commands.[26,38,39]

During intentional movements, an EP component—the equilibrium position of the effector (such as the hand during reaching)—gradually changes and forms an equilibrium trajectory.[40] Although the equilibrium and actual hand trajectories of fast arm reaching movements in the natural gravitational field are spatially close,[41] they are not isochronous: the equilibrium position reaches its final destination at the time when the hand just approaches its peak velocity and has moved only through about 1/3 of the whole movement distance (Figure 6).[42] When EP shifts are completed, muscle and reflex properties are sufficient to decelerate the movement.[39,43,44] The final equilibrium position may not coincide with the targeted position of the hand because of movement error, which necessitates a change in the threshold position to eliminate the error.

Complex, curvilinear, and nonmonotonic equilibrium trajectories can occur in many actions, such as those involving obstacle avoidance, adaptations to complex force fields, and jumps (e.g., Ref 31). However, as confirmed by experiments and modeling,[38,39,42,45] simple, fast point-to-point arm movements without corrections result from short-lasting monotonic, rather than from complex, nonmonotonic EP shifts, with overshoots past the final position ceasing only with movement offset.[46,47]

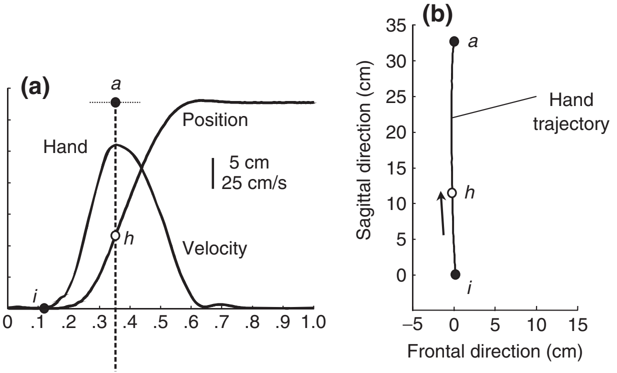

FIGURE 6 | In fast point-to-point arm movements, shifts in the arm equilibrium position are ceased substantially before the end of movements. An example of fast arm movements in temporal (A) and spatial coordinates (B). Point *i* is the initial hand position. Point *h* is the hand position at the time when the shifts of the hand to the final equilibrium position, *a*, has been completed. Thus, the equilibrium position substantially leads the actual hand position. Because of this discrepancy, muscles generate forces sufficient for a high-speed movement. Curves and points *i*, *a* and *h* were experimentally measured (Reprinted with permission from Ref 42. Copyright 2001 Springer).

MAJOR DEPARTURE FROM CONVENTIONAL VIEWS ON MOTOR CONTROL

In the following sections, threshold position control will be linked to the ability of the brain to choose and shift the spatial FRs in which action and perception take place. By specifying, say, a threshold position of the arm, the brain predetermines *where*, in spatial coordinates, the neuromuscular elements will work but it does not instruct them *how* they should work: *muscle activity and forces emerge* only if peripheral feedback indicates that the arm position is within the specified spatial boundaries. Therefore, central changes in threshold positions do not represent 'motor commands' to muscles *per se*. A proposed terminology for threshold positions is 'central commands' (see earlier text) or 'control variables', so as not be confused with the term 'motor commands'.

Also, the threshold position cannot be interpreted in terms of servo-control theory (e.g., Ref 48) as an internal representation of the targeted position that the system should reach. Although the threshold position may occasionally coincide with the targeted position, it is not specified as such (Figure 5).

Threshold position control thus signifies a major departure from the conventional view that actions result from central pre-programming of the anticipated pattern of motor commands (efference copy) computed according to the desired movement trajectory or other kinematic and kinetic characteristics.[49,50] The nervous system is released from the burden of pre-programming of any variable characterizing the motor output, including the movement trajectory. As mentioned before, the brain can influence but cannot directly predetermine the EP since it is also affected by external forces, which limits the capacity of the nervous system to control the EP. Figure 5 illustrates the important points of this section.

Feed-Forward Nature of Threshold Position Control

Figures 2 and 5 show that threshold position control is accomplished in a feed-forward way, i.e., in advance of motor actions. This control strategy is helpful in anticipatory adjustment of motor performance, such as increasing grip force to prevent object slippage when moving the arm[13] or preparing responses to arm perturbations.[51] It also allows the system to overcome destabilizing effects of reflex and electromechanical delays.[26]

By rapidly shifting the threshold position before the onset of fast movement, the system forces the stretch reflex to powerfully activate agonist muscles (Figure 5(A), vertical arrow), such that only comparatively strong perturbations are able to influence the initial agonist EMG burst.[43] Thus, threshold position control invalidates the conventional view that in fast movements, the contribution of the stretch reflex to the initial agonist EMG burst is minimal (e.g., Ref 52).

Predicting Movement Errors before the End of Motion

As mentioned before, experimental data and computer simulations have shown that the final value of the arm referent position (R_a) in fast movements is established substantially before movement offset, about the time when the movement speed reaches its peak velocity[42] (Figure 6). Thus, the next motor action in a sequence of actions can be started without waiting for the end of the motor output from the previous action, for example, during rapid speech production or piano playing. Moreover, ending control processes early in the movement gives the system sufficient time to *predict* whether the target will be reached, so that corrections can be initiated beforehand. Piano players may actually detect errors before they hit the wrong piano keys.[53]

The forward nature of threshold position control is a natural consequence of the integration of control and sensory inputs at the motoneuronal membrane level (Figure 2). This confirms the suggestion that natural processes may manifest feed-forward and predictive properties in the absence of any computations based on internal models of the system dynamics.[54–57]

Posture–Movement Problem and Its Empirical Solution

Von Holst and Mittelstaedt[58] emphasized that each posture of the body or its segments are stabilized such that deviations from the posture are met with position- and velocity-dependent resistance generated by various muscle, reflex, and central posture-stabilizing mechanisms. In contrast, intentional movements away from previously stabilized postures do not evoke resistance from these same mechanisms. The understanding of why these mechanisms react differently to intentional and unintentional deviations from a stable posture is the essence of the classical posture–movement problem. Von Holst and Mittelstaedt[58] assumed that, to prevent resistance to intentional motion, efference copy (a copy of motor commands to muscles) is used to suppress motion-evoked afferent feedback (reafference), i.e., a major source of resistance to motion. However, in isotonic arm movements, the EMG activity can return to its premovement level when the final arm posture is reached[7,59] (Figure 7). This implies that the efference copy that reflects this activity also returns to its premovement level, leaving the position-dependent reafference accumulated during the intended transition to the new arm posture uncompensated. Therefore, the efference copy theory is unable to explain why uncompensated posture-stabilizing feedback does not drive the arm back to the initial position at the end of movement. The failure of the efference copy theory to solve the posture–movement problem complements the growing concern that the theory does not explain other aspects of action and perception[55,60] (for review see Ref 2).

Posture-stabilizing mechanisms function only when muscles are active, i.e., when the threshold position is reached. Therefore, by shifting the threshold position, say, of the arm, the system resets ('re-addresses') posture-stabilizing mechanisms to a new referent arm posture (R_a). The initial posture appears as a deviation from the new referent posture and the same posture-stabilizing mechanisms that otherwise

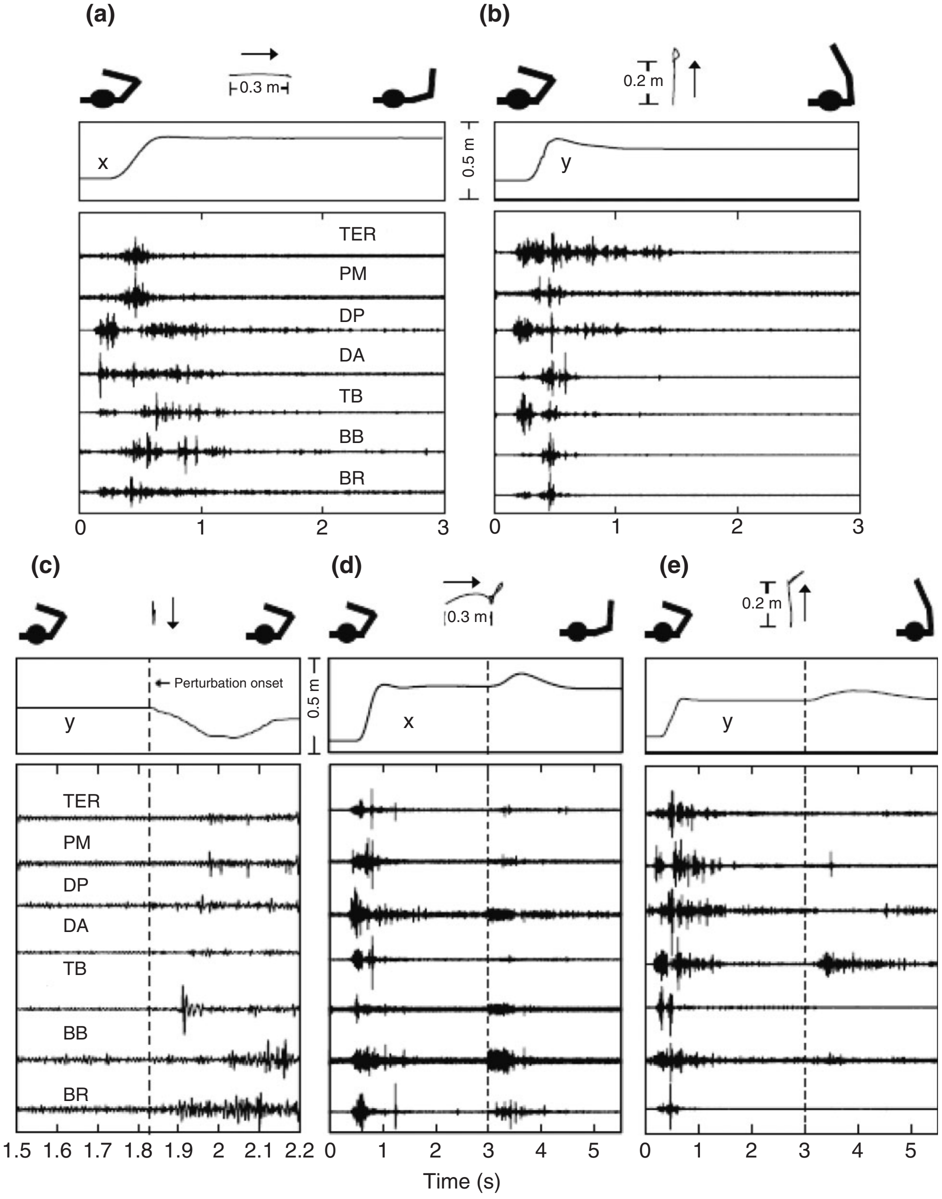

FIGURE 7 | Resetting of threshold arm configuration in point-to-point arm movements in frontal (*x*) and sagittal (*y*) directions. Note that the activity of seven muscles at the initial arm position is practically zero (background noise level) and, after transient EMG bursts, returns to zero at the final positions (A, B). Muscles are activated in response to perturbations of the arm at the initial (C) and final (D, E) positions. The results imply that motoneurons of arm muscles were near their activation threshold and that the threshold arm position was reset when movement was made. On the top of each panel, the hand trajectories as well as the initial and final arm configurations are shown; *x* and *y* are major components of trajectories for the motion to the frontal and sagittal targets, respectively. Muscles that remained active at the final position could be deactivated in response to perturbation in appropriate direction (e.g., DP in E) (Reprinted with permission from Ref 7. Copyright 2006 Springer).

would resist the movement now drive the limb to the new posture. Thus, by shifting the threshold position, the nervous system *converts movement-resisting into movement-producing forces*, which solves the posture–movement problem (Figure 5(A)). By changing the rate and duration of threshold shifts, the system may influence the speed, duration, and extent of the resulting motion (e.g., Ref 38,39).

Note that the solution of the posture–movement problem implies that posture-stabilizing mechanisms are used to produce movement. It does not exclude the possibility of separate modifications of postural and movement aspects of motor actions, as shown in numerous studies (e.g., 61). For example, by increasing the rate of shifts in threshold hand position, the system may speed up hand motion to the same final position. By changing the direction of shift in the threshold hand position in the arm workspace, the system can elicit movements to different final positions while maintaining similar dynamics of motion to them.

Posture–Gait Problem and its Solution

This problem is a particular case of the posture–movement problem. According to the usual biomechanical interpretation, with a forward step, the center of body mass is shifted away from the body support area, creating the risk of falling and necessitating 'catching' the body. The notion of FR offers a solution to the posture–gait problem that eliminates the falling risk (Figure 8). By influencing body location neurons (defined earlier), control levels shift the referent location (R_l) of the body forward. These neurons generate activity that signals the difference between the actual and the referent location of the body in the environment. The activity of these neurons is transmitted to body configuration neurons that tend to diminish the input by changing the referent body configuration (R_c), thus virtually translating the body toward the new location and readdressing the posture-stabilizing mechanisms to the new, referent posture. The difference between the actual and referent body postures results in muscle forces that support the stance phase of one leg and propel the other leg into the swing phase, thus generating a step to the new, projected body location. Biomechanically, although the center of mass leaves the initial body support area, it moves toward the new, projected support area without any threat of falling. The feasibility of this control strategy was demonstrated by Günther and Ruder[62] who simulated planar human gait based on changes in the referent body configuration.

Kinesthesia

Kinesthesia (sense of motion and position of body segments) is predominantly based on information from group Ia and II spindle afferents.[63,64] However, efferent, γ-influences on muscle spindles often make discharges of these afferents ambiguously related to the position of body segments. In particular, spindle afferent discharges hardly change during slow isotonic finger motion.[65] Nevertheless, despite the position-independence of spindle discharges, position sense remains fairly accurate in this situation: the finger is perceived as moving, even when movement is made without vision. Another example of positional ambiguity of spindle afferent activity is that, in isometric conditions, discharges of spindle afferents increase with increasing isometric force[66] whereas

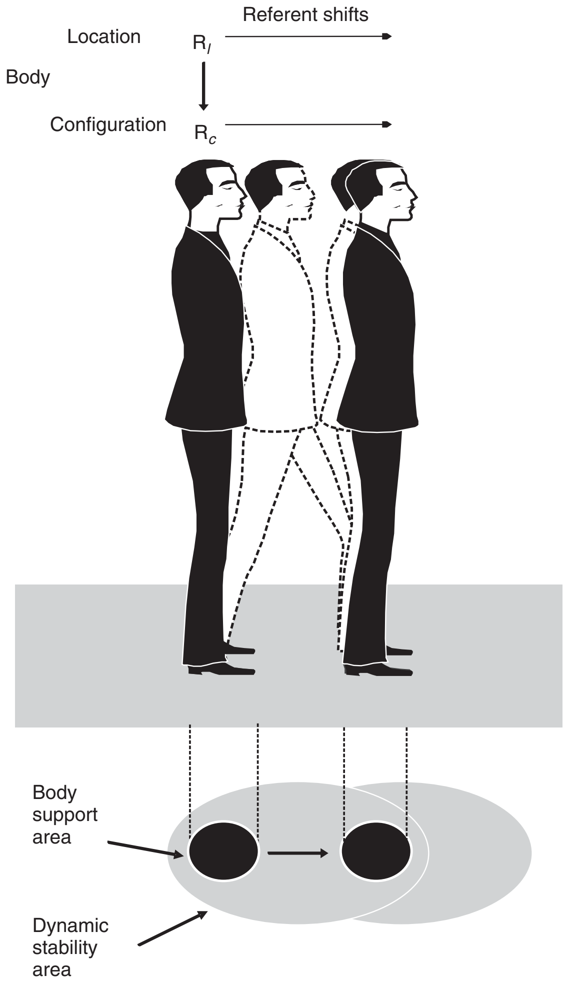

FIGURE 8 | Human step as an emergent response to changes in the gap between the actual location (Q_l) of the body and its centrally specified referent location (R_l) in the environment. During standing, body posture Q_c (solid figure) is stabilized such that the center of the body mass is within the area of body support. Externally elicited deviations from posture Q_c evoke position- and velocity-dependent muscle resistance. The area from which the center of body mass should move at some speed to reach the foot support area without a fall of the body is called the dynamic stability area. Posture-stabilizing mechanisms would generate resistance in response to an intentional step if it were made without any concerns with these mechanisms (classical posture–movement problem). To make a step, the nervous system shifts the referent location of the body (upper horizontal arrow and dashed figure) until it virtually reaches a final position, R_l, located at some distance from the initial position of the body. The virtual relocation of the body elicits (vertical arrow) step-like changes in the referent body configuration, R_c. Following an increase in the gap between Q_c and R_c, muscles are activated, and produce a real step. Although the center of body mass initially appears outside the initial body support area resulting from the referent shifts, it moves toward and eventually reaches the new body support area, thus excluding the risk of body fall. Multiple steps (gait) result from continuous shifts in the referent body location in the environment. Since the posture-stabilizing mechanisms are shifted with the virtual body displacement, they do not resist but rather produce the step or gait.

the limb is correctly perceived as being motionless. Discharges from other proprioceptive afferents are not less ambiguous than spindle afferents in transmitting positional information.[2]

McCloskey[67] and Gandevia[68] proposed that the nervous system overcomes the positional ambiguity of proprioception by taking into account a copy of motor commands (efference copy) while interpreting proprioceptive signals. This proposal, however, is inconsistent with data showing that after isotonic movements, not only spindle discharges[65] but also motor commands to muscles can return to their premovement values (Figure 7). In this case, efference copy in isolation or in combination with constant spindle discharges would mistakenly report to the brain that the limb returned to or remained at the initial position.

In the framework of the EP theory, proprioceptive signals reflect not the absolute position of the limb but the *deviation of the limb from the referent position* specified by the brain. Therefore, adequate position sense, i.e., correct evaluation of the actual angle, Q, is derived at some brain level by adding the referent (threshold) joint angle (R) to positional measure P of proprioceptive signals[2,4] (Figure 9):

$$Q = R + P. \qquad (1)$$

In other words, R plays the role of a reference not only for motor action but also for perception of position.

An isotonic elbow flexion is produced by a monotonic decrease in R, which appears to be a component of position sense. The joint angle is perceived as changing following this decrease in R, even though the proprioceptive component, P, of position sense can remain unchanged and motor commands to muscles return to their premovement levels.

The kinesthetic rule (1) helps explain position sense not only in isotonic movements (Figure 9(B)) but also in isometric torque production[2] (Figure 9(C)). It also explains kinesthetic illusions, phantom limb and pain phenomena in amputees,[69–71] and the sense of effort (Weber–Fechner's law).[2] In particular, in the absence of the limb, the proprioceptive component (P) of position sense is missing but the absent limb may still be sensed as present (phantom) because of the central, referent component (R) of position sense.

Like perception of body segments, perception of the whole body ('self') may be formed based on a combination of the centrally specified referent body configuration (R_c) and deviation from it defined by sensory inputs. By electrical stimulation of certain brain regions, the combination of R and P underlying whole body perception can be artificially changed, eliciting the awkward sense of 'split personality'—an illusion of the presence of a person who mirrors motions of the stimulated person.[72]

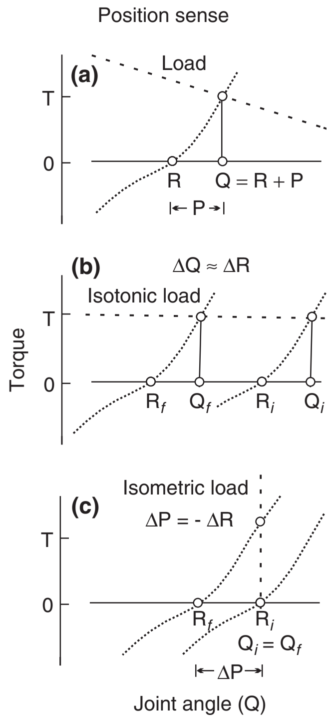

FIGURE 9 | Central and afferent components of position sense. (A) When muscles compensate an external load, the segment arrives at position Q deviated from the threshold position R by P. Position Q can be sensed adequately by combining the control signal responsible for setting the threshold position, R, with deviation from it, P, delivered by proprioceptive signals. (B) An isotonic movement is produced by changing the threshold position (ΔR). The resulting change in the joint angle (ΔQ) can be perceived based on the central component (ΔR) of position sense even if its afferent component remains constant ($\Delta P = 0$). (C) When movement is prevented (isometric condition), changes in the threshold position (ΔR) results in an increase in proprioceptive feedback (by ΔP) and isometric torque. In this case, the central and afferent components of position sense are equal but opposite ($\Delta P = -\Delta R$) and, taken together, elicit no sensation of motion ($\Delta Q = 0$) (Reprinted with permission from Ref 2. Copyright 2009 Springer).

One can assume that self-awareness of arm motor actions in healthy subjects also relies on changes in the central component of kinesthesia, R_a. Parietal lobe stimulation in awake patients undergoing brain surgery evoked the sensation of arm movement even though no overt movement was made.[73] In contrast, premotor lobe stimulation triggered limb movements but patients denied that they had moved. It is likely that parietal lobe, but not premotor region, stimulation excited neurons responsible for the central component of kinesthesia. Therefore, the patients believed that they had really performed the movement only when the parietal lobe was stimulated. In healthy humans, self-awareness of motor actions based on the central component of kinesthesia also relies on afferent feedback (P in rule (1)) to perceive that the movement was actually made.

SPATIAL FRAMES OF REFERENCE FOR ACTION AND PERCEPTION

The notion that the nervous system produces actions in task-specific FRs is broadly accepted.[74] The EP theory advances this notion in several ways.

Different Forms of Threshold Position as Attributes of Neural FRs

Each FR has attributes—origin point, metrics and geometry. Different forms of threshold position (e.g., λ, R_a, R_c, R_l) can be considered as the origin (referent) points of the respective spatial FRs in which the system operates.[28,29,32] For example, R_l is the origin of an FR comprised of all possible locations of the body in the peripersonal environment. This FR and its shifts are used for actions in the environment, such as walking or running (Figure 8), jumping, reaching for an object on a table, shaking hands with another person, or playing tennis. The referent body configuration (R_c) is the origin point of a personal FR that consists of all possible spatial configurations (Q_c) of the body.[7,11,31,32] In the absence of coactivation of opposing muscle groups, the R_c is the threshold configuration of the body, i.e., the body posture at which all skeletal muscles are silent but are prepared to generate activity and forces in proportion to the difference between Q_c and R_c*.

Physical Nature of FRs

In each FR, neuromuscular elements may or may not be activated depending on the difference between the actual and the referent positions of the system in the chosen FR as well as on the rate of change in this difference. Therefore, by changing the referent position, the nervous system shifts the FR and thus elicits an appropriate motor action. On the basis of this characteristic, neural FRs are said to be physical or action-producing: such FRs are tools for motor actions.[2]

Physical versus Mathematical FRs

Physical reference frames used by the nervous system are fundamentally different from symbolic or mathematical FRs used to *describe* motor behavior. Specifically, unlike physical FRs, changes in attributes of symbolic FRs only influence the way we *describe* the system behavior without influencing this behavior.

Common FRs for Action and Perception

It has been suggested that adequate kinesthetic sense is achieved by combining proprioceptive signals with the referent limb position that is simultaneously used to control motor actions (see Eq. (1)). A more general suggestion is that the brain interprets sensory signals in specific spatial FRs and, moreover, these FRs are identical with the FRs for actions (*common, action–perception FRs*).[2]

Neural FRs as Continuously Functioning Structures

The nervous system does not need to create FRs for action and/or perception: they have been formed ontogenetically, and all body parts and the body itself are continuously functioning in the respective FRs (Figure 4). In particular, during standing, the whole body is already localized in a neural FR associated with the environment. Thereby, during quiet standing, the major attribute of the body frame—R_c—is close to the actual body configuration, Q_c, such that the small difference between them is sufficient to provide muscle torques maintaining body stance. For the body to lean, the system does not need to recreate an R_c—one can lean the already existing R_c and actual body leaning will follow.

Transitions from One FR to Another

In abstract, mathematical descriptions of system behavior, different FRs are interrelated by matrix (Jacobean) transformations. The brain does not need to make such transformations to perform actions in one FR or another. As an analogy, consider the places we live in and work in as different spatial FRs. The physical relations between these FRs help us to decide how to get from home to work. Similarly, spatial FRs used by the brain are existing neural structures selected in a task-specific way. To switch to another FR, the system relies on the physical relations of the desired FR with other FRs, without concerning itself with matrix transformations. Consistent with this view is the demonstration that subjects can easily, without learning, switch between different FRs according to the task demand.[75]

Mapping between Desired Movements and Associated Referent Shifts

A shift in the referent hand position is the tool used by the brain to reach a desired point or object in space.[2,28,29,76] To clarify the tool concept, consider driving a car: the steering wheel is a tool that the driver rotates to move the car in the desired direction without any concern or pre-programming of the position of the steering wheel associated with the driving direction.

Therefore, in contrast to conventional views in which control signals are identified with motor commands, no pre-programmed mapping of control signals—shifts in the threshold hand position—is required for reaching different spots in peripersonal space: the system simply shifts the referent hand position such that the hand moves in the direction of the target.

Hierarchy of FRs

Although FRs are numerous, they are organized in a specific way so that they can be managed by the nervous system without redundancy problems. We can think of the body as occupying a place in the environment. This means that the FR for the body configurations (personal FR) would be embedded in the FR defining all possible body locations in the peripersonal environment. This is reflected in the relationship between the origins of these FRs: the R_l controls the R_c, as illustrated for gait (Figure 8). FRs for individual joints and muscles are sub-FRs of the personal FR defined by its origin, R_c, which is simultaneously the origin (center) of the FR defining the coactivation range (C) for opposing muscle groups (see earlier text). The FR hierarchy allows the nervous system to choose only one 'leading' FR in a task-specific way and all subordinated FRs will be involved automatically: This rule has been illustrated for locomotion: to elicit gait or running, it is sufficient to choose an appropriate rate and direction of shifts of the referent localization of the body in the environment. To reach for an object in the environment, one can correspondingly shift the referent position of a desired effector whereas subordinated referent positions of other body segments will expediently be involved in the task performance.

ISOMORPHISM BETWEEN BODY BIOMECHANICS AND NEURAL CONTROL

In the present context, we use the mathematical term *isomorphism* (similarity) to illustrate a *correspondence (mapping) between the biomechanical structure of the body and the neural organization underlying the control of this structure*. Isomorphism also implies that the structural relationships between elements of the body correspond to the neural relationships between the neural structures that control these elements, and vice versa. To clarify, the referent body configuration is apparently geometrically similar to the body. Moreover, taken together, different forms of referent position control comprise a neural structure that is isomorphic to the geometrical structure of the body placed in the environment. The next examples and section might be helpful in illustrating how the isomorphism principle can advance the understanding of control of action and perception.

Reformulation of the Size Principle for Motoneuronal Recruitment

The formula $A = [x - \lambda^*]^+$ for muscle activation (Figure 3) implies that the first motor unit is recruited when $x = \lambda^*$ and subsequent *motor units are recruited according to their threshold muscle lengths*. This rule thus establishes isomorphism between the mechanical variable x and neurophysiological variable λ^* in defining the order of motor unit recruitment. Compared to the original formulation ('size principle'),[77] the new formulation of the rank-ordered recruitment of motor units has several advantages: it places the principle in the framework of a general theory of motor control; it is less rigid in terms of allowing modifications of the recruitment order depending on the movement speed, degree of freedom used in the motor task (if the muscle is polyfunctional), and fatigue.[6]

The Principle of Biomechanical Correspondence in Recruitment of Muscles

As mentioned earlier, during quiet standing, the difference between the actual and referent configurations of the body is relatively small. During micro-oscillations of the body, they may transiently match each other such that $Q_c = R_c$. A similar matching, $Q_c = R_c^*$, can transiently occur in many other motor tasks.[30,31] This isomorphism has two consequences. First, at the configuration at which matching occurs, all skeletal muscles of the body, regardless of their biomechanical function, reach their activity minimum. The depth of this minimum will be defined by the degree (C) of muscle coactivation. Several studies have confirmed the existence of global minima in the EMG activity of multiple skeletal muscles at certain phases of jumping (Figure 10), sit-to-stand movements, stepping in place, and jeté movements in skilled ballet dancers.[30,31,33] Second, in the absence of coactivation ($C = 0$), the R_c is the threshold configuration of the body at which all muscles, regardless of their biomechanical functions, reach their threshold lengths. This means that once an R_c is specified, the values of individual thresholds (λs) for all skeletal muscles of the body *emerge without any redundancy problem*. Thereby, the relationship between the *threshold lengths* of different muscles at this body posture mirrors the relationship between the *actual muscle lengths*. This isomorphism is called *the principle of biomechanical correspondence in the control of* actions.[32] It was used to successfully

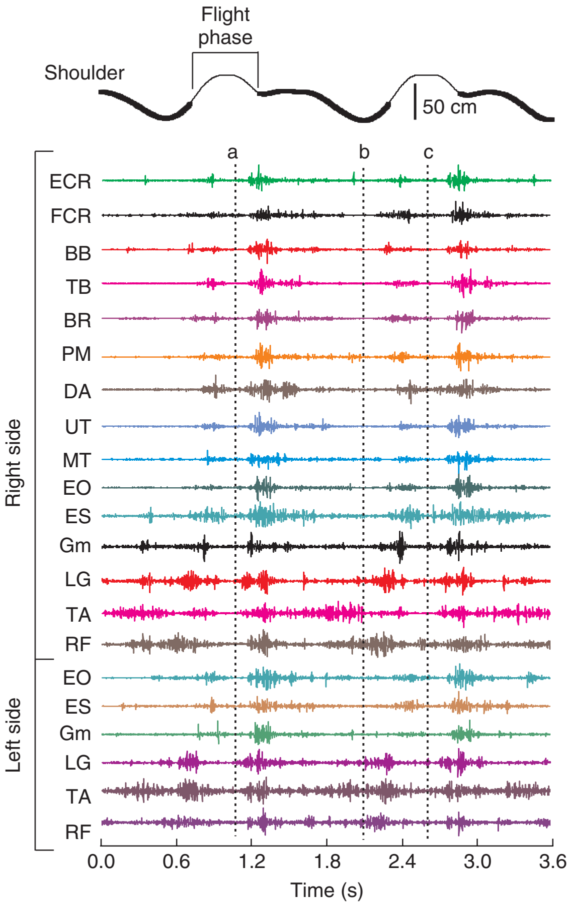

FIGURE 10 | A verification of the concept of the referent body configuration: the occurrence of global EMG minima during vertical jumps. EMG minima in 21 muscles across the body occur during the flight phase in each jump (at time *a* and *c*) and during transition from body flexion to extension (at time *b*) in preparation to jumps (in about 80% of jumps). Surface EMG activity of 16–21 functionally diverse muscles of the legs, trunk, and arms was recorded, typically, from the pectoralis major (PM), deltoid anterior (DA), upper trapezius (UT), middle trapezius (MT), lattissimus dorsi (LD), erector spinae (ES), thoracic back extensors (TBE), lumbar back extensors (LBE), lateral abdominus (LA), rectus abdominus (RA), external oblique (EO), extensor carpi radialis (ECR), flexor carpi radialis (FCR), bicepsbrachii (BB), triceps brachii (TB), brachioradialis (BR), gluteus medius (Gm), tensor fascia latae (TFL), rectus femoris (RF), semitendinosus (ST), vastus medialis (VM), biceps femoris (BF), lateral gastrocnemius (LG), and tibialis anterior (TA) (Reprinted with permission from 31. Copyright 2004 Springer).

simulate sit-to-stand movements in humans based on central changes in the referent body configuration[28,29] in a model that included all anatomically defined muscles of the legs.

Adaptation of Referent Shifts to Gravity

During reaching for objects in the peripersonal environment, the hand is deviated downward from its referent position by the weight of the arm. Therefore, taking gravity into account, the shifts in the hand reference configuration should be made to a point somewhat higher than the object. It is possible that centrally the referent shifts are still made directly toward the object as if there were no gravity whereas signals from pressure and force-sensitive cutaneous, articular and proprioceptive receptors elevate these referent shifts in proportion to the distance of the hand from the body, thus compensating for the increasing torque due to the arm weight.

Minimization Rule

We have seen that there is no redundancy problem in choosing specific muscles for a given motor task: they are all constrained to function in the personal FR depending on the difference between the actual and the referent body configuration and try to minimize this difference in the limits defined by mechanical and internal constraints (cf. Ref 78). At first glance, there is still redundancy in choosing appropriate referent body configurations for a given motor task. Consider, however, a specific task, say, a forward step. A step is proposed to minimize the distance between the actual (Q_{l}) and desired location of the body in the environment. To achieve this, the system shifts the referent location, R_{l}, of the body by influencing neurons that signal the difference between Q_l and R_{l}^* to other body configuration neurons. As a group, the latter neurons will change the already existing referent body configuration to make a virtual (referent) step since only in this case will the input to these neurons ($Q_{\mathrm{l}} - R_{\mathrm{l}}^*$) be minimized. The subsequent muscle recruitment converts the virtual into a real step with actual minimization of the distance between Q_{l} and R_{l}^*. Indeed, with such a minimization strategy, each new step may not be exactly a repetition of the previous one because of the natural variability of the pattern of step-like shifts in the R_{l}, external perturbations, and history-dependent changes of properties of neuromuscular elements (Figure 11).

A similar minimization process may underlie other motor actions. In particular, reach to grasp movement can be considered as being accomplished by minimizing the distance and difference in the shapes of the hand and object, with subsequent development of grasping force within certain margins.[76] Leading in this action may be neurons responsible for changes in the referent hand configuration R_{h} that subordinate neurons responsible for changes in the referent arm configuration, R_{a}. The minimization process brings the hand to the object. Changes in the referent position

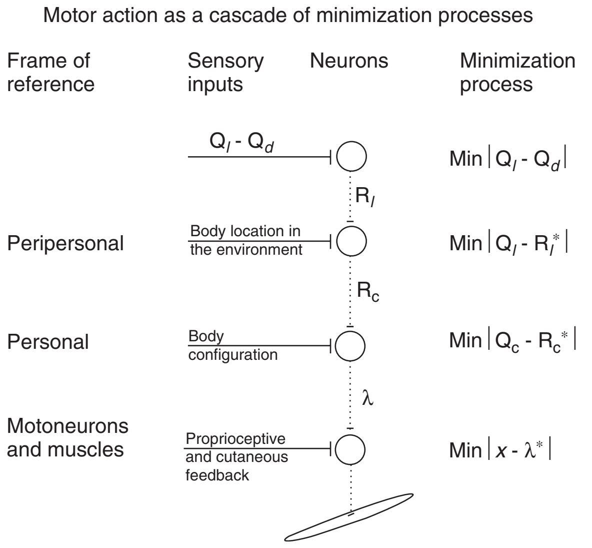

FIGURE 11 | Basic rules in solving the redundancy problems in the control of multiple muscles and degrees of freedom. First, the brain reduces the amount of redundancy by constraining neuromuscular elements to function in task-specific spatial frames of reference (FRs). Second, neuromuscular elements within each and in different FRs interact to minimize the gaps between the actual and referent values of variables at any level of control hierarchy. Sensory signals from subordinated levels are delivered to higher levels to make, if necessary, corrections of referent variables. Asterisk (*) implies that the respective variable might depend on velocity.

of the fingers continue such that they begin to virtually penetrate the object (Figure 4(C)) until cutaneous receptors signal that the grip force has reached safety margins.[13]

The minimization process elicited by shifts in the referent hand position during reaching movement attracts all degrees of freedom that can contribute to this process. As a consequence, the hand trajectory may remain invariant if the number of degrees of freedom involved in the task changes either intentionally, or following mechanical perturbations. This prediction of the minimization strategy has been validated.[79]

How the Brain Solves Redundancy Problems

Mathematically, redundancy is associated with the problem of choosing a unique element from a set of many equivalent elements (actions, variables, patterns). The previous analysis suggests that the brain does not directly solve redundancy problems: it only limits the amount of redundancy by predetermining where, in spatial coordinates, a task-specific action should emerge and allows all motor elements, including the environment, to interact to deliver a unique action thus solving the redundancy problem, a process that can be called *natural selection of action*. The existence of *physical FRs, their hierarchy, FR--body isomorphism as well as the minimization rule eliminate redundancy problems at any level of motor control*. If the emerging action does not meet the task demands, it can be modified or replaced with another action by adjusting the previously chosen form or using a different form of threshold position control.

CONCLUSION

The review illustrates that the EP theory is valuable in solving several problems of action and perception, some of which have remained controversial for over a century. The strength of the theory lies in the fact that it has progressed hand in hand with rigorous experimental testing. The explanatory and predictive power of the theory as well as its potential for further development, especially in terms of the explanation of cognitive function of the brain, is far from being completely exploited. One challenging task in advancing the theory is to explain how practically all sensory information is integrated in order to produce a referent image of the body—a central facet in action, perception, and cognition.

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