

Threshold position control of arm movement with anticipatory increase in grip force

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Abstract The grip force holding an object between fingers usually increases before or simultaneously with arm movement thus preventing the object from sliding. We experimentally analyzed and simulated this anticipatory behavior based on the following notions. (1) To move the arm to a new position, the nervous system shifts the threshold position at which arm muscles begin to be recruited. Deviated from their activation thresholds, arm muscles generate activity and forces that tend to minimize this deviation by bringing the arm to a new position. (2) To produce a grip force, with or without arm motion, the nervous system changes the threshold configuration of the hand. This process defines a threshold (referent) aperture (R_a) of appropriate fingers.

The actual aperture (Q_a) is constrained by the size of the object held between the fingers whereas, in referent position R_a , 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_a and R_a . Thus, grip force emerges since the object prevents the fingers from reaching the referent position. (3) From previous experiences, the system knows that objects tend to slide off the fingers when arm movements are made and, to prevent sliding, it starts narrowing the referent aperture simultaneously with or somewhat before the onset of changes in the referent arm position. (4) The interaction between the fingers and the object is accomplished via the elastic pads on the tips of fingers. The pads are compressed not only due to the grip force but also due to the tangential inertial force (“load”) acting from the object on the pads along the arm trajectory. Compressed by the load force, the pads move back and forth in the gap between the finger bones and object, thus inevitably changing the normal component of the grip force, in synchrony with and in proportion to the load force. Based on these notions, we simulated experimental elbow movements and grip forces when subjects rapidly changed the elbow angle while holding an object between the index finger and the thumb. It is concluded that the anticipatory increase in the grip force with or without correlation with the tangential load during arm motion can be explained in neurophysiological and biomechanical terms without relying on programming of grip force based on an internal model.

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Introduction

In everyday life, we often behave in a predictive or anticipatory way, which helps us to improve the efficiency of habitual and acquire new motor skills as well as to prevent undesirable consequences of our own actions. For example, when rapidly lifting an arm during standing, we initially activate our leg muscles to stabilize the body, a phenomenon called the anticipatory postural adjustment (Belen'kii et al. 1967). During quiet standing, small rhythmical trunk movements resulting from respiration are also compensated by appropriate changes in the body configuration (the respiratory synergy; Gurfinkel et al. 1988; Hodges et al. 2002). When we move the arm while holding an object between fingers, we unconsciously increase the grip force to prevent the object from sliding (Flanagan and Wing 1997). If a person lifts a heavy book from the palm of his hand, the hand usually remains motionless (another case of anticipatory postural adjustment; Forget and Lamarre 1995). This behavior is usually contrasted with the absence of such adjustment when the book is suddenly lifted from the palm by another person: in this case, the hand involuntarily moves upward and stops at another position (the unloading reflex; Asatryan and Feldman 1965).

The capacity of different biological and artificial systems to produce predictive or anticipatory actions has been analyzed in different theoretical studies resulting in the identification of two types of anticipation, weak and strong (Dubois 2001). Weak anticipation refers to anticipation of events predicted from symbolic computations of desired outcome based on an internal model of the system (see also Rosen 1985, p. 341). The results of such computations are then used to physically implement the programmed outcome. Weak anticipation is used in artificial systems, for example, in robotics when an internal model of the system in the form of inverted equations of motion is used to compute and then specify joint torques to produce the desired trajectory of the end point of an artificial arm.

Strong anticipation is manifested by natural, physical laws. In other words, in strong predictive systems, anticipatory properties are inherent in system's natural dynamics and thus do not rely on internal models. For example, predictive properties of mechanical laws can be seen from the fact that, given initial conditions, they pre-determine future motion of the body.

In studies of motor control, the term "internal model" is used in two different, often inconsistent ways (Ostry and Feldman 2003). We will use this term to denote the hypothesis that implies that basic aspects of motor actions, including learning, adaptation, anticipation, and execution are based on *neural imitations* or *emulations* of

system's natural or inverted input/output relationships characterizing, in particular, the dynamics of the body interacting with the environment (e.g., Wolpert and Kawato 1998; Kawato 1999). Formulated in this way, the hypothesis can be tested and either confirmed or rejected. By using the term internal model only in this sense will we avoid the widespread use of the same term in a metaphorical sense, as a symbol of any change in motor behavior or neural activity, related in particular, to anticipation and learning, even in those cases when reliance of such changes on internal emulators of system's dynamics is unfounded.

Internal models have been postulated for many motor actions, including movement adaptation to different force fields (for review see Ostry and Feldman 2003). However, some of these actions have been simulated based on known properties of the neuromuscular system, without internal models, raising the possibility that the neuromuscular system belongs to the class of strong anticipatory systems not relying on internal models (Ostry and Feldman 2003). In experimental studies made in the theoretical framework of internal models, there is a tendency to disregard this possibility. As a consequence, the observations of anticipatory actions are considered as an unequivocal sign that the nervous system uses internal models to plan and produce motor actions. In particular, the possibility that dynamic systems may manifest anticipatory behavior in the absence of internal models has been unnoticed in the analysis of grip forces during arm movements (Flanagan and Wing 1997; Blakemore et al. 1998), biasing the researchers to the conclusion that the anticipatory nature of grip force unambiguously points to force programming based on internal models imitating the interaction of hand with the object. Recent studies, however, have questioned the physiological feasibility of such a conclusion (Ostry and Feldman 2003; Feldman and Latash 2005; Foisly and Feldman 2006). It is natural to describe motor actions in terms of mechanical and EMG variables. However, a major idea of internal model hypothesis that control processes underlying motor actions are involved in pre-programming of these variables appears physiologically unrealistic. In particular, unlike the threshold control approach, the pre-programming approach failed to provide a physiologically feasible solution to the classical posture-movement problem of how movement can be produced without evoking resistance of posture-stabilizing mechanisms. This conclusion has been derived from the analysis of several models of point-to-point movements simulated in the framework of the internal model hypothesis (Ostry and Feldman 2003) as well as from results of direct testing of this hypothesis (Foisly and Feldman 2006). Nevertheless, since anticipatory genera-

tion of grip force during arm movements is still considered as evidence of internal models, we feel that it is important to offer alternative explanations of the same phenomenon.

In the present study, we analyzed and simulated elbow movements and pinch-grip forces when subjects rapidly changed the elbow angle while holding an object between the index finger and the thumb. We investigated the possibility of neural control levels not relying on internal models to increase the grip force before or simultaneously with the onset of elbow movement. The simulation was based on the finding that various descending systems (cortico-, reticulo-, vestibulo- and rubro-spinal) can reset the threshold limb position. At this position all limb muscles may remain silent but, if the limb deviates from this threshold position, electromyographic (EMG) activity emerges and elicits forces resisting the deviation (Asatryan and Feldman 1965; Feldman and Orlovsky, 1972; Nichols and Steeves 1986; Ostry and Feldman 2003; Archambault et al. 2005). Such resetting is mediated by pre- and post-synaptic, direct or indirect inputs to α - and/or γ - motoneurons (Matthews 1959; Feldman and Orlovsky 1972; Capaday 1995). These findings imply that the nervous system only constrains the possible values of kinematic, EMG and kinetic variables without being able to pre-determine their specific values. Within the limits defined by the activation thresholds, specific values of these variables emerge following the interaction of the neuromuscular and reflex components of the system between themselves and with the environment.

The efficiency of threshold position control has been demonstrated in simulations of several single- and multi-joint arm movements, including locomotion (Flanagan et al. 1993; Feldman and Levin 1995; Laboissière et al. 1996; St-Onge et al. 1997; Gribble et al. 1998; Günther and Ruder 2003; Pilon and Feldman 2006). Threshold position control has also been used to analyze and simulate such aspects of motor actions as adaptation, anticipation and learning (Gribble et al. 1998; Weeks et al. 1996; Foisy and Feldman 2006; Pilon and Feldman 2006).

To simulate arm movement with an anticipatory increase in the grip force, we used a specific form of threshold position control applied to multiple skeletal muscles and joints. Such control is accomplished by changes in the referent (R) configuration of the body or its segments (Feldman and Levin 1995; Feldman et al. 1998; Lestienne et al. 2000; St-Onge and Feldman 2004; Lepelley et al. 2006). In the absence of co-activation of agonist and antagonist muscles, the R configuration represents the threshold position (posture) of the body or its segments. As defined above, threshold posture is associated with a specific state of the neuromuscular

system (threshold state). In this state, muscles are silent but they become active and generate resistance in response to any deviation from this state. The threshold state is thus different from the state of full muscle relaxation characterized by the absence of EMG responses to mechanical perturbations, unless they are very rapid (e.g., when the quadriceps tendon is hit by a hammer causing a knee jerk). The threshold or R posture can be described by the set of joint angles at which the threshold state is achieved. It is assumed that co-activation of agonist and antagonist muscles induced at the R posture is balanced so that the zero net muscle torques associated with the R configuration of the arm remains zero. In other words, co-activation does not influence the R posture, which resembles the observation that the arm remains motionless when arm muscles are intentionally co-activated.

We use the concept of referent limb configuration to simulate discrete elbow movements and grip forces holding an object between the index and the thumb. For this case, the R configuration consists of two components: the referent hand configuration characterized by the *referent aperture* (R_a) and the referent elbow angle (R_e), so that $R = (R_a, R_e)$. When a rigid object is held between the fingers, the actual aperture (Q_a) is determined by the size of the object. In contrast, the centrally-specified referent aperture (R_a) can be smaller than Q_a , as if the fingers virtually penetrate the object (Fig. 1a). Due to the deviation from the threshold aperture, the hand muscles generate activity and resistive forces that tend to diminish the gap between Q_a and R_a . In other words, the resistive (grip) force emerges since the object prevents the fingers from reaching the referent aperture. In the present study, the validity of these notions is tested by simulating experimental discrete elbow movements and grip forces that prevent an object held between the tips of the index finger and thumb from slipping. Results have been reported in abstract form (Pilon et al. 2005a, b).

Methods

The model: basic neurophysiological concepts and equations

We first describe the physiological mechanisms underlying threshold position control, which will allow us to postulate the existence of different types of neurons and neuronal ensembles that produce changes in the referent elbow-hand configuration. Second, we numerically simulate motor responses to changes in this configuration and investigate whether or not these responses resemble experimental data for elbow movement and grip forces.

Physiological origin of threshold position control in different neurons

Thresholds of motoneurons and other neurons are usually measured in electrical units (threshold membrane potentials or currents). The observations that the nervous system can modify the *threshold position* at which muscles become active imply that the electrical thresholds are somehow transformed into positional variables, thus placing our actions in a spatial frame of reference associated with the body or with the environment. Physiologically, such transformation can be explained by considering how proprioceptive and other afferent inputs are combined with central inputs at the level of the membrane of motoneurons and other neurons, a process called *sensory-control integration* (Fig. 2a).

Motoneurons First, consider the case when descending central influences on the neuromuscular system remain unchanged or absent. Due to proprioceptive feedback from muscle spindle afferents, the membrane potential of motoneurons depends on the current muscle length (x).

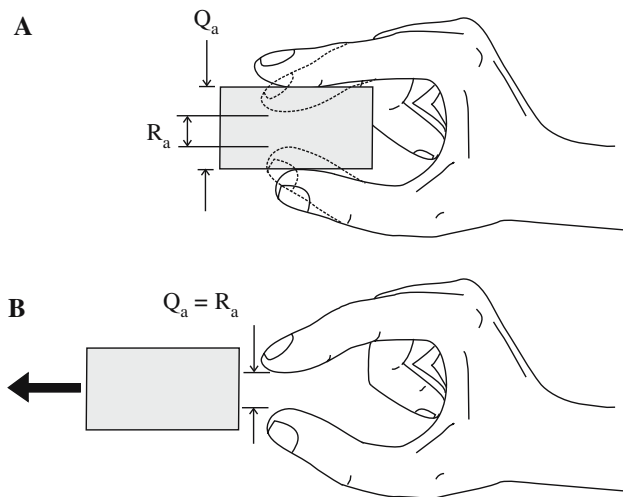


Fig. 1 Threshold control of grip force. **a** By influencing the activation threshold of motoneurons of hand muscles, the nervous system specifies a referent aperture (R_a) that defines a virtual distance between the index and the thumb. In the presence of the object, the actual aperture (Q_a) is constrained 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_a and R_a . Thus, grip forces emerge because the object prevents the fingers from reaching the referent position. Both central modifications in the threshold position (R_a) or/and changes in the size of the object (Q_a) influence the grip force. **b** The referent aperture is reached when the object is forcefully pulled away from the fingers (*horizontal arrow*), a phenomenon similar to the unloading reflex usually demonstrated by unloading of other limb segments

This means that a slow, quasi-static stretch of this muscle results in a gradual increase in the membrane potential of the motoneuron (Fig. 2b, lower diagonal line). The motoneuron begins to generate spikes when the current membrane potential begins to exceed the threshold potential (V_+). In the presence of length-dependent feedback, the same event becomes associated with spatial variables: the motoneuronal recruitment occurs when the muscle length (x) reaches a specific, threshold length (λ_+). Now, consider the case when a constant control input is added by descending systems (Fig. 2b, vertical arrows). The primary effect of this control input is a shift in the membrane potential of the motoneuron. If the net effect of such an input is facilitatory, the same muscle stretch elicits motoneuronal recruitment at a shorter threshold length, λ . The electrical effect of control inputs is thus transformed into a spatial variable—changes in the threshold muscle length. When

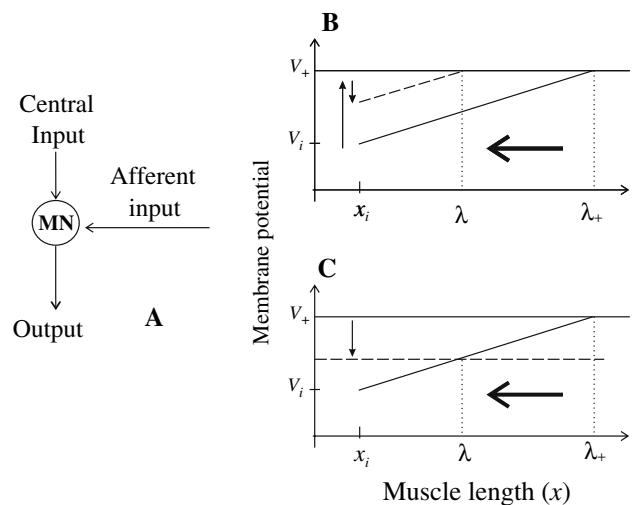


Fig. 2 Physiological origin of threshold position control. **a** Rather than reflecting individual properties of motoneurons, threshold position control originates from integration of spatial (length-dependent) afferent signals and central control signals on the motoneuronal membrane. Threshold position control relies not only on such a sensory-control integration but also on the existence of an electrical threshold (V_+) for motoneuronal recruitment. **b** When a muscle is stretched quasi-statically from an initial length (x_i) in the absence of control inputs, the motoneuronal membrane potential increases according to afferent length-dependent feedback from the muscle (*solid diagonal line*). The electrical threshold (V_+) is eventually reached at length λ_+ , at which the motoneuron begins to be recruited. When independent control inputs are added (*Up arrow* depolarization, *Down arrow* hyper-polarization), 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

the muscle is stretched beyond its activation threshold, the firing frequency of already active motoneurons increases and additional motoneurons are recruited in the order of their individual thresholds, a process resembling the size principle for recruitment of motor units (Henneman 1981).

As mentioned in the **Introduction**, the threshold muscle length can be changed by different descending systems that influence α -motoneurons either directly or indirectly via interneurons or γ -motoneurons. Recently, it has been found that some descending systems can also change the membrane potential (V_+) of motoneurons (e.g., Fedirchuk and Dai 2004), implying that this might be an additional way of controlling the threshold length (Fig. 2c).

Physiological data also indicate that the threshold length comprises several additive components with only one component controlled centrally (Matthews 1959; Feldman and Orlovsky 1972; Feldman 2007). To reflect these findings, we use symbol λ^* for the composite (net) threshold, whereas symbol λ is reserved for its central component:

$$\lambda^* = \lambda - \mu\omega - \rho + \varepsilon(t) \quad (1)$$

where λ and μ are controllable parameters; μ is a time-dimensional parameter related to the dynamic sensitivity of muscle spindle afferents (Feldman and Levin 1995); ω is the velocity of change in the muscle length ($\omega = dx/dt$); ρ is the shift in the threshold resulting from reflex inputs such as those responsible for the inter-muscular interaction and cutaneous stimuli (e.g., from pressure-sensitive receptors in the finger pads); $\varepsilon(t)$ represents history-dependent changes (not considered in the present model) in the threshold resulting, in particular, from intrinsic properties of motoneurons. The net threshold, λ^* , is also the threshold length for the first motoneuron from which the recruitments of motor units of a muscle starts. In other words, the muscle begins to be activated if the difference between the actual and the net threshold length is not negative, i.e. when $x - \lambda^* \geq 0$. Otherwise, the motoneuron and the whole muscle are silent (relaxed). In a supra-threshold state, the frequency and the number of recruited motoneurons increases with the increasing difference between the actual and the threshold muscle length, so that the activity of the muscle (EMG magnitude) is proportional to A , where A is

$$A = [x - \lambda^*]^+ \quad (2)$$

Here $[u]^+ = u$ if $u \geq 0$ and 0 otherwise.

The sensory-control integration described for motoneurons implies that it is the motoneuronal membrane that is the site where electrical control inputs are transformed into a spatial quantity—a shift in the threshold muscle length (λ^*) that the length-dependent afferent signals should ex-

ceed to begin motoneuronal recruitment. In addition, by switching from a silent to an active state or vice-versa, motoneurons signify that the values of the actual and threshold muscle length match each other. This event can be considered as a *cognitive aspect* in the initiation of motor action. Once the difference between the current and threshold lengths becomes positive, the emerging activity of the neuromuscular system tends to diminish the gap between these lengths in the limits defined by internal and external constraints. Based on these general notions, we will postulate the existence of hierarchically high neurons that can produce coordinated changes in the activation thresholds of multiple muscles to influence arm movement and grip force.

Elbow neurons It is assumed that elbow neurons, possibly with the participation of intermediate neurons, receive afferent signals from muscle, joint and skin afferents that relate to the elbow angle, Q_e so that the membrane potential of such neurons increases depending on Q_e (Fig. 3a). At a certain angle called the referent angle (R_e), the neurons begin to be recruited. The firing frequency of already recruited neurons and their number increase depending on the difference between the actual and the referent joint angle. Similar to motoneurons, a central signal (vertical arrow in Fig. 3a) sets a new referent angle, R_e' . Elbow neurons influence elbow flexor and extensor motoneurons in a reciprocal way—they facilitate one muscle group and inhibit (or de-facilitate) the opposing muscle group. These neurons thus accomplish the reciprocal command previously considered in the λ model (e.g., Gribble et al. 1998).

Aperture neurons It is assumed that there are neurons, called aperture neurons, that receive afferent signals from muscles, joint and skin receptors but, unlike the elbow neurons, these signals are related to the distance, Q_a , between the pads of the index and thumb so that the membrane potential of these neurons increases when the aperture increases (Fig. 3b). The threshold of the most sensitive neuron from this group is reached when a specific aperture, called the referent aperture (R_a) is established. The number of recruited aperture neurons increases in proportion to the difference between the actual and the referent aperture. Control influences on aperture neurons produce shifts in the membrane potentials of these neurons or, equivalently, changes in the referent aperture. Once activated, the aperture neurons influence the thresholds (λ -s) of motoneurons of hand muscles that tend to narrow the distance between the pads of fingers to the value defined by the referent aperture. When the object prevents movement of the fingers, the remaining gap between Q_a and R_a gives rise to an isometric, grip force.

Co-activating neurons It is assumed that there are neurons that co-facilitate motoneurons of opposing (antagonistic) muscle groups acting on the elbow and/or hand muscles. A primary effect of this facilitation is a shift in the muscle activation thresholds of opposing muscle groups from their common referent positions (R_a and/or R_e) of the segments. For example, by producing facilitation of motoneurons of elbow flexor and extensor muscles, the co-activating neurons *decrease the threshold lengths of both elbow flexors and extensors*. To express these shifts in angular coordinates, it is necessary to take into account that changes in the elbow angle produces *reciprocal changes* in the lengths of flexor and extensor muscles. We define the elbow angle as increasing with the lengthening of elbow flexor muscles. Therefore, co-facilitation of flexor and extensor motoneurons decreases the threshold angle for the former and increases for the latter muscles (Fig. 4). These shifts thus create a spatial zone within which both muscle groups become co-active (*co-activation zone*). Such a zone contains the respective referent positions (R_a and/or R_e) within it and changes the width of the zone leaving the position unchanged (for details see Feldman 1993; Levin and Dimov 1997). Co-activation neurons thus produce co-activation commands previously considered in the λ model.

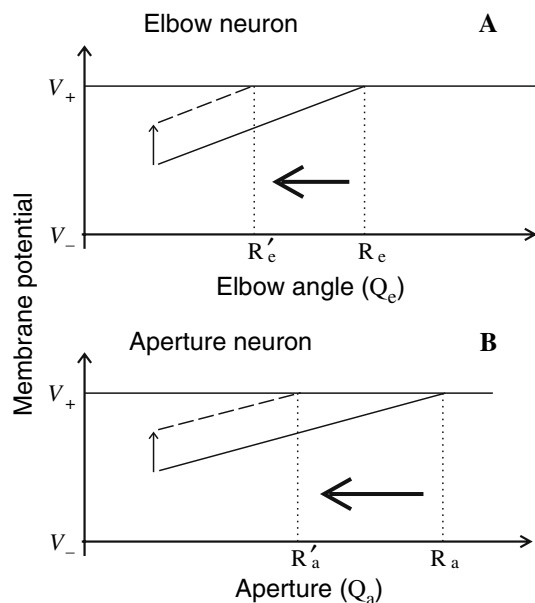


Fig. 3 Elbow and aperture neurons in the model. **a** It is assumed that elbow neurons receive afferent feedback that monotonically shifts their membrane potential in proportion to the elbow angle (Q_e). By analogy with motoneurons (Fig. 2), central shifts in the membrane potential (vertical arrow) elicit changes in the referent value of the joint angle from R_e to R'_e (horizontal arrow). **b** In aperture neurons, the membrane potential depends on the distance (aperture, Q_a) between the index finger and the thumb. Central shifts in the membrane potential (vertical arrow) elicit changes in the referent (threshold) aperture, from R_a to R'_a

Neural ensembles controlling elbow, aperture and co-activating neurons

It has been assumed that shifts in the referent elbow angle (R_e) are accomplished by a line-ordered neural ensemble that is able to propagate excitation by sequential recruitment of neurons (Adamovich et al. 1984). The propagation of excitation can be visualized as motion of the front of the excitation along the ensemble (Fig. 5a). The onset time, rate (velocity) and duration of the shift in the excitation front can be controlled centrally. The recruitment of neurons may increase, decrease or remain unchanged, implying that the propagation velocity can be positive, negative or zero so that the number of recruited neurons in the ensemble can respectively increase, decrease or remain unchanged. The position of the excitation front defines the current value of R_e . In the present model, we assume that a similar neural ensemble is used to control the referent aperture, R_a . Physiologically, such ensembles may be similar to that in the superior colliculi that propagate excitation during saccades (Munoz et al. 1991) or to the multi-segmental neural structure that propagates the excitation along the spinal cord during swimming in the lamprey (Grillner 2003). In the present model, we only assume that the neural ensembles controlling R_a and R_e has the properties described above and therefore may produce shifts in R_a and R_e that are mathematically described by ramp-shaped functions of time (Fig. 5b). The slope of the ramp is defined by the specified velocity at which the excitation propagates. The ramp height (the product of

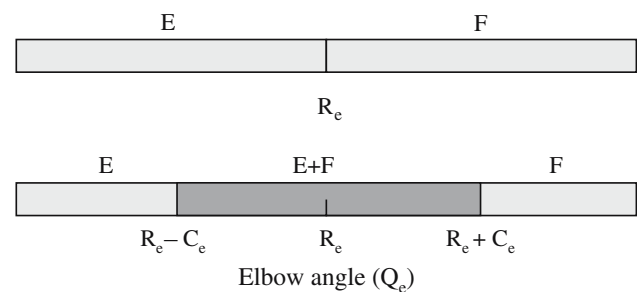


Fig. 4 Co-activation zone for opposing muscle groups, exemplified for muscles acting at the elbow (e) joint. *Upper panel* In the absence of co-activation, the referent position (R_e) represents the threshold angle at which both flexor (F) and extensor (E) muscles are silent. Flexor muscles are active when $Q_e < R_e$ and extensor muscles are active when $Q_e > R_e$. *Lower panel* When elbow flexor and extensor motoneurons are co-facilitated, the angular threshold decreases for flexor but increases for extensor muscles, so that the referent position (R_e) occurs within a co-activation zone (dark segment). The zone is scaled with the strength of co-facilitation. With a shift in the referent position, the co-activation zone shifts as well. This hierarchy in the relationship between the R and C commands allows the system to avoid the potential resistance of muscles to the deviation from the previously stabilized initial position

the velocity and duration of propagation) represents the total shift in the respective referent variable. Depending on the task demand, shifts in the referent values of variables in the two ensembles can be triggered simultaneously or sequentially, in the same or opposite directions. It is also assumed that the co-activating neurons are controlled by similar neural ensembles. As a consequence, changes in the C commands for either elbow or hand muscles are also described by ramp-shaped functions of time.

Decision making

Moving the arm while holding an object between fingers is just one of the many actions involving the upper limb. For example, if we pick up a small stone on a river bank, we usually want to throw it as far as possible by rapidly moving the arm and releasing the stone at a certain phase of arm movement. In contrast, if we hold a cup, we do not want to drop it and hold it more firmly when moving the arm. If there is no object between fingers, one can narrow or, vice-versa, widen the gap between the tips of fingers and begin to move the fingers simultaneously with, before or after the arm movement onset. One can also vary the extent of the arm or/and finger actions. In the present model, all these actions can be accomplished by appropriately changing the referent elbow–finger configuration, $R = (R_a, R_e)$. The involvement of command $C = (C_a, C_e)$ in these actions is dictated by the necessity to stabilize and

provide the desired speed of the motor action (see Feldman and Levin 1995).

In the experimental situation when a subject is required to move the arm while holding an object between the fingers, the decision to make this but not other actions involving the elbow and fingers is imposed by the instruction given to the subject. Further, from everyday experiences, the system has already learned that objects tend to slip from the fingers when the arm begins to move. In the model, this knowledge and the necessity to prevent slipping are expressed in changes in the referent elbow–finger configuration. Specifically, neural control levels not only modify the referent elbow angle, R_e , to produce the elbow movement but also narrow the referent aperture, R_a , to hold the object stronger when the arm moves (Fig. 1). These changes can be graded based on previous experiences and motor memory as well as on the sensation of the initial grip force and properties of the object's surface stemming from muscle and cutaneous afferents (Johansson and Westling 1984; Flanagan and Wing 1997). This strategy, not relying on an internal imitation of the arm–hand system interacting with external forces, might be mostly successful but sometimes results in slipping, which, as is known, occurs in everyday life. Dealing with unfamiliar objects, the system may initially exaggerate the decrease in the R_a and thus elicit unnecessary high grip forces. However, the change in the referent aperture can be adjusted either during the first motion (if the object does not collapse) or in the next trials based on feedback from receptors in the finger pads. In this scheme, grip force adjustment can be expressed as a decrease in the magnitude of the initially exaggerated referent aperture until the emerging grip force is diminished to a value just sufficient to prevent slipping.

We considered the cases when the changes in the R_a started simultaneously with or preceded the onset of R_e . We thus could simulate empirical grip forces and elbow movements that either started simultaneously (in 42% of trials) or sequentially (in 58%).

Although ramp-shaped patterns were used for both R_a and R_e , these patterns were not identical for the following reason. With the movement offset, the final value of the referent elbow angle should be maintained to hold the final position. In contrast, it is unnecessary to maintain an enhanced value of grip force after the end of movement and, to diminish the grip force, the system gradually returns the referent aperture to its pre-movement value. Similarly, an enhanced C command is only required during the movement (Feldman and Levin 1995) and this command can be gradually diminished after the movement offset. Each ramp was defined by two parameters—the rate and duration of changes in the respective referent variable. These parameters were adjusted to fit experimental data (see Results). This process may be similar to what subjects do when they

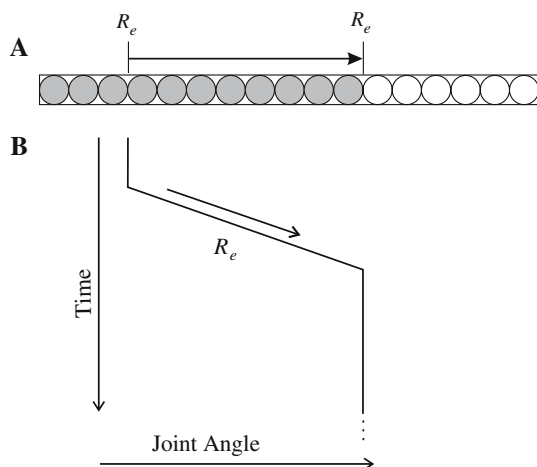


Fig. 5 Neural ensembles specifying referent variables. **a** It is assumed that the value of each referent variable is defined by the number of recruited neurons in a specialized group (ensemble) of neurons. In response to a triggering input, the ensemble begins to propagate excitation at specified rate and duration, resulting in a ramp-shaped pattern of changes in the appropriate referent variable (e.g., variable R_e , in **b**). Similar ramp-shaped patterns may exist for C commands, except that after the end of motor action, a high level of these commands is usually unnecessary so that they can be attenuated by backward propagation of excitation

optimize the action with repetition (learning). For example, the initially selected parameters of control variables could result in a movement error or/and exaggerated grip force. By adjusting the rate and duration of changes in the R_a , R_e and C , subjects might enhance the movement precision and reduce the grip force to the limits allowed by safety margins.

Integral control scheme

The above description of decision-making represents a qualitative, conceptual part of our model. It is assumed that, once the decision to move the arm is made, the propagation of excitation is triggered in the neuronal ensembles (N) that generate ramp-shaped shifts not only in the elbow referent position (R_e) but also in the referent aperture (R_a ; Fig. 6). These shifts can be initiated either simultaneously or sequentially and can be accompanied by ramp-shaped co-activating commands, C_e and C_a . Delivered to motoneurons (directly or indirectly via interneurons or γ -motoneurons) the R and C inputs influence the activation thresholds of motoneurons.

For simplicity, the elbow joint, index finger and thumb are considered as having one degree of freedom each. Two opposing muscles groups (agonists and antagonists) act on each of the three joints (six muscle groups in total). All variables, including those in Eqs. 1–3 are considered in the respective angular coordinates. We define the elbow angle as increasing with the lengthening of elbow flexor muscles. Then, given an elbow referent angle (R_e) and co-activation command (C_e), the angular measure of the central components of activation thresholds for elbow flexors (subscript F) and extensors (subscript E) are defined as:

$$\lambda_F = R_e - C_e \text{ and } \lambda_E = R_e + C_e \quad (3)$$

The causal chain of events resulting from changes in the referent aperture and respective co-activation command is shown in Fig. 6 (bottom panel). For the elbow system, the causal sequence can be obtained by replacing subscript ‘‘a’’ with ‘‘e’’ in the same diagram. The referent aperture is defined by appropriate referent angles for the index and thumb. In the presence of co-activation commands, the angular thresholds for muscles acting on each finger are defined by formulas resembling those for elbow muscles (Eq. 3). Muscle activation (A) defined by Eq. 2 elicits gradual, time-dependent muscle torque development. This torque also depends on the muscle length and velocity coming from two sources: (1) The properties of the contractile apparatus explained by the sliding-filament theory (Huxley and Hanson 1954); mod-

ifications of muscle forces depending on these kinematic variables are accomplished practically *without delay*. (2) The properties of proprioceptive feedback that influences muscle activation depending on the same kinematic variables but after *some delay*. In addition, muscle activation elicits muscle torques after electromechanical delay (EMD). However, this delay only influences the latency of motor actions with no effect on their dynamics (Pilon and Feldman 2006). The effect of EMD was likely to be about the same for the elbow and finger actions and thus could not be responsible for simultaneous or sequential onsets of elbow and finger actions. The overall latency of motor actions was not the focus of our study and therefore we used zero EMD.

It is known that the action of the contractile muscle component is transmitted to appropriate body segments via passive, series elastic component. In the model, the action of this component was indirectly accounted for by the gradual torque development and by taking into account the elastic properties of the pads on the tips of the fingers (see below). One can also consider the series elastic component as introducing some delay in the transmission of muscle torque to body segments. To imitate this effect, we somewhat exaggerated the reflex delay to 50 ms compared to usual values of 25–30 ms used in other simulations.

The dynamic equations that characterize all transformations represented in Fig. 6 for the elbow joint have been published (Pilon and Feldman 2006). Except for one essential supplement (see the next section), the same equations with subscript ‘‘a’’ instead of ‘‘e’’ were used to simulate grip forces. All simulations were made using Matlab software and parameters listed in Table 1.

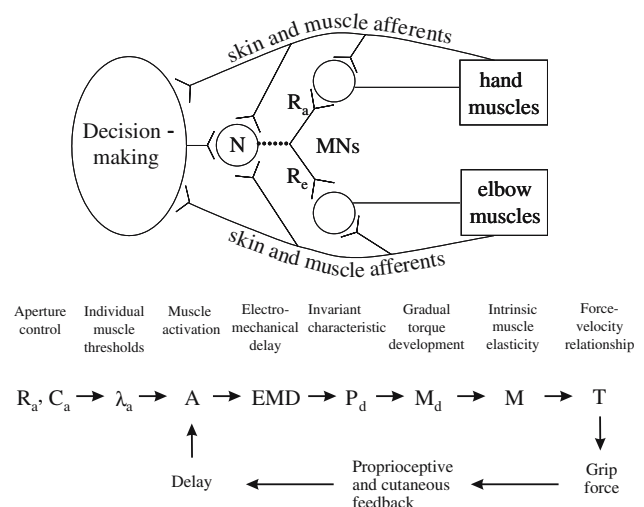


Fig. 6 Integral control scheme. For details see text

Properties of finger pads

To realistically represent the interaction between the fingers and the object, we took into account the fact that the tips of fingers have a deformable pulp or pads (Fig. 7). In the model, this pulp was represented by an elastic layer between the bones in the fingers and the object. The bones of the index finger and the thumb could thus move a few millimeters towards the surface of the object, even if the fingers were initially in contact with it. The pulp layer was compressed depending on the normal component of grip force. It could also somewhat be shifted and compressed in the horizontal direction due to the horizontal, inertial forces (“load”) acting from the object following the elbow acceleration–deceleration. As has previously been found, the pulp resistance increases exponentially with compression (Serina et al. 1997, 1998; Wu et al. 2003). These characteristics of the pulp were incorporated into the model. To evaluate the mechanical role of horizontal pulp compression on the shape of the normal component of grip force (Fig. 7c), simulations were made with and without this compression.

Experimental procedures

Right-handed healthy adults ($n = 10$, three males, seven females; 29 ± 5 years) participated in the study after signing an informed consent form approved by the institutional ethics committee (CRIR). Experiments were similar (although not identical) to those of Flanagan and Wing (1993, 1997). Each participant sat in a chair with a solid back support. His/her right forearm was strapped in a pronated position to a light horizontally manipulandum that had negligible resistance to rotation. The elbow rotation axis was aligned with that of the manipulandum. The wrist was somewhat extended from its neutral position to avoid hand contact with the manipulandum. The shoulder abduction and extension angles were about 55 and 45°, respectively. Subjects were instructed to make fast discrete elbow flexion and extension movements while holding an object (force transducer) between the index finger and the thumb (Fig. 8). The fingers contacted two parallel, Teflon-covered surfaces of the transducer, 28 mm apart. After practice (one–two trials), subjects made five discrete flexions and five extensions (movement distance of about 60°), resting 10–20 s between trials. They were instructed to make single movements without corrections. The longitudinal axis of the transducer was aligned with the movement direction so that the vector representing the normal component of grip force was directed vertically, along the other major axis of the transducer (Fig. 8).

The transducer (ATI Industrial Automation, weight 80 g, sample rate 1,080 Hz) measured two components of

Table 1 Values of parameters characterizing central commands selected individually for each subject’s data and constant parameters in simulations of elbow movement and grip forces (see also Pilon and Feldman 2006)

	Elbow	Index	Fingers	Thumb
Central commands				
r_R (deg/s)	[350 500]	[64 75]		[64 70]
r_C (deg/s)	[240 300]	[24 63]		[24 63]
μ (ms)	[50 80]	[5 10]		[5 10]
t_C (ms)	100		[80 100]	
p_C (ms)	[10 100]		[50 300]	
p_R (ms)	–		[60 85]	
d_C (ms)	–		[55 90]	
Constant parameters				
a (N·m)	1.2	0.1		0.1
α (1/deg)	0.05	0.05		0.05
κ (N/m)	[0.0055 0.0081]	0.0006		0.0006
d (ms)	50	50		d (ms)
G_ρ	0	0.1		[0.1 0.15]
h (deg)	10	10		10
τ_1 (ms)	10		[10 30]	
τ_2 (ms)	40		50	
τ (ms)	40	50		50
v_m (deg/s)	[500 750]	–		–
b (deg/s)	[90 200]	–		–
I (kg·m ²)	0.1	–		–
L (kg)	0.08	0.06		0.06
l (m)	0.375	0.04		0.025
Object parameters				
s (mm)	–		30	

Parameters of central commands: r_R , r_C , rates of change in the R and C commands; μ , dynamic sensitivity of the activation threshold (see Eq. 2); t_C , C command ramp duration; p_R , p_C , durations of R or and C command plateau; d_C , delay of the onset of C command relative to that of the R command. Other parameters: a , α , constants defining the shape of torque-angle (invariant) characteristics; κ : coefficient of muscle elasticity at a given activation level; d , reflex delay; g_ρ : gain of Ia reciprocal inhibition; h : angular difference in the thresholds for recruitment of motoneurons and Ia interneurons of reciprocal inhibition; τ_1 , τ_2 , time constants of gradual torque development; τ , time constant for the first derivative of gradual torque development; v_m , constant determining critical velocity (when torque is zero) in the torque-velocity relationship for active muscle; asymptotic velocity in torque-velocity relationship for active muscle; I , moment of inertia of the force transducer; L : mass of the forearm with the manipulandum and force transducer; l , length of segments; s : object size (distance between two contact surfaces)

grip force, normal to its surfaces (F_n) and tangential to it (F_t). With the proper orientation of the transducer (see above) these components were respectively normal and tangential to the movement trajectory. The tangential component was responsible for the acceleration and deceleration of the transducer. Since no slipping occurred

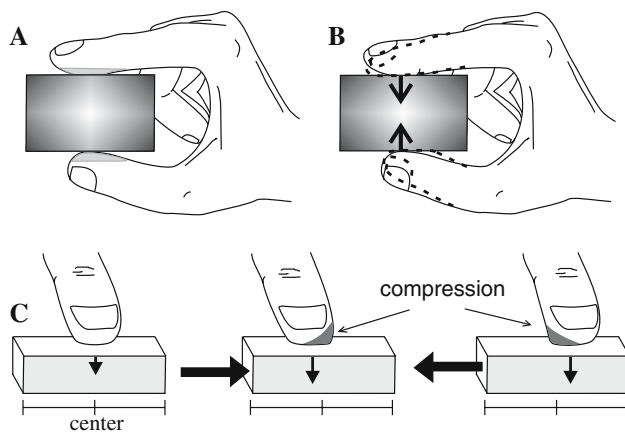


Fig. 7 Mechanical effects of finger-object interactions via finger pads. **a, b** When the gap between the tips of the index finger and the thumb narrows, the pads are compressed, resulting in an increase in the normal component of grip force (vertical arrows). **c** When the hand moves, the object resists in proportion to the movement acceleration and deceleration. The pads are then compressed in the direction of the movement trajectory. The compressed pad becomes thicker, thus increasing pressure on the finger bones and the object. Inevitably, the horizontal pulp deformation gives rise to an increase in the normal component of grip force, both during movement acceleration and deceleration. This pad-related contribution to the normal grip force dips to zero when the acceleration changes sign

in our experiments, this acceleration coincided with that of the arm motion so that $F_t = m \times a$ where m is the mass of the transducer. Since F_t was relatively small, the signal from the transducer measuring this force was affected by other forces resulting from inevitable variations in the alignment of the transducer with the hand trajectory. Therefore, the values of F_t computed from the movement acceleration were considered as more reliable than those measured by the force transducer. The equal and opposite force ($-F_t$), acting on the fingers can be considered as the load force resulting from the inertia of the object and applied to the fingers.

To record elbow movement, four infra-red light reflecting markers (Vicon, six cameras, sampling rate 120 Hz) were placed on the tip of the index finger, on the forearm near the elbow rotation axis and on the shoulder (Fig. 8). The data were filtered (a non-delayed low-pass fifth order Butterworth filter with a cut-off frequency of 8 Hz). Linear and angular displacement of the marker on the right index finger was used to determine the position of the transducer and the movement trajectory. By finding time derivatives of filtered signals we determined the movement velocity and acceleration. To determine the movement onset in each trial, we first found 5% of the hand acceleration peak. We then calculated the mean acceleration and its standard deviation for the points below the 5%-threshold. The movement onset was determined as the time when the hand began to leave the zone of the

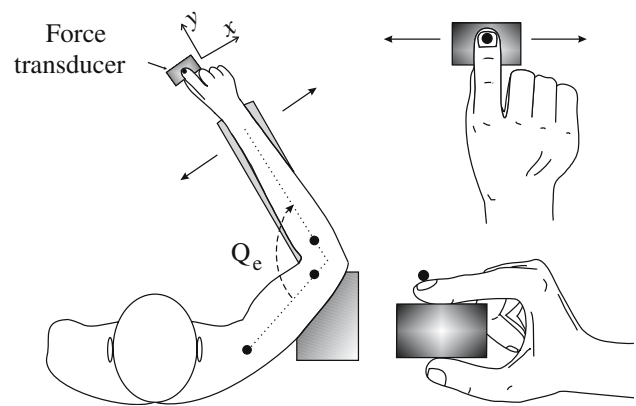


Fig. 8 Experimental setup. The forearm was attached to a horizontal manipulandum allowing flexion and extension movements about the elbow axis. A force transducer was held between the tips of the index finger and thumb during motion of the forearm (arrows). Four infrared reflecting markers (filled circles) and Vicon system were used to record the elbow angle (Q_e). The upper and bottom surfaces of the force transducer were parallel to the plane of elbow rotation. One axis of the transducer (x) was oriented along the hand trajectory whereas the z -axis was oriented vertically and thus orthogonally to the trajectory. Normal (z, y) and tangential (x) components of grip force were measured

mean ± 2 SD. The onset of normal grip force was computed in a similar way, except that the force had a non-zero initial value that was subtracted before using the above procedures. We thus could determine whether or not the grip force started prior to the elbow movement.

Simulations

The parameters in the model were subdivided into two groups: (1) constant parameters that describe the properties of muscle, reflex and other components of the system; (2) parameters characterizing the shape and timing of control variables R_a , R_e and C . When possible, the values of constant parameters were chosen from the ranges reported in other studies. Specific values of such parameters were identified by simulating elbow movement and grip force patterns taken from a representative trial, individually for each subject. Once identified, these values remained unchanged in the simulation of data from the remaining trials of the same subject and only parameters of control variables could be modified to reproduce the movement and grip force patterns in all trials.

The resemblance between simulated and experimental curves (“goodness of fit”) was evaluated by the coefficient of correlation (r^2) between them and by the root mean square error (rms). Experimental and simulated patterns were also compared in terms of the mean magnitude and duration of the normal component of grip force. The duration was measured as the width of the force curve at a

height corresponding to its half maximum. The discrepancy between the simulated and experimental data was considered significant for $P < 0.05$.

Results

Empirical data

Elbow movements ($61 \pm 6^\circ$, mean \pm SD) were comparatively rapid (peak velocity was in the range of 218–641°/s). The kinematic profiles of these movements (solid curves in two upper panels in Fig. 9) were similar to the known kinematic profiles of elbow movements made without any object between fingers (e.g., St-Onge et al. 1997). The tangential component of grip force (Fig. 9, curve F_t) changed sign with the transition from the movement acceleration to deceleration. It also had a small terminal swing before reaching zero level after the end of movement. In contrast, the normal component (F_n) of grip force monotonically increased during elbow movement and gradually decreased to the pre-movement level 1–2 s after the end of movement. This force component was variable for each subject and across subjects, both in terms of amplitude and shape. We distinguished single-peak (Fig. 10a), double-peak and intermediate profiles of this component (Fig. 10b, c). Single-peak patterns were observed in a majority of subjects (Fig. 10 for S2, S3E, S4E, S5E, S6, and S9E; symbols ‘E’ and ‘F’ refer to the elbow extension and flexion, respectively). In each subject, trials with double-peak patterns (S1E, S7E, and S8F) were always mixed with trials with single-peak patterns. Intermediate patterns were only seen in flexor movements in S1, S3–S5, S7, and S9). For the group of nine subjects, peak values of normal force broadly varied (9.6 ± 4.8 N; range from 4.1 to 17.4 N). As a rule, the peak values of grip force in single-peak patterns exceeded those in double-peak patterns (Fig. 10). Variations of force half-width (the period when the force exceeded 50% of its peak) were also large (341 ± 111 ms, range from 168 to 469 ms).

The elbow movement and the normal component of grip force were considered synchronized if the absolute value of the interval between their onsets did not exceed 25 ms, which was the case in 42% of all the trials for the group (10 ± 11 ms). In 58% of trials, the normal grip force emerged before elbow movement (55 ± 32 ms, range 25–165 ms).

The coupling between the normal grip component and the inertial load (or the tangential grip component) was estimated by the correlation coefficient (r^2) between these variables computed for the period between the movement onset and offset (the time between the two vertical lines in Figs. 9, 11, 12). The movement onset was defined as

described in [Methods](#). The movement offset was defined as the instance when the movement velocity crossed the zero level for the first time after the movement onset. Computed in this way, the value of correlation coefficient was low (range 0.002–0.058). In some studies (Flanagan and Wing 1993, 1995, 1997), in which mostly double-peak force pattern was observed, the force pattern was correlated not with the actual, inertial load force (that changes sign when the elbow movements goes from acceleration to deceleration) but with its absolute value (that remains positive before and after the transition from acceleration to deceleration). Applying this procedure to the trials with and without double-peak patterns in our study, we got much higher values of r^2 (0.64–0.85). For single-peak patterns of normal grip force, the correlation with the absolute value of the load force remained low.

Comparisons of simulated and experimental data

Like in previous studies (e.g., St-Onge et al. 1997), ramp-shaped referent inputs R_e and C_e were effective in eliciting the motor output that perfectly matched ($r^2 = 0.97$ – 0.99 , $P < 0.01$) experimental elbow movements, both in terms of position and velocity (two upper panels in Figs. 9, 11, 12). In the same figures, both elbow movements and grip forces were simulated. In Fig. 9, the normal component of experimental grip force began to increase by 37 ms before the elbow movement onset. To reproduce this sequence, the referent inputs R_a and C_a influencing the finger aperture were initiated before those influencing the elbow movement (Fig. 9, bottom panel). For simulations of either the elbow or finger actions, the changes in the R and C components were synchronized. The model was equally robust in reproducing experimental elbow kinematics and grip forces in those cases when they started simultaneously (Fig. 11). To simulate these cases, the referent commands underlying the elbow movement and grip force were also initiated simultaneously. Figure 12 shows another example of simulation of elbow movement and grip force. In this case, the grip force started somewhat after the elbow movement onset. According to our criterion (see [Methods](#)), these actions were still considered as practically initiated simultaneously since the difference in the onset times did not exceed 25 ms.

In simulations shown in Figs. 9, 11 and 12, we took into account the fact that the pulp on the tips of fingers was compressed due to the normal component of grip force but disregarded the tangential component of pulp compression arising due to the object inertia. With this simplification, we were able to easily reproduce single- and intermediate but *not double-peak patterns* of grip force. At a first glance, the tangential component of pulp compression could not influence the normal component of grip force since the

Fig. 9 Typical simulation of elbow movement and single-peak pattern of grip force. *Upper panel* Experimental (solid curve) and simulated (dotted) elbow angle shown together with elbow central commands R_e and C_e used in the simulation (dashed and dash-dotted, respectively). *Middle panels* Experimental and simulated elbow velocity and grip force. *Bottom panel* Central aperture commands R_a and C_a for muscles of the index finger and the thumb (dashed and solid, respectively); C_a is the same for both fingers)

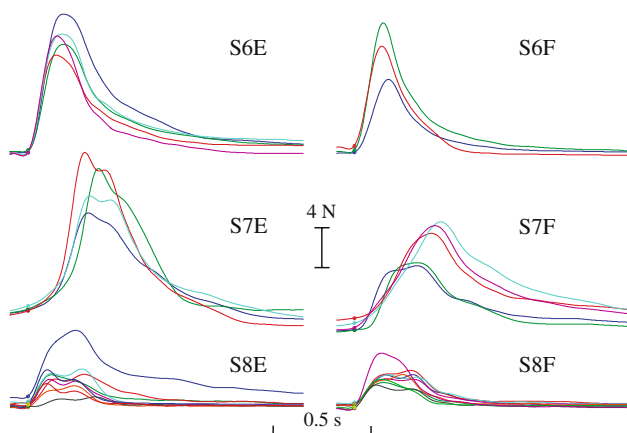
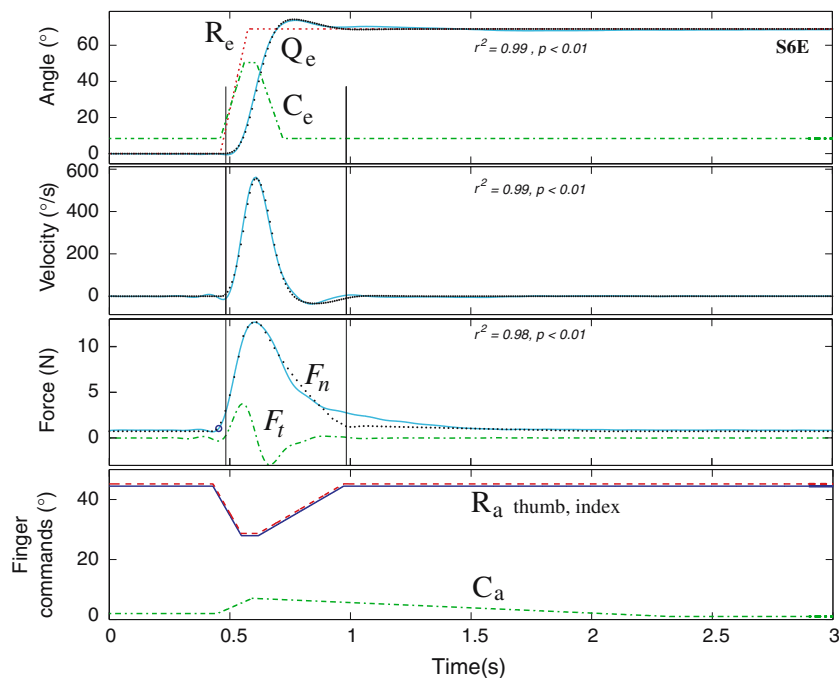


Fig. 10 Examples of single- and double-peak grip force patterns

former was orthogonal to the latter. Consider, however, possible effects of pulp compression in more detail.

First, because of the normal grip force, the pulp was compressed in the normal direction, by 1–2 mm (Fig. 13). Second, the inertial, tangential force (F_t in Fig. 14a) was transmitted from the object to the fingers via the deformable pulp. As a consequence, the bones of the index and the thumb slightly moved laterally from their neutral position on the object, thus shifting and compressing the pulp back and forth in the horizontal direction following the hand acceleration and deceleration. Compressed horizontally, the pulp became thicker (Fig. 14b) and increased the vertical pressure between the

finger bones and the object (F_c in Fig. 14a). Thus, because of pulp compression, the normal grip component somewhat increased not only when the movement was accelerated but also when it was decelerated and only went to zero when the acceleration changed sign. In other words, following elbow acceleration–deceleration, the pulp effect could transform a single-peak pattern of grip force (dashed in Fig. 14c) into a double-peak pattern and the peaks would be synchronized with the respective peaks in the movement acceleration and deceleration (solid curve in Fig. 14c).

We found that the amplitude of the normal component of pulp compression should be equaled to about 1/3 of the inertial force amplitude to explain experimental double-peak patterns of the normal component of grip force. In this case, the pulp was tangentially compressed by about 1 mm (Fig. 14b). Experimental double-peak patterns of the normal component of grip force could be converted into single- or intermediate patterns by subtracting the normal effect of pulp compression (Fig. 14c). By appropriately grading the pulp compression, we could effectively reproduce both elbow movements and any experimental patterns of normal grip forces ($r^2 \geq 0.96$, $P < 0.01$). The error in the reproduction of the elbow position, velocity and normal grip force was less than 7% from the respective amplitude values of these variables (absolute error: 1.51°, 25°/s, and 0.43 N, respectively). The relative error in the reproduction of half-width of the normal grip force (range 220–359 ms for different subjects) in all cases was less than 5% or 23 ms.

Fig. 11 Simulation of experimental elbow movement and an intermediate pattern of grip force. Traces as in Fig. 9

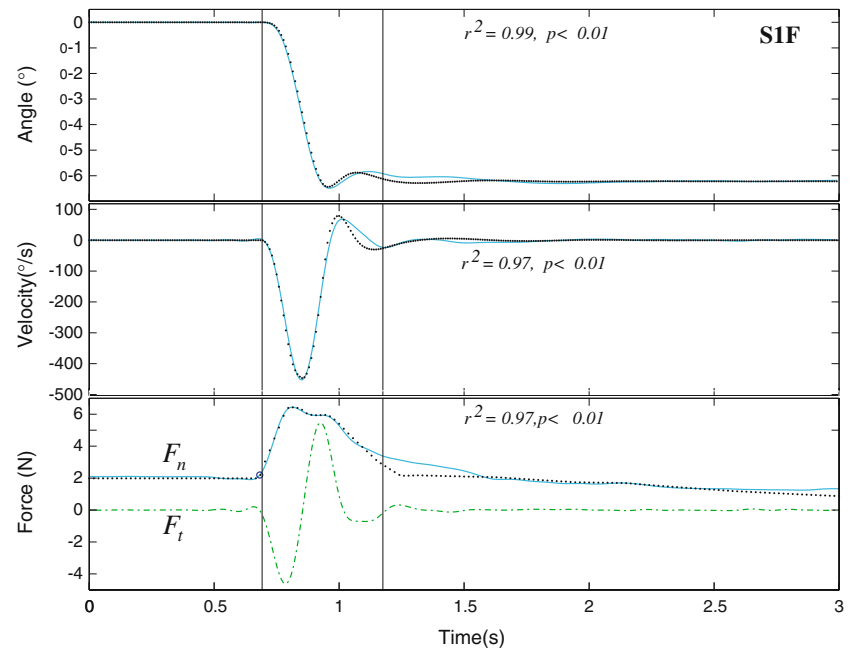
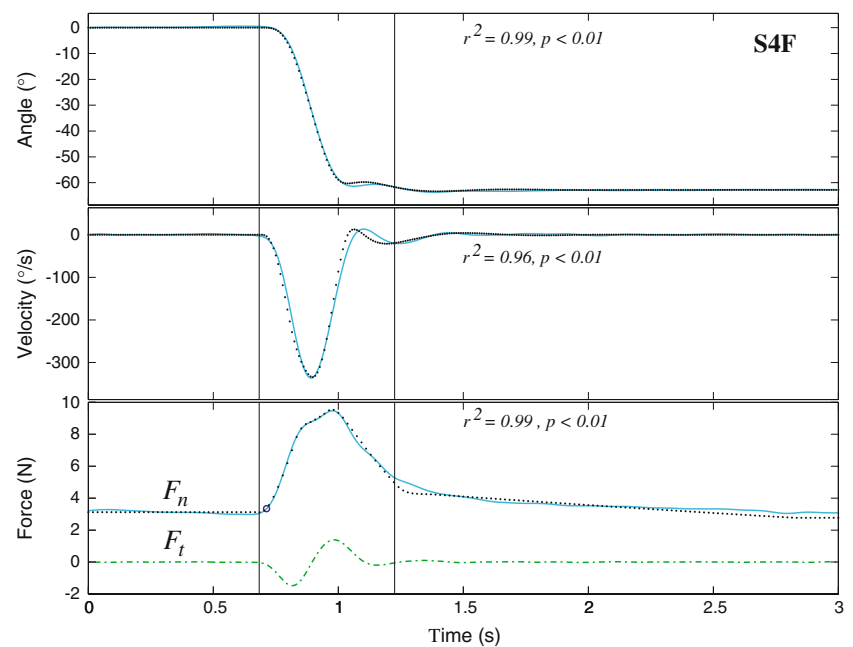


Fig. 12 Another example of simulation of experimental elbow movement and an intermediate pattern of grip force. Traces as in Fig. 9



Discussion

Basic findings

Our analysis showed that threshold position control expressed in terms of appropriate modifications of the referent arm–hand configuration is efficient not only in providing arm movement but also grip force that prevents slipping of the object from the fingers. It also showed that these actions could be controlled without any programming

of muscle activations (“motor commands”), forces and kinematics. The values of these variables emerged depending on the difference between the physical arm–hand configuration and its virtual, referent configuration modified by neural control levels. Depending on the timing of the elbow and aperture components of the referent configuration, the increase in the grip force could start either before or simultaneously with the arm movement onset (in 58 and 42% of cases, respectively). The model was robust in reproducing the empirical patterns of elbow

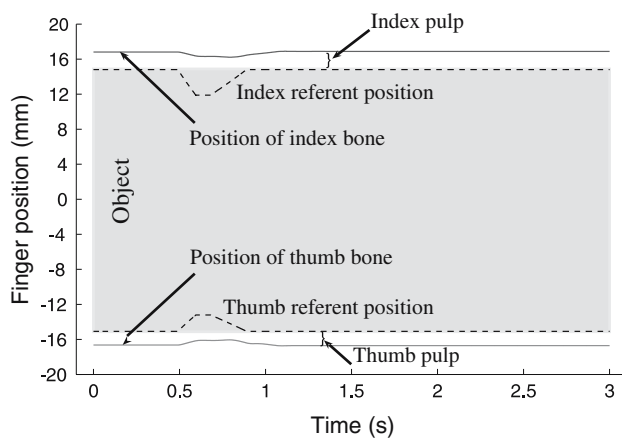


Fig. 13 Vertical compression of the finger pads resulting from the changes in the referent aperture variables R_a and C_a (simulation)

movement and grip force. The mechanical properties of the fingers' pulp appeared essential in the explanation of occasional changes of single- to double-peak grip force patterns in different trials, as well as of observable correlations of grip force with the orthogonally acting inertial load.

Grip-load relationship in our study

It seems likely that the double-peak pattern of grip force resulted from mechanical properties of the contact between the fingers and the object: during horizontal acceleration and deceleration of the object, the pulp on the tips of the fingers was deformed and shifted back and forth in the gap between the finger bones and the object. The pulp deformation thus *increased* pressure on the object and fingers and influenced the normal component of grip force, in synchrony with the elbow acceleration and deceleration. In other words, the pulp pressure and the modification of the normal component of grip force elicited by it increased twice in the course of elbow movement and only transiently reduced to zero when the movement acceleration changed sign (Fig. 14a). This mechanical effect explains the characteristic double-peak pattern of the grip force with a dip in between these peaks.

Two factors could be responsible for changes of the pattern of grip force from double- to single-peaked in various trials. First, the inertial force in our study was comparatively low (2–6 N), so that the pulp effect on the normal grip force was likely hidden in those trials in which the grip magnitude was high, resulting in single-peak grip forces. Second, pulp compressibility and translation decrease exponentially with increasing grip force (Serina et al. 1997, 1998; Wu et al. 2003). Therefore, the pulp-related influences on the orthogonal, grip force likely diminished when subjects produced comparatively high

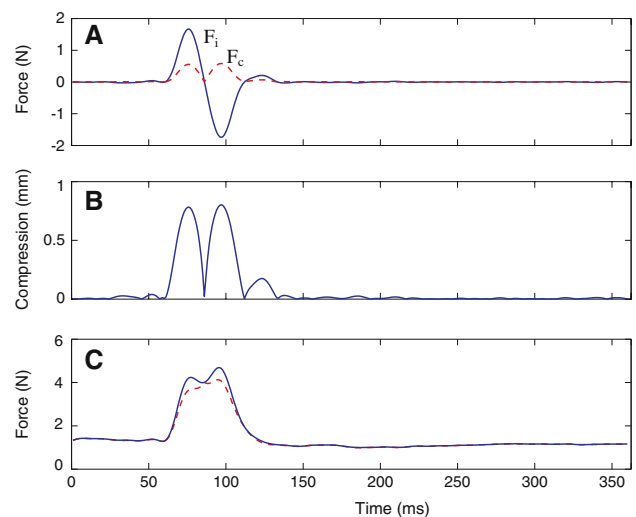


Fig. 14 Pulp compression elicited by tangential inertial force mechanically influences the normal component of grip force and converts single-peaked patterns of normal grip force into double-peaked patterns. For details see text

grip forces. This explains why correlation between the load and grip forces was high in one but was absent in other trials without any direct involvement of control levels in switching between these correlation patterns.

In the study by Flanagan and Wing (1997) the mass of the object was bigger (1.41 kg) but the arm movements were slower than in our study. Therefore, the inertial load (mass multiplied by acceleration) was in the range of low values when the pulp compressibility and mobility was high. Therefore, like in our study, correlation of grip and load forces in the study by Flanagan and Wing could also result from the mechanical interaction of the object and fingers via finger pads, and not only when inertial but also when viscous or spring-like loads were used. They selected a block of trials after about forty repetitions so that the performance was more stereotypical than in our trials taken from the start of experiments. In addition, our instruction “to make fast movements” was less restrictive in terms of movement speed. Therefore, our subjects showed more large variations in grip force and grip-load correlation.

Explanations of behaviors involving grip forces in other studies

Our analysis illustrates that threshold position control is efficient in meeting the task demand (to move the object without slipping) without any concerns about correlation between the grip and load forces. We reiterate this point by discussing results of other studies of grip force production. We will focus on those results that at a first glance might be seen as conflicting with the notion of threshold position control.

In two experiments conducted by Blakemore et al. (1998), load force was generated by subjects themselves. In one experiment, an object (similar to that in our study) was fixed in a clamp and subjects gripped it with their right thumb and index finger oriented horizontally. They were required to rhythmically pull down on the object to track a target load waveform. In the framework of threshold control, to produce the load force, subjects could make appropriate rhythmical changes in the referent vertical position (R_v) of the tips of the fingers holding the object. To prevent slipping the fingers off the object, they could simultaneously change the referent aperture (R_a) and thus rhythmically modulate the grip force, in synchrony with the load force, as was actually observed in this experiment. The task did not prevent subjects from changing R_a just below the actual aperture (Q_a) defined by the horizontal size of the object, eliciting comparatively small grip forces (on average, about 3.5 N in the experiment). In this situation, the mechanical, pulp-related influence of load force on grip force could be robust (see above) and contributes to the modulation of the grip force elicited by the central signals.

In the second experiment, subjects were required to steadily hold the same but non-clamped object with the right hand while pushing the object upward from underneath with the left index finger. Mechanically, the hand is an elastic system so that the rhythmical force from the left finger could change the object's position unless the right hand did something to minimize the object's displacement. In terms of threshold position control, the change in the position could be diminished by using a constant co-activation (C) command, thus increasing hand stiffness. In addition, the rhythmical referent signal that drove the muscles of the left finger, could be appropriately attenuated and used to modulate the referent position of the right fingers (R_v) to rhythmically counteract the force produced by the left finger. Guided by the general strategy of preventing object's slipping, the system could simultaneously modulate the referent aperture (R_a) in synchrony with and in proportion to the R_v command. This explains why the emergent load and grip force patterns were similar to those in the first experiment except that the amplitude of grip force modulation was smaller. This explanation is also consistent with the notion that acting on the same object, all effectors (left and right fingers) usually cooperate in meeting the task demands (e.g., Li et al. 2000, 2001; Latash et al. 2002).

In two other experiments by Blakemore et al. (1998), a robot was used to generate load force. The object was attached to the arm of the robot, which was programmed to produce rhythmical modulations of load force on the right hand gripping the object if the position of the object was maintained, as instructed. Unless appropriately trained,

subjects could not produce appropriately modulated referent control signals to elicit rhythmic muscle forces to minimize the object's displacement by the robot (unlike the previous experiment in which such referent control signals were available). Nevertheless, subjects could meet the task demand by specifying constant values of referent variables R_v and R_a . To minimize the object's motion, it was necessary to co-activate the hand muscles and grip the object stronger. This could be achieved by increasing the C command and decreasing the referent aperture, compared to the previous experiment. The emergent, stronger grip force (about 10 N in the experiment compared to 3.5 N in the two previous experiments) could limit the compressibility and mobility of the pulp (see above), virtually decoupling the grip and the load force, as actually occurred in this experiment.

In the other experiment with the same robot, subjects used the left hand to move a joystick placed on a table to guide the robot in generating the load for the right hand. In this case, the left and the right hand dealt with different objects and met different task demands so that the control signals underlying the joystick motion could not be transferred without practice to the right hand, especially when the joystick-robot transfer function was not known to subjects. In this situation, subjects could control the right hand as in the other experiment with the robot. This control strategy could also result in a nearly constant but relatively high (about 10 N) grip force despite rhythmical load force generated by the robot, as was shown in the study by Blakemore et al. (1998). For all control strategies employed in all the four tasks, the relationship between grip and load force could apparently be frequency-dependent since viscous-elastic properties of muscles, pulp, homonymous and heteronymous reflexes strongly depend on frequency of perturbations, which explains why the amplitude ratio, phase and lag in the grip-load force relationship changed with frequency in these experiments.

Our analysis shows that threshold control can be easily adjusted to accommodate various task demands without any internal models, contrary to what suggested by Blakemore et al. (1998).

The role of afferent systems in arm movement with grip force production

The notion of threshold position control shows that afferent feedback is critically important in transforming electrical signals resulting from descending, control influences on motoneurons and interneurons into spatially-dimensional variables—changes in the threshold position of the body and its segments (Figs. 2, 3). It is because of this transformation that our actions are placed in a frame of reference associated with the body or environment (Feldman

2007). This point is emphasized by sensory and motor deficits in deafferented subjects. In the absence of proprioceptive feedback in these subjects, the electrical control signals issued by descending systems cannot be transformed into spatially dimensional variables, resulting in inability to recognize and stabilize the arm position when the eyes are closed, not to mention that these subjects cannot stand or walk without assistance (Forget and Lamarre 1995).

It is also important to emphasize the *forward nature* of threshold position control. Consequences of this are numerous. In particular, according to the traditional view, proprioceptive feedback comes to motoneurons too late to contribute to the initial activity of agonist muscles during fast movements or isometric force productions and that this feedback is only efficient in slow motor actions. This view was applied not only to arm but also to eye movements and was used to justify the opinion that the oculomotor system lacks proprioceptive stretch reflexes, which appeared incorrect (Dancause et al. 2007). The traditional view does not take into account the fact that the changes in the motoneuronal membrane potentials and the associated changes in the state of spinal neurons preceding the initial activity of muscles deeply affect the state of the neuromuscular system before any visible changes in the motor output and pre-determine this output for some time ahead, i.e., in a *forward way* (Fig. 2). As has been shown (Pilon and Feldman 2006), the forward nature of threshold control allows the system to overcome destabilizing effects of reflex and electromechanical delays. Most important, the forward nature of threshold control implies that substantial changes in the state of the neuromuscular system start before any changes in EMG activity so that the latter emerges with a substantial contribution of proprioceptive feedback.

Threshold position control also implies that, rather than representing the desired goal of motor actions or actions as such, control variables (R_a and R_e in the present study) play the role of *tools or means* that are used by the nervous system to influence emerging actions. This is most obvious for the control variable called the referent aperture: as a position-dimensional variable, it does not represent the goal of the task (to generate an appropriate grip force that prevents object's slipping) but it does represent the means to reach this goal. Although it is less obvious, the same is true for the referent arm position. The system changes the R_e until visual and/or kinesthetic feedback start signaling that the desired position Q_e was reached (see also below). Thereby, it does not matter whether or not the final R_e coincides with the desired position (in the absence or in the presence of gravitational loads, respectively). These tools indicate where, in spatial coordinates, neuromuscular elements should work without

specific instructions on how they should work (Feldman and Levin 1995).

The notion that control variables are just neural tools that are used to shape emerging motor actions is a major point of departure from the traditional view that the nervous system programs motor actions, a view most strongly reflected in the internal model hypothesis. We will further this major point by considering how threshold position control can be used to explain adaptation of arm movements and grip forces to sudden changes in the load.

Adaptation of arm movements without grip force generation has been analyzed experimentally in the framework of threshold control in several studies (Feldman 1980; Weeks et al. 1996; Foisy and Feldman 2006), with the following conclusions. Rather than EMG patterns, muscle forces and load, subjects store in working memory the referent arm position that was efficient in reaching the target in the load condition in the previous trial. On the next trial, they recall and reproduce this referent arm position. Since the referent position is condition-specific, a sudden change in the load brings the arm to a new position. Based on visual and somatosensory feedback, subjects quickly adjust the referent arm position so that, typically after one trial, the movement with the new load becomes adequate.

These results may help explain how the system adjusts not only arm movements but also grip forces to a new load. In a study by Johansson and Westling (1988), subjects had to grip an object between the index finger and the thumb, lift it by moving the forearm, hold it in the air, and return to the table. After several trials with a heavy object, it was suddenly replaced with a light one. The task was similar to that simulated in our study, except that in the latter, the object was not replaced with another object and the forearm with the hand moved in a horizontal plane. In terms of threshold control, the lifting task could also be performed by simultaneously changing the referent arm position and hand aperture. Specifically, to reach the desired arm position (Q_e), subjects were forced to shift the referent arm position (R_e) *higher* than Q_e so that the difference $R_e - Q_e$ elicited muscle activation and torques that were sufficient to balance the gravitational torque of the arm with the object at position Q_e . In addition, subjects had to scale the referent aperture according to afferent signals that reflect the pressure in the pulp depending on the weight of the object. Thus, when the referent arm position was previously adjusted to a heavy load and then was suddenly reduced in some trial, the equilibrium at the target position became impossible. The arm continued to move beyond the target position (overshoot) until the arm reached a position at which the lighter load could be balanced. To correct the movement error (overshoot), subjects started changing the arm referent position by gradually diminishing it until

the object returned to the previous position, Q_e . In the next trial, subjects could reproduce the new referent position to make precise lifting of the light load. An overshoot in the arm movement and rapid, one-trial re-adaptation to a new load were indeed observed by Johansson and Westling (1988). In their experiments, afferent feedback from the pulp receptors could be used to make corrective changes in the referent aperture. This can be achieved by increasing the referent aperture until afferent signals from the pulp inform the controller that the grip force reached a safety margin in holding the light object without slipping, an assumption which is consistent with the observations of optimization of grip force with repetitions (Johansson and Westling 1984; Edin et al. 1992). Indeed, the feasibility of the suggested threshold control strategy can be verified by simulating not only kinematic and kinetic but also EMG patterns in this task in the framework of threshold control. While simulating this behavior, one can also consider the possibility that a sudden decrease in the weight of the object can produce an illusion of losing the object. Therefore, reacting to this illusion, subjects may first decrease the referent aperture, thus gripping the object stronger before increasing the referent aperture to a value that is adequate for the light load.

The threshold-mediated changes in the grip force resulting from tactile signals can also be effective in preventing losing the object when the properties of its contact with the fingers are suddenly worsened as was the case in the study by Fagergreen et al. (2003). Despite delays in the transmission to muscles, these signals can be efficient in preventing or even stopping the ongoing slip of the object during the hand motion (see also Boudreau and Smith 2001; Picard and Smith 1992a, b). This is in addition to the role of tactile information in the forward preparation and adjustment of grip forces from trial to trial. It is known (Deuschl et al. 1995; Issler and Stephens 1983; Jenner and Stephens 1982; Boudreau and Smith 2001) that cutaneous influences can be transmitted to muscles via spinal (latency 30–50 ms) and trans-cortical pathways (latency 55–75 ms). Central control levels can likely prevent slipping based on signals from cutaneous and other receptors and eliciting triggered reactions (latency 80–120 ms). In our model, the short-latency, spinal reaction to the properties of the fingers–object contact is expressed in a change in the peripheral component, ρ , of the threshold, whereas the long-latency reactions (including triggered reactions) as a change in the central component of the threshold. The model can be used to simulate and investigate these properties of afferent systems, which can be the focus of future studies.

In conclusion, the major aspects of grip force production with or without arm movement in our or other studies can be explained in terms of basic neurophysiological and

biomechanical notions without invoking the idea of internal models. This study, thus complements other studies that question the physiological feasibility of the internal model hypothesis. The threshold control theory also suggests the existence of several types of neurons responsible for different forms of threshold position control (see the first section of [Methods](#)). Most likely, these neurons are localized in the respective segments of the spinal cord whereas neurons that send control inputs to them are possibly located in many areas of the brain, including the motor cortex. These suggestions can be tested in appropriately designed electrophysiological studies in animals so that the threshold control theory can further be verified.

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