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MOVING A HAND-HELD OBJECT: RECONSTRUCTION OF REFERENT COORDINATE AND APPARENT STIFFNESS TRAJECTORIES

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Abstract—This study used the framework of the referent configuration hypothesis and slow changes in the external conditions during vertical oscillation of a hand-held object to infer the characteristics of hypothetical control variables. The study had two main objectives: (1) to show that hypothetical control variables, namely, referent coordinates and apparent stiffness of vertical hand position and grip force can be measured in an experiment; and (2) to establish relation(s) between these control variables that yield the classic grip-force–load-force coupling. Healthy subjects gripped a handle and performed vertical oscillations between visual targets at one of five metronome-prescribed frequencies. A HapticMaster robot was used to induce slow changes in the vertical force applied to the handle, while the size of the handle was changed slowly leading to changes in the grip aperture. The subjects were instructed not to react to possible changes in the external forces. A linear, second-order model was used to reconstruct the referent coordinate and apparent stiffness values for each phase of the vertical oscillation cycle using across-cycle regressions. The reconstructed time profiles of the referent coordinates and apparent stiffness showed consistent trends across subjects and movement frequencies. To validate the method, these values were used to predict the vertical force and the grip force applied to the handle for movement cycles that were not utilized in the reconstruction process. Analysis of the coupling between the four variables, two referent coordinates and two apparent stiffness values, revealed a single strong constraint reflecting the coupling between the grip force and vertical force. We view these data as providing experimental support for the idea of controlling natural, multi-muscle actions with shifts in a low-dimensional set of referent coordinates.

Key words: referent configuration hypothesis, referent trajectories, endpoint stiffness, grip force, grip apparent stiffness, grip-force–load-force coupling.

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Abbreviations: EP, equilibrium point; F_{GRIP}, magnitude of the grip force; PMP, Passive Motion Paradigm; RC, referent configuration; RMS, root mean squared.

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INTRODUCTION

The equilibrium-point hypothesis (EP-hypothesis, Feldman, 1966, 1986) and its recent development in the form of the referent configuration hypothesis (RC-hypothesis, Feldman and Levin, 1995; Feldman, 2009) have been highly influential over the past 50 years. According to these hypotheses, the neural control of a motor action can be adequately described as time functions of spatial referent coordinates (*referent trajectories*) for salient variables. For single-muscle control, the EP-hypothesis considers threshold of the tonic stretch reflex (λ) as the salient referent coordinate, which is specified via subthreshold depolarization of the corresponding alpha-motoneuronal pool. Changes in λ lead to movement, active force production, or both depending on external loading conditions. In Fig. 1A, the dependence of active muscle force on muscle length (the bold curves) for two values of the threshold of the tonic stretch reflex (λ_i) are shown. For a given external load and λ_i, an equilibrium point (EP_i) is characterized by a specific muscle length and a specific force exerted on the environment. A shift from λ_1 to λ_2 can lead to changes in both muscle length and force (a change from EP_1 to EP_2) depending on the external load characteristic. One such characteristic is illustrated in Fig. 1A. By a simple extension, a centrally specified time function $\lambda(t)$ dashed bold curve in Fig. 1B) leads to changes in equilibrium values of muscle length and force ($L_{EP}(t)$ and $F_{EP}(t)$ in Fig. 1B) and to actual muscle length changes $L(t)$ (solid curve in Fig. 1B) that would also depend on other factors, e.g., inertia.

Further extension of these ideas to multi-muscle movement is illustrated in Fig. 1C, D. A hierarchical control scheme has been developed in which the central controller is presumed to specify a RC at the highest, i.e., task, level (Feldman and Levin, 1995). While components of RC are spatial referent coordinates, their specification for an agonist–antagonist muscle pair controlling a joint results in two commands defined as the reciprocal command and co-activation command (Feldman, 1980). The former defines the joint referent coordinate (see details in Discussion), while the latter is reflected in its apparent stiffness. This description can be generalized for a multi-joint system. For example, to execute vertical movement of a hand-held object ($h(t)$ in Fig. 1D), the centrally specified RC is reflected in the *referent height* $r_H(t)$ and the *apparent stiffness* (cf. Latash and Zatsiorsky, 1993) of the hand $k_H(t)$. The movement of the object $h(t)$ emerges due to the specified input and external force field. Furthermore, one can view the task-level control

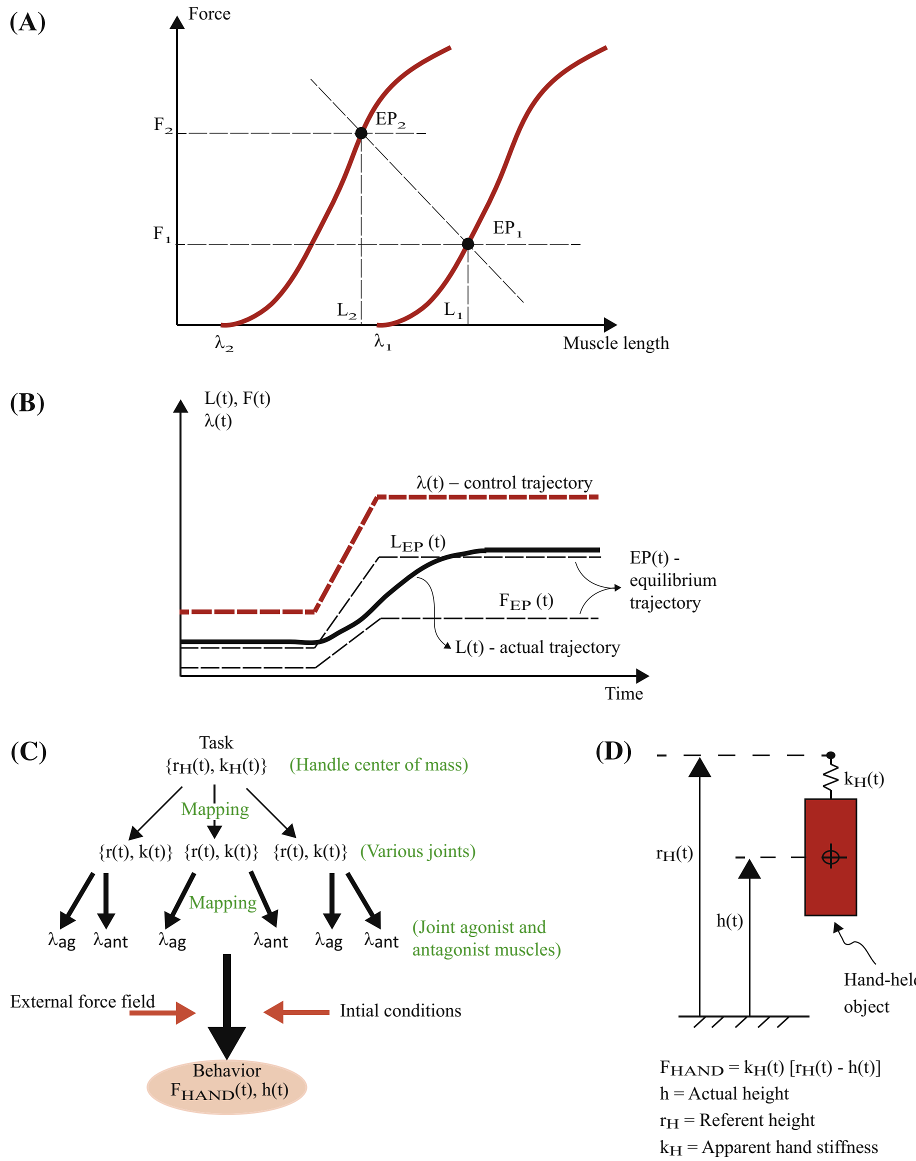

Fig. 1. Panel (A) illustrates the dependence of active muscle force on muscle length (the bold curves) for two values of the threshold of the tonic stretch reflex (λ_i). For a given external load and given λ_i, an equilibrium point (EP_i) is achieved and is characterized by a specific muscle length and a specific force. A shift from λ_1 to λ_2 can lead to changes in both muscle length and force (a change from EP_1 to EP_2) depending on the external load characteristic. One such characteristic is illustrated in Panel (A). Panel (B) depicts the time profile $\lambda(t)$, which is a control trajectory (bold, dashed line). It leads to changes in the equilibrium values of muscle length and force, $L_{EP}(t)$ and $F_{EP}(t)$. Taken together, these time functions comprise the equilibrium trajectory. Actual trajectory of muscle length and force (only $L(t)$ is illustrated) depends on many factors such as the inertia of the moving system. Panel (C) depicts a scheme in which hypothetical central control commands (i.e., referent variables) are transformed into tonic-stretch-reflex thresholds for all the muscles involved in the action via a series of few-to-many mappings. Behavior, such as measured mechanical variables, emerges as a consequence of the central commands and external conditions. The object in Panel (D) experiences a force from the subject's hand. As a first approximation, the hand force is modeled as a linear relation between the difference in the current, $h(t)$, and referent, $r_H(t)$, heights. The apparent hand stiffness, $k_H(t)$, is the proportionality constant.

input as being transformed by a sequence of few-to-many transformations that yield referent coordinates at lower hierarchical levels all the way down to λs for all involved muscles (for more detail see Latash, 2010).

One major obstacle in the development of the RC-hypothesis has been the lack of a method to measure RCs and their time changes during natural movements. The first attempt to develop such a method was made over 20 years ago and applied to reconstruction of referent trajectories during single-joint movements (Latash and Gottlieb, 1991, 1992; Latash, 1992).

To obtain the time course of the hypothetical control signals, Latash and Gottlieb developed a method based on comparing actual joint trajectories during repetitive movements in slightly varying external loading conditions. They assumed that the profiles of control variables were reproduced across trials. Regression analysis of the force–displacement data across trials at identical phases of the movement allowed the computation of referent joint coordinate and apparent stiffness values, which were later interpolated to approximate the assumed referent trajectories. This