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SYNERGIES IN THE SPACE OF CONTROL VARIABLES WITHIN THE EQUILIBRIUM-POINT HYPOTHESIS

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Abstract—We use an approach rooted in the recent theory of synergies to analyze possible co-variation between two hypothetical control variables involved in finger force production based on the equilibrium-point (EP) hypothesis. These control variables are the referent coordinate (*R*) and apparent stiffness (*C*) of the finger. We tested a hypothesis that inter-trial co-variation in the {*R*; *C*} space during repeated, accurate force production trials stabilizes the fingertip force. This was expected to correspond to a relatively low amount of inter-trial variability affecting force and a high amount of variability keeping the force unchanged. We used the "inverse piano" apparatus to apply small and smooth positional perturbations to fingers during force production tasks. Across trials, *R* and *C* showed strong co-variation with the data points lying close to a hyperbolic curve. Hyperbolic regressions accounted for over 99% of the variance in the {*R*; *C*} space. Another analysis was conducted by randomizing the original {*R*; *C*} data sets and creating surrogate data sets that were then used to compute predicted force values. The surrogate sets always showed much higher force variance compared to the actual data, thus reinforcing the conclusion that finger force control was organized in the {*R*; *C*} space, as predicted by the EP hypothesis, and involved co-variation in that space stabilizing total force.

Key words: uncontrolled manifold hypothesis, synergy, finger force, isometric, apparent stiffness, equilibrium-point hypothesis.

INTRODUCTION

The human body is redundant: It typically possesses infinite ways to accomplish any given motor action. Recently, the problem of motor redundancy (Bernstein, 1967) has been reinterpreted within the principle of motor abundance (Gelfand and Latash, 1998; Latash, 2012). Based on this principle, a *synergy* is defined as an organization of a set of elemental (input) variables that co-vary to stabilize a fewer number of task-specific output performance variables (Latash, 2008).

In the past, most synergy analyses assumed an abundant set of elemental variables that could be kinetic (digit forces and moment), kinematic (joint rotations) or electromyographic (reviewed in Latash, 2008). In this work, we demonstrate for the first time the existence of a synergy in the space of control variables defined within an influential hypothesis in the field of motor control, the equilibrium-point (EP) hypothesis (Feldman, 1966, 1986, 2009, 2015). According to the EP hypothesis, the control of an effector is associated with setting values of neural variables that translate into referent coordinate (*R*) and apparent stiffness (*C*) for the effector (see Discussion for more detail). Thus, a one-dimensional task of pressing with a finger in isometric conditions – the task studied in this paper – is associated with setting values of two elemental variables, the fingertip referent coordinate (R_{FT}) and its apparent stiffness (C_{FT}) (Fig. 1A; cf. Pilon et al., 2007; Latash et al., 2010; Ambike et al., 2014). The task is, therefore, abundant in the two-dimensional space of control variables, {R_{FT}; C_{FT}}. We examine whether there exist synergies in the space of the control variables, {R_{FT}; C_{FT}}, stabilizing the force produced by the finger.

In a linear approximation, the solution space for the single-digit force production task is represented by the function: $C_{FT}(R_{FT} - X_{FT}) = f$, where X_{FT} is the fingertip actual coordinate and *f* is force (Fig. 1A). This function, a hyperbola, represents the uncontrolled manifold (UCM, Scholz and Schöner, 1999) in the {R_{FT}; C_{FT}} space. If a person accurately performs this task several times, the data points in the {R_{FT}; C_{FT}} plane are expected to show small deviations from the UCM. Their deviations along the UCM, however, do not affect fingertip force and can be larger, smaller, or equal to those orthogonal to the UCM. We hypothesize that deviations along the UCM will be larger than those orthogonal to the UCM. This hypothesis is based on two assumptions: (1) The control of this action is organized in a space adequately reflected by {R_{FT}; C_{FT}}; and (2) It is associated with a synergy in this space that stabilizes fingertip force

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Abbreviations: ANOVA, analysis of variance; EP, equilibrium-point; MVC, maximum voluntary contraction; UCM, uncontrolled manifold.

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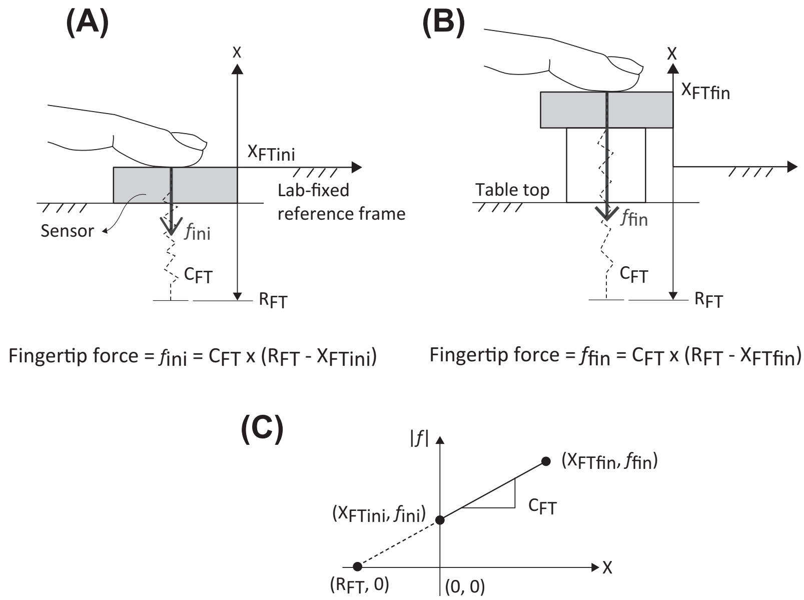

Fig. 1. Model for finger force generation. Finger force generated by the fingertip in proportion to the difference between the nervous-system-defined referent coordinate (R_{FT}) and the fingertip actual configuration (X_{FT}). In Panels (A) and (B), the lab-fixed coordinate frame is conveniently located at the actual fingertip position, and the distance coordinate is measured positive upward. Panels A and B depict the initial configuration and the configuration at the end of the upward perturbation of the sensor, respectively. Panel (C) depicts the sensor displacement vs fingertip force (absolute value) relation. The slope provides an estimate of the apparent fingertip stiffness (C_{FT}), and the force-axis intercept provides the estimate of R_{FT}.

(Latash, 2008, 2010). If either assumption is false, the hypothesis should be falsified.

We used the "inverse piano" device (Martin et al., 2011a) to introduce smooth positional perturbations to fingers. Subjects were instructed and trained "not to interfere" with possible force changes produced by the inverse piano (cf. Feldman, 1966; Latash, 1994). When a finger is lifted by the inverse piano, its X_{FT} is moved away from R_{FT} (Fig. 1B). This is expected to increase the finger force magnitude in proportion to the lift magnitude. We observed linear relations between the fingertip coordinate and force that allowed computing R_{FT} (intercept) and C_{FT} (slope) values for the fingertip (Fig. 1C). We also explored possible differences among the fingers and between the right and left hands.

This study provides three novel contributions to the field. First, it introduces a method to measure the hypothetical control variables as suggested by the EP hypothesis for steady-state, force-production tasks. Second, it is the first study that 'pierces the skin without puncturing it' and investigates the existence of synergies in the $\{R_{FT}; C_{FT}\}$ space. Finally, the current study is also the first to apply the UCM analysis to variables that reflect hypothetical control variables within the EP-hypothesis.

EXPERIMENTAL PROCEDURES

Subjects

Ten healthy subjects voluntarily participated in this study (six males and four females; age: 25.2 ± 5.18 year, height: 1.70 ± 0.09 m, mass: 71.14 ± 7.85 kg; mean ± SD). All subjects were right-hand dominant by self-report and had no history of discomfort or injury in the upper arm for the past 6 months. All subjects provided informed consent in accordance with the procedures approved by the Office for Research Protection of the Pennsylvania State University.

Equipment

The "inverse piano" device (details in Martin et al., 2011a, b) was used to provide controlled positional displacements of the fingers during the course of the trial (see Procedures). This equipment consists of four unidirectional piezoelectric force sensors (model 208C01, PCB Piezotronics, Depew, NY, USA) connected to linear actuators (PS01–23 × 80; LinMot, Spreitenbach, Switzerland). The force sensors were mounted within slots in a steel frame (140 × 90 mm), 3-cm apart in the medio-lateral direction and could be adjusted in the anterior-posterior direction to accommodate different hand sizes. A wooden board (460 × 175 × 27 mm) was attached to the frame to support the subject's arm. Sandpaper (100-grit) was placed on the contact surface of the sensor to increase the friction between the digits and sensors. In addition, a laser sensor was used (resolution, 0.015 mm; AR200–50 M, Schmitt Industries, Portland, OR, USA) to record the displacement of the force sensors. The laser was projected onto a reflective surface screwed to the index-finger sensor. The signals from the force transducers were routed through a PCB 484B11 signal conditioner and then digitized along with the laser signal at 200 Hz using a 16-bit National Instruments PCI-6052E analog-to-digital card (National Instruments, Austin, TX, USA). The sensor reading was zeroed with the subject's fingers resting on the sensors with the hand relaxed just before