

Neural Control of Motion-to-Force Transitions with the Fingertip

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The neural control of tasks such as rapid acquisition of precision pinch remains unknown. Therefore, we investigated the neural control of finger musculature when the index fingertip abruptly transitions from motion to static force production. Nine subjects produced a downward tapping motion followed by vertical fingertip force against a rigid surface. We simultaneously recorded three-dimensional fingertip force, plus the complete muscle coordination pattern using intramuscular electromyograms from all seven index finger muscles. We found that the muscle coordination pattern clearly switched from that for motion to that for isometric force ~ 65 ms before contact ($p = 0.0004$). Mathematical modeling and analysis revealed that the underlying neural control also switched between mutually incompatible strategies in a time-critical manner. Importantly, this abrupt switch in underlying neural control polluted fingertip force vector direction beyond what is explained by muscle activation-contraction dynamics and neuromuscular noise ($p \leq 0.003$). We further ruled out an impedance control strategy in a separate test showing no systematic change in initial force magnitude for catch trials where the tapping surface was surreptitiously lowered and raised ($p = 0.93$). We conclude that the nervous system predictively switches between mutually incompatible neural control strategies to bridge the abrupt transition in mechanical constraints between motion and static force. Moreover because the nervous system cannot switch between control strategies instantaneously or exactly, there arise physical limits to the accuracy of force production on contact. The need for such a neurally demanding and time-critical strategy for routine motion-to-force transitions with the fingertip may explain the existence of specialized neural circuits for the human hand.

Key words: motor control; neural control; finger; hand; contact transition; force

Introduction

Fine manipulation using fingertips is an integral part of the human identity. A fundamental element of manipulation is the acquisition of precision pinch: abruptly making contact with external surfaces to produce static force with the fingertips. Numerous studies show that the apparently trivial task of making contact using any limb is surprisingly difficult to understand (Lacquaniti and Maioli, 1987, 1989; Bizzi et al., 1992; Hogan, 1992; Wolpert et al., 1995; Gribble et al., 1998; Todorov, 2000; Ostry and Feldman, 2003; Kurtzer et al., 2005; Lackner and DiZio, 2005) or to successfully mimic with robots

(Whitney, 1987; Kazerooni, 1990; Hogan, 1992; Hyde and Cutkosky, 1994; Akella and Cutkosky, 1995; Cavusoglu et al., 1997). Contact discontinuously changes the mechanical constraints of the task. Therefore the joint torques (and muscle forces in turn) for producing motion and force with the end-point of a limb in a given direction are necessarily different (Hogan, 1985, 1992). However, the underlying neural control strategy need not change. One hypothesis known as impedance control in robotics and equilibrium point control in motor control proposes that to exert a limb force against a surface, we can simply regulate the viscoelastic muscle behavior so as to move the controlled “virtual” position of the limb inside the surface. In this case, a contact force emerges from the mismatch between actual and virtual position, without a direct need to code it in the neural signal (Feldman, 1986; Bizzi et al., 1992; Hogan, 1992; Hyde and Cutkosky, 1994; Mussa-Ivaldi and Bizzi, 2000; Ostry and Feldman, 2003). Alternatively, others hypothesize that the nervous system switches between two distinct control strategies, one to produce limb motion but that cannot produce limb force in the same direction as the motion, and vice versa. Hence, the contact transition is executed through accurate anticipation of contact time and careful feedforward/feedback control of joint torques (Whitney, 1976, 1987; Hogan, 1988; Kazerooni, 1990) or muscle activations (Lacquaniti and Maioli, 1987, 1989; Todorov,

Received May 18, 2007; revised Dec. 7, 2007; accepted Dec. 10, 2007.

This work was supported by the Whitaker Foundation, National Science Foundation (NSF) Grants 0312271 and 0237258, and National Institutes of Health (NIH) Grants HD048566, AR050520, and AR052345 (F.J.V.-C.). M.V. was supported by the NSF Frontiers in Integrative Biological Research Grant 0425878 during manuscript preparation. The contents of this manuscript are solely the responsibility of the authors and do not necessarily represent the official views of the National Institute of Arthritis and Musculoskeletal and Skin Diseases, the National Institute of Child Health and Human Development, the NIH, the Whitaker Foundation, or the NSF. We thank R. V. McNamara III for technical support and experiment execution, F. A. Medina for EMG processing, Dr. V. J. Santos for help with study design, S. Song for machining and instrumentation, Drs. M. Price and S. Backus for fine-wire electrodes placement, and Drs. J. Guckenheimer, A. Ruina, M. Srinivasan, K. J. Keenan, E. Todorov, F. Mussa-Ivaldi, and the anonymous reviewers for critical comments.

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DOI:10.1523/JNEUROSCI.4993-07.2008

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2000). Regardless of where the reader may stand on this debate, to our knowledge contact transitions have not been studied in the realm of finger function.

Given the biomechanical (Valero-Cuevas et al., 2007) and neural (Penfield and Boldrey, 1937; Schieber and Hibbard, 1993; Scott, 2004) specialization of human fingers, it is unclear whether conclusions from studies of dynamic interactions of whole limbs with the environment extend to neuromuscular control of human fingers. Studies of typing (Kuo et al., 2006) involve tasks where the contact surface is not rigid and the goal is not to produce a well directed sustained static force against it. In contrast, the acquisition of precision pinch for manipulation of rigid objects requires abruptly making contact with the object to immediately generate well directed static fingertip forces. Here, we investigated whether the neural control of finger musculature switches when the index finger abruptly transitions from motion to isometric force production (i.e., a tap-to-push task). When we found that a switch occurred, we studied the timing, mechanical consequences and neuromuscular implications of the switch.

Materials and Methods

Consenting subjects (11 male; 7 female; age range, 19–39 years; mean, 22.8 years) with no history of neurological or hand pathology or injury participated in this study. This study was approved by Cornell University's Committee on Human Subjects. We recorded motions and forces in 18 subjects, and intramuscular electromyograms in nine of them. Subjects wrapped the thumb and unused fingers of their dominant hand around a fixed horizontal dowel to produce force using their index finger against the flat, top surface of a cylindrical pedestal mounted on a six-axis load cell (model 20E12A-I25; JR3, Woodland, CA). The surface position and height was adjusted such that the index finger was in a neutral ad-abduction posture and the metacarpo-phalangeal, proximal-interphalangeal and distal-interphalangeal joints in ~30, 45, and 15° of flexion, respectively. Resembling our previous work (Valero-Cuevas, 2000), subjects wore a custom-molded thimble with a spherical Teflon bead embedded at its tip. This rigorously defined the mechanical task via a unique contact point and friction cone for force direction.

We instructed subjects to ramp-up fingertip force against a flat target surface to a self-selected high magnitude [~100% maximal voluntary contraction (MVC)] as quickly as possible (i.e., tap-to-push task). This ensured that the transition from motion to force production was indeed abrupt. They were instructed to, on contact, keep the finger static and the force pointed vertically to the best of their ability. The trials started from three initial conditions: “relaxed,” “preactivated,” and “motion.” In the motion condition, subjects tapped the target surface five times at a 1 Hz rhythm set by a metronome (1 s for the up-and-down motion) and pushed down on the surface at the end of the fifth cycle (Fig. 1a, blue traces show the last cycle). In the relaxed condition, the subject rested the fingertip on the target surface for two metronome beats (i.e., 2 s) before pushing down (Fig. 1b, green traces). In the preactivated condition, subjects produced a downward vertical force vector of a self-selected minimal magnitude for two metronome beats before pushing down (Fig. 1b, red traces). Subjects typically produced between 0.5 and 1 N of force magnitude in the preactivated condition.

Electromyograms. The seven muscles actuating the index finger are *flexor digitorum profundus* (FP), *flexor digitorum superficialis* (FS), *extensor indicis proprius* (EI), *extensor digitorum communis* (EC), *first lumbrical* (LUM), *first dorsal interosseous* (DI), and *first palmar interosseous* (PI). We recorded and digitally processed EMGs using fine-wire intramuscular electrodes from all seven muscles in nine subjects using previously reported techniques (Valero-Cuevas, 2000). Amplified EMGs were sampled at 2000 Hz, bandpass filtered at 20–800 Hz, full-wave rectified, and normalized by the largest EMG level recorded

during maximal voluntary contractions of that muscle. Maximal voluntary contractions of individual muscles were done immediately before and after fingertip force production, with the index finger braced in the same posture used during the study. We multiplied the normalized EMG from each muscle by its maximal muscle stress and then by its physiological cross-sectional area values obtained by us in three previous biomechanical studies (Valero-Cuevas et al., 1998; Valero-Cuevas, 2000; Valero-Cuevas and Hentz, 2002) to find a time-varying muscle-force vector $\mathbf{m}(t)$, the “muscle coordination pattern” (Valero-Cuevas et al., 1998; Valero-Cuevas, 2000, 2005) $[\text{FP, FS, EI, EC, LUM, DI, PI}]^T$. Finally, we smoothed $\mathbf{m}(t)$ using a symmetric moving average with a 50 ms window. As in our past work (Valero-Cuevas, 2000), the reference coordination pattern vector ($\mathbf{m}^{\text{ref}}$) for each trial was defined as the average of $\mathbf{m}(t)$ during 100 ms of peak force (always occurring >500 ms after contact). We calculated the angle $[\theta(t)]$ between $\mathbf{m}(t)$ at every sample and $\mathbf{m}^{\text{ref}}$ using the unit-vector dot-product formula given as follows:

$$\theta(t) = \cos^{-1} \left(\frac{\mathbf{m}(t) \cdot \mathbf{m}^{\text{ref}}}{\|\mathbf{m}(t)\| \|\mathbf{m}^{\text{ref}}\|} \right), \quad (1)$$

where a larger θ means a larger misalignment of the measured coordination pattern with respect to the reference pattern, and $\theta = 0$ means perfect alignment.

We found average of θ for each trial in six windows of 50 ms width as shown in Figure 2a, performed one-way repeated measures ANOVA to test whether θ differed across the six time intervals. We applied a Tukey–Kramer adjustment for multiple comparisons when reporting p values. We verified that the residuals were normally and identically distributed.

Fingertip force analysis. We used the vertical force (F_z) to detect contact or start of force-ramps. Force production was said to start when F_z exceeded 6 SDs above mean F_z during the relaxed, preactivated or no-contact period. Through trial and error we found a threshold of 6 SDs to yield the most reliable detection of force onset and manually verified each automatically detected force onset. We discarded trials where the finger slipped or bounced after contact, or if the flight phase during motion trials was <400 ms (despite the metronome).

We low-pass filtered (80 Hz cutoff) the force data from all three axes before calculating the angular deviation of the force vector from vertical $[\phi_{\text{force}}(t)]$. We then found $\max(\phi_{\text{force}})$ and $\text{var}(\phi_{\text{force}})$ in the time interval between +10 and +65 ms after contact (see Fig. 3a–c). To be judiciously conservative, we excluded force data for the first 10 ms after contact to remove high-frequency sensor noise transients that subdued typically by 5 ms, and always well within 10 ms (Fig. 1a). We also limited our analysis to +65 ms because sensory feedback will affect force production subsequently (Venkadesan et al., 2007). Both $\max(\phi_{\text{force}})$ and $\text{var}(\phi_{\text{force}})$ were log transformed to ensure normality. We then performed repeated measures ANOVA to test for differences in $\max(\phi_{\text{force}})$ and $\text{var}(\phi_{\text{force}})$ between different initial conditions. We applied a Tukey–Kramer adjustment for multiple comparisons when reporting p values.

Index finger model. To objectively evaluate the mechanical consequences of the contact transition on the initial angular deviation of the force vector, we developed a torque-driven planar index finger model with an ideal inelastic contact collision. This model produced motion when unconstrained, or force immediately on contact with a surface (for nonslip conditions). Finger motion was modeled using a three-link open kinematic chain; and initial force production as a four-bar linkage closed kinematic chain. We switched between the separate formulations for the motion and force production at contact.

We calculated net joint torques for motion (τ_{motion}) while ensuring that two features of our experimental trials were emulated. First, we designed model finger kinematics to emulate the subjects' preference to keep the distal phalanx vertical (i.e., perpendicular to the target surface). Second, to emulate the fact that subjects' fingertip made contact with a nonzero vertical velocity, we prescribed a sigmoidal vertical velocity profile for the model fingertip, starting with zero velocity 500 ms before contact (highest finger posture) and peak velocity at contact. These two

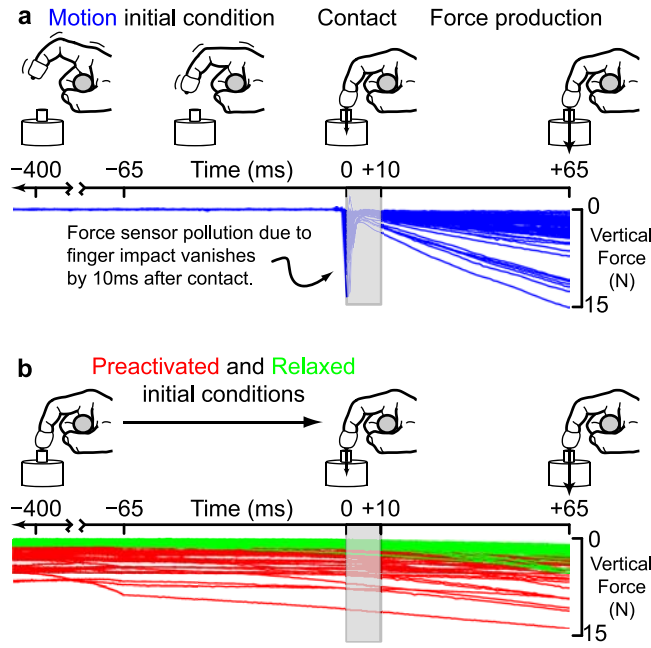


Figure 1. Experimental setup and force production under different initial conditions. *a*, For the motion initial condition, subjects tapped the surface five times before pushing against it to maximize vertical force. The blue traces show vertical force data from all subjects. Data from the first 10 ms (gray box) were excluded to remove high-frequency impact sensor noise transients that subsided typically by 5 ms, and always well within 10 ms. *b*, For the relaxed (green) and preactivated (red) initial conditions, subjects produced force-ramps in a static posture (no previous finger motion), and from nearly zero, or low force ($\sim 25\%$ of maximal voluntary force), respectively.

requirements uniquely specified the joint angles $[\varphi(t)]$ and joint angular velocities/accelerations throughout the motion phase. Given that the left-hand side of Equation 2 is known for every instant of time during the motion phase, we directly calculated the unique joint torques for producing this motion:

$$M(\varphi)\ddot{\varphi} + C(\varphi, \dot{\varphi})\dot{\varphi} + N(\varphi) = \tau_{\text{motion}} \quad (2)$$

where φ is the vector of joint angles, M represents the inertial properties of the finger, C represents Coriolis and centrifugal forces on each phalanx, and N is the gravitational term.

The dynamical equation for initial force production when the fingertip makes contact with the surface is as follows:

$$M(\varphi)\ddot{\varphi} + C(\varphi, \dot{\varphi})\dot{\varphi} + N(\varphi) + A(\varphi)^T \mathbf{f} = \tau_{\text{force}} \quad (3)$$

where

$$\mathbf{f} = (AM^{-1}A^T)^{-1}(AM^{-1}(\tau_{\text{force}} - C\dot{\varphi} - N) + \ddot{\varphi}), \quad (4)$$

where the posture dependent matrix A is the manipulator Jacobian that maps joint angular velocities to translational velocities of the fingertip and $\mathbf{f}$ is the fingertip force vector produced when in contact with a surface. The beaded thimble used in the experiment precludes the fingertip from producing any torques while maintaining a static posture (for a detailed description of the torque output of the fingertip, see Valero-Cuevas et al., 1998). By definition, the unique joint torques needed to produce static vertical force (τ_{force}) are calculated by setting joint angular velocities and accelerations to zero in Equations 3 and 4; in other words, $\tau_{\text{force}} = A(\varphi)^T \mathbf{f} + N(\varphi)$, where $\mathbf{f}$ is the desired fingertip force vector.

We calculated $\tau_{\text{motion}}(t)$, such that under the assumptions outlined for Equation 2, it would take 500 ms to travel from the height of the metacarpophalangeal joint to the height of the target. Also, the posture at contact emulated the reference posture used in our experiments, namely, 30, 45, and 15° of flexion, from the proximal to the

distal joints, respectively. We calculated joint torques at contact such that for the reference contact posture, τ_{force} would produce static vertically oriented fingertip force vector of 0.15 N in magnitude. We simulated various durations (0 to 65 ms) of transition between τ_{motion} and τ_{force} , as well as various errors in timing, i.e., the instant when the transition is completed (0 to 20 ms before contact occurs). We assumed an ideal inelastic collision (i.e., fingertip and joint motions come to a standstill on contact). This allowed us to examine the mechanical consequences (i.e., causal relationships) between a non-instantaneous transition in joint torques and initial misdirection in fingertip force vector on contact, independently of the viscoelastic properties of the finger and collision dynamics.

Test of impedance control. We directly tested whether impedance control was used in a parallel study with six consenting subjects (three male; three female; average age, 19.5 years; range, 19–20 years) in which EMGs were not recorded. The task was identical to the with motion condition, with the difference that blindfolded subjects, while wearing the thimble, continuously tapped a 50 mm diameter rough sensor surface. Each tap motion lasted 3 s: the up–down tapping motion lasted 1 s as in the “motion” initial condition, followed by a 2 s period when subjects pushed to a self-selected low force ($\sim 25\%$ MVC). Each subject performed a total of 150 taps in 10 batches of 15 taps. For all taps a robot lowered the surface to touch a bell, to allow the subject to phase-lock their tapping cadence, and then randomly raised the surface to either the reference height (in 95% of the taps) or to a different height (in 5% of the taps). The surface height for the 5% of “catch” trials was selected at random from a uniform distribution with ± 6 mm range. This prevented the blindfolded subject from using auditory cues to identify catch trials. The dependent variable for the regression (Fig. 5) was peak $\|\mathbf{f}\|$ for $t = +10$ ms to $t = +65$ ms after contact, normalized by the steady-state force the subjects reached at each tap. The variability in steady state force across subjects precluded our detecting systematic changes (if any) in initial force magnitude with surface height. Thus, we used normalization as a means to best detect a systematic change in initial force magnitude across trials with disparate self-selected steady-state static force magnitude.

Results

The 7D muscle coordination patterns $[\mathbf{m}(t)]$ for motion (Fig. 2a, dark boxes) and force production (Fig. 2a, light boxes) were significantly different ($\Delta\theta \geq 20^\circ$, $p < 0.0001$). However, even 65 ms before contact (Fig. 2a, during finger motion, shaded box), the coordination pattern had already changed abruptly (in a span of ~ 60 ms) and was significantly different from the preceding periods of finger motion (Fig. 2a, dark box at $[-150, -100]$ vs shaded box at $[-90, -40]$) ($\Delta\theta = 14^\circ$, $p = 0.0004$), but statistically indistinguishable from the pattern for static force production (Fig. 2a, light box at $[+20, +70]$ vs shaded box at $[-90, -40]$) ($\Delta\theta = 6^\circ$, $p = 0.28$). This clear and abrupt transition between coordination patterns occurred before contact could alter the mechanical condition (i.e., the switch in muscle coordination pattern cannot be explained by the onset of contact). Moreover, the coordination pattern $[\mathbf{m}(t)]$ after contact was well aligned with $\mathbf{m}^{\text{ref}}$, the reference pattern for maximal static force production (Fig. 2a, light boxes) ($\theta < 20^\circ$).

In addition, the increase in the vector magnitude of the muscle coordination pattern parallels that for the vector direction but is initiated later (i.e., closer to the contact time) (Fig. 2b). That is, the nervous system begins by increasing the alignment of the coordination pattern vector with that for force production over 100 ms before contact (Fig. 2a). In contrast, the vector magnitude of the coordination pattern begins to increase to match that for initial force production < 70 ms before contact (Fig. 2b). Thus, we find that the transformation of the muscle coordination pattern vector from that

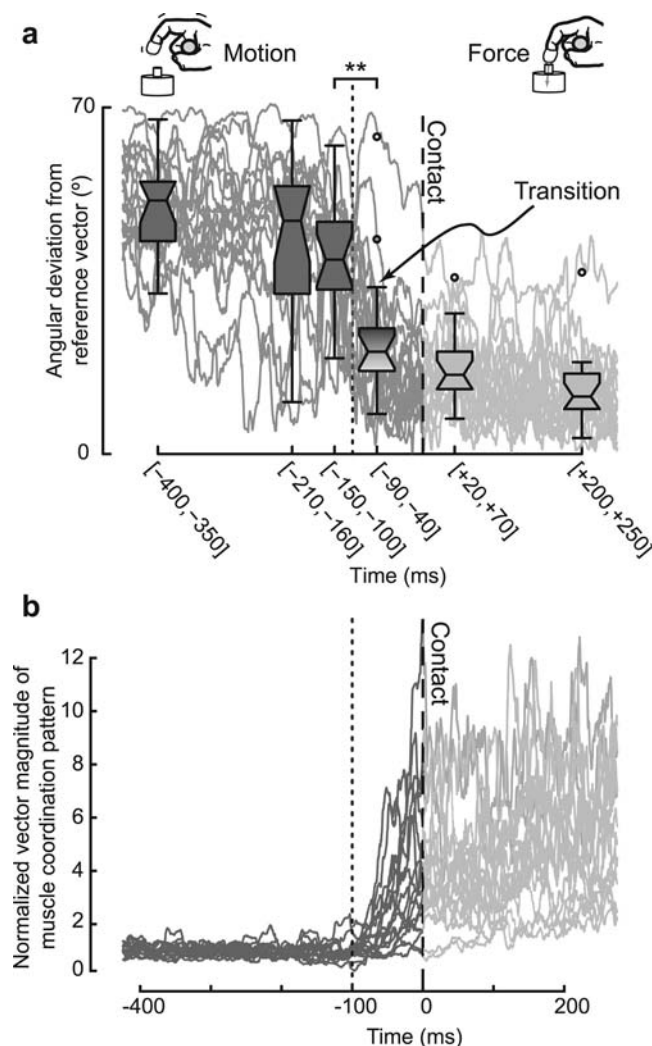


Figure 2. Switch in direction and magnitude of the muscle coordination pattern vector between motion and static force production. *a*, Muscle coordination patterns (dark and light traces) are represented by their angular deviation (θ) from a reference coordination pattern (namely, the coordination pattern when fingertip force was the highest). The box plots are 50 ms wide averages of θ . The central line is the median, the notches are the robust 95% confidence limits of the median, the lower and upper limits of the box are the quartile limits, whisker lengths are 1.5 times the interquartile distance, and outliers are shown with circular markers. The switch between patently different patterns for motion and for force occurred very abruptly and before contact (the shaded box extending from -90 ms to -40 ms). *b*, The vector magnitude of the muscle coordination pattern was normalized by the mean magnitude for each trial during the first 200 ms of motion. This enabled an objective comparison of how the magnitude scaled over the time course of each trial. The vector magnitude was higher even for initial force production compared with the motion phase. Much like the switch in vector direction (*a*), this increase in vector magnitude started before contact. However, unlike the vector direction that started switching over 100 ms before contact, the vector magnitude started increasing less ~ 70 ms before contact.

for motion to that for static force resembles a nonlinear interpolation.

A mathematical analysis of the time course of the transition of muscle coordination patterns shows that there was necessarily a switch between mutually incompatible underlying neural control strategies: from one for finger motion to another for fingertip force production (for full details, see the supplemental material, available at www.jneurosci.org). By “incompatible” neural control strategies we mean incompatible with each other by virtue of each strategy being able to

meet only one set of mechanical constraints: either those for motion or those for force. Briefly, our analysis formalizes the following statement: given that the finger’s mechanical state and external constraints do not change as it approaches contact, a change in muscle coordination pattern necessitates a change in the underlying neural control strategy. That is, the switch in muscle coordination pattern is of neural origin because it cannot be explained by the mechanical transition at contact. The proof of this argument follows the *reductio ad absurdum* argument. If one assumes the underlying neural control strategy to be constant as the finger undergoes contact, then the resulting relationship among muscle coordination patterns directly contradicts our experimental finding that they change rapidly before contact. This result applies even when the underlying neural control strategy undergoes changes compatible with neural and muscle redundancy (e.g., changes in neural signals that do not affect the muscle coordination patterns). Importantly, this analytical conclusion holds for a general underlying neural control strategy that could, for example, encode either muscle forces directly, or other properties of the neuromuscular system like motoneuron excitability.

We also found that the abrupt switch in underlying neural control strategy polluted fingertip force vector direction beyond what is explained by muscle activation-contraction dynamics (Zajac, 1989), neuromuscular noise (Harris and Wolpert, 1998), and premotor planning (Sober and Sabes, 2005). We used two quantifiers of fluctuations in force production between $+10$ and $+65$ ms after contact (Fig. 3): peak angular deviation [$\phi_{\text{force}}(t)$] of the fingertip force vector from the vertical [$\max(\phi_{\text{force}})$] and its variance [$\text{var}(\phi_{\text{force}})$]. Repeated measured ANOVA found both $\max(\phi_{\text{force}})$ and $\text{var}(\phi_{\text{force}})$ to be significantly larger for the motion initial condition, and significantly and progressively lower for the “relaxed” and “preactivated” initial conditions (Fig. 3; highest *post hoc* pairwise p value < 0.018).

Importantly, our mechanical torque-driven planar index finger model found that switching between control strategies is time critical, and the likely source of pollution in force direction. Such force misdirection on contact is predicted to occur in this model even though the contact collision is ideally inelastic and the viscoelastic properties of the finger and force transducer are not present. If the switch in neural control strategy could occur instantaneously and exactly on contact (i.e., resembling an ideal step function at contact) the model predicted the fingertip force vector to be perfectly perpendicular to the surface immediately after contact (Fig. 4, origin). However, a more realistic sample simulation compatible with muscle excitation-contraction delays where the transition takes 35 ms to be completed and ends exactly at contact shows that the fingertip force misdirection at the instant of contact is at least 7° (Fig. 4), which is realistically compatible with our experimental results. Moreover, repeated iterations of the model show that the force vector misdirection is very sensitive to both the timing and duration of the transition. Force misdirection errors arise simply because transition duration and/or imprecise timing cause the finger to make contact in a posture different from the planned posture. Figure 4 underscores the time criticality of this switching in control strategies because even small (i.e., 10 ms) increases in both the onset and duration of the transition can lead to $>60\%$ increase of errors in initial force vector direction (Fig. 4) (e.g., vertical line at 35

ms). The effectiveness of compensatory strategies in the face of such time criticality is addressed in the Discussion.

Last, a necessary prediction of impedance control is that force output ($\|F\|$ shortly after contact) will systematically change with surface height. However, we saw no such systematic change in the catch trials where subjects tapped on the surreptitiously elevated/lowered surface ($n = 6$; $p = 0.93$) (Fig. 5).

Discussion

By recording EMGs from all muscles of the index finger, we found that muscle coordination patterns changed abruptly in a nonlinear, time-critical manner between characteristic motion and “force” patterns. Because this clear and abrupt transition occurred before contact could alter the finger’s mechanical condition, our mathematical analysis finds this necessarily reflects a switch between mutually incompatible underlying neural control strategies. Additionally, because force output did not vary systematically with surreptitious changes in the tapping surface height, we could directly rule out impedance control as the dominant form of control. Importantly, we find that this switch between underlying neural control strategies results in pollution of the initial fingertip force vector direction above and beyond neuromuscular noise or muscle activation-contraction dynamics. A mechanical index finger model found that these unavoidable errors in initial force direction are a consequence of the inability of the nervous system to switch instantaneously and exactly between incompatible control strategies. Thus, the physiological limitations of the neuromuscular system plus the time criticality of this switching in control strategies conspire to impose physical limits on the accuracy of force production on contact. We speculate that such a neurally demanding and time-critical strategy for the transition from the control of fingertip motion to force production may explain the existence of specialized neural circuits for the human hand.

Finding a switch between mutually incompatible underlying neural control strategies has important consequences to the study of motor control of the fingers. For human fingers, our findings challenge hypotheses like equilibrium point control that propose constant control strategies capable of bridging abrupt changes in mechanical constraints (Feldman, 1986; Bizzi et al., 1992; Gribble et al., 1998; Mussa-Ivaldi and Bizzi, 2000; Ostry and Feldman, 2003). A proposed advantage of equilibrium

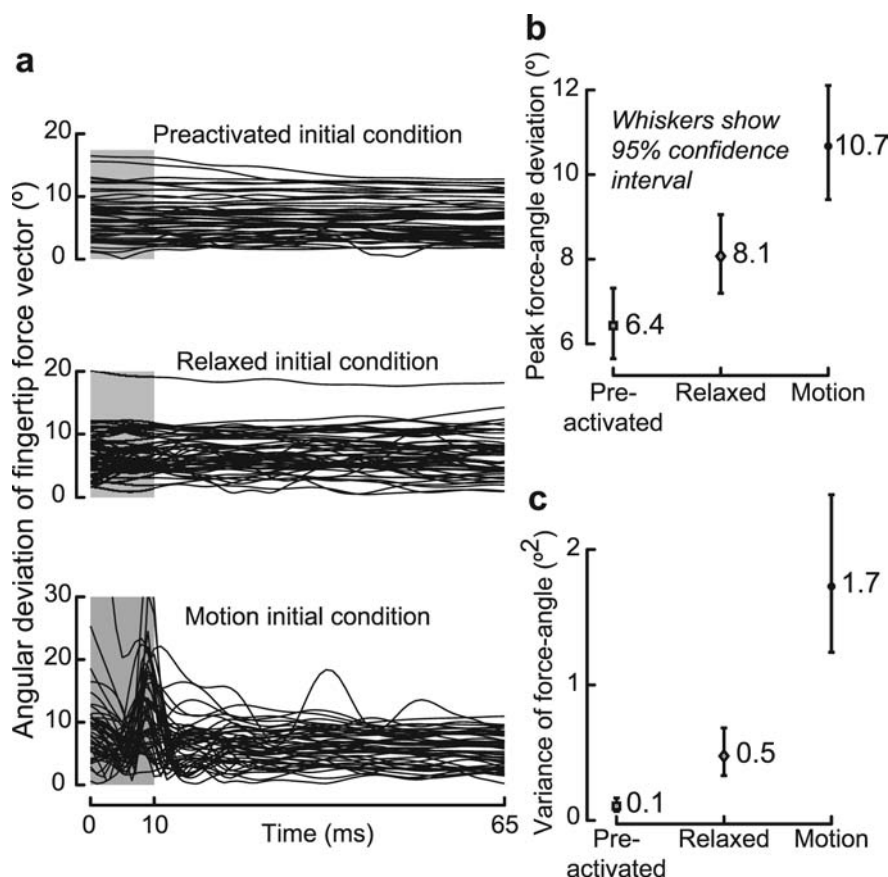


Figure 3. Fluctuations in direction of the fingertip force vector after finger contact. *a*, Force angle data [$\phi_{\text{force}}(t)$] from all subjects for all three initial conditions. The first 10 ms are grayed out and excluded for all analyses. Even for the remaining time segment, the force direction appears to fluctuate much more for the motion condition than for either the relaxed or preactivated conditions. The peak force angle deviation for the motion condition (blue) occurs around 8 ms. We are conservative in our analyses by excluding the first 10 ms because the force data were clearly reliable well before 8 ms (Fig. 1*a*, blue traces). *b*, The peak force angle deviation [$\max(\phi_{\text{force}})$] decreased from motion to relaxed to preactivated conditions. All differences were statistically significant. *c*, The variance in force direction [$\text{var}(\phi_{\text{force}})$] also decreased from motion to relaxed to preactivated conditions and all differences were statistically significant.

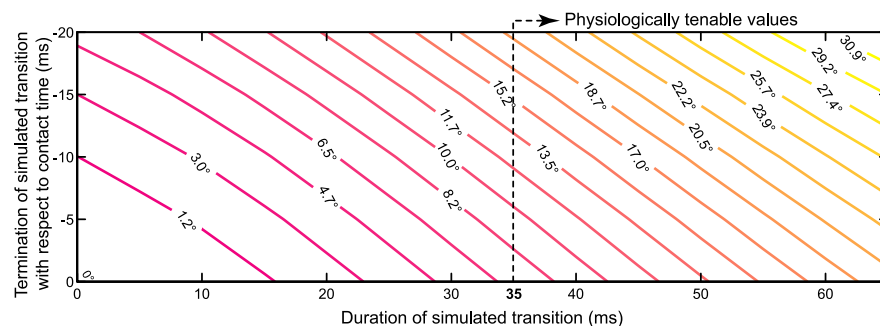


Figure 4. Simulations reveal that just muscle activation-contraction dynamics impose a physical limit on directional accuracy of the initial fingertip force vector on contact. The labeled contour lines show the misdirection of the initial fingertip force vector with respect to the surface normal. The abscissa shows the duration of the transition between the joint torque pattern for motion and that for force; and the ordinate shows inaccuracies in the timing of this transition, represented by its termination time with respect to contact time. For physiologically tenable values of transition duration (> 35 ms), the initial fingertip force vector is misdirected by at least 7°, and the misdirection increases by over 60% for every 10 ms increase in timing inaccuracy (contour values along vertical dotted line at 35 ms abscissa).

point control is that it can mediate transitions between posture and movement “automatically,” without the nervous system explicitly computing or actively controlling it (Ostry and Feldman, 2003). In contrast, our data and analysis show a clear example of

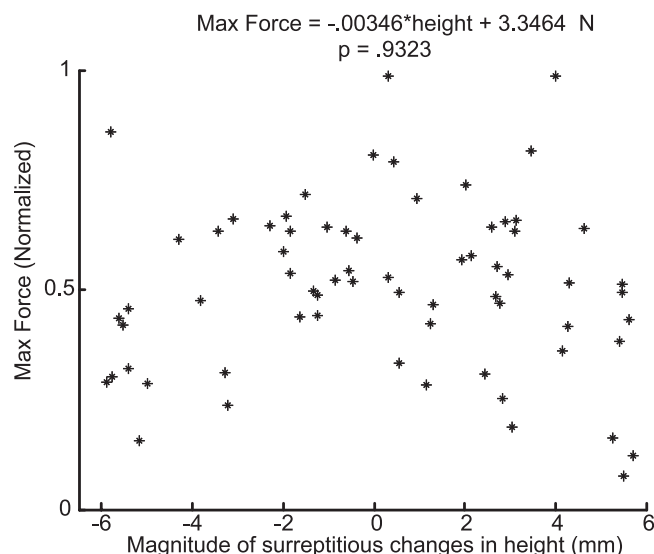


Figure 5. Simple impedance control was not observed. The peak fingertip force magnitude (ordinate) within 65 ms after contact (the first 10 ms excluded) did not change systematically with surreptitious changes in the surface height (abscissa). This shows that a simple impedance control strategy could not have been the dominant form of control for finger contact transitions.

the nervous system using a neurally demanding and time-critical switch between mutually incompatible underlying neural control strategies to transition from motion to force production. Independently of current debates on plausible control strategies, our results support the more fundamental idea that the neural control of the fingers fits well within the emerging framework of hybrid control systems characterized by dynamical systems subject to continuous controls and discrete transitions (Guckenheimer, 1995; Branicky et al., 1998).

Our results reveal that the time-critical transformation of the muscle coordination pattern vector before contact resembles a nonlinear transformation. We find that the change in the vector direction of the muscle coordination pattern is well underway at least 100 ms before contact (Fig. 2*a*). In contrast, the vector magnitude begins to change only within 70 ms of contact (Fig. 2*b*). A linear transformation would cause simultaneous and proportional scaling of both the vector magnitude and direction. Three possible explanations come to mind: (1) there exist neuro-musculo-skeletal constraints which prevent or bias against the implementation of a linear transformation (e.g., neural coupling, motoneuron pool spillover, anatomical coupling among finger musculature); (2) the limitations of EMG artifactually distort estimates of linearity of the transformation; or (3) a nonlinear path is conducive to reducing errors in the fingertip trajectory, the finger posture at contact and, hence, initial force production. We have previously presented fine-wire EMG evidence that the nervous system is able to control index finger muscles independently in a similar force production paradigm (Valero-Cuevas et al., 1998; Valero-Cuevas, 2000). This argues against neuro-musculo-skeletal constraints or EMG artifacts being the dominant explanation for the nonlinear transformation in our present data. By this process of elimination we speculate that, while the finger is still in motion, the nervous system reduces the deviation from the planned posture for contact by postponing the necessary increase in coordination pattern magnitude. Establishing whether this specific nonlinear transformation is task-optimal requires additional experimental and

modeling work that is beyond the scope of this first report of the phenomenon. The time criticality of this transformation is discussed below.

Our work extends current understanding of the control of finger musculature by showing that during abrupt transitions between neural control strategies, muscle physiology imposes physical limits to the accuracy of static force production on contact. Our simulations quantify the mechanical sensitivity of initial force direction to the duration and timing of the switch between mutually incompatible strategies (Fig. 4). That is, switching between mutually incompatible control strategies for motion and static force will unavoidably pollute force production after contact if not done exactly and instantaneously. For realistic switching durations constrained at a minimum by 35 ms of muscle activation-contraction dynamics (Zajac, 1989), deviations from a planned completion of the switching by even 10 ms increase force misdirection by >60% (Fig. 4, vertical line at 35 ms in duration). In the biological system, timing errors of ~10 ms are tenable given unavoidable neuromuscular noise (Harris and Wolpert, 1998) and physiological delays (Venkadesan et al., 2007). It is conceivable that the nervous system could plan joint torques for motion using compensatory strategies so that the finger lands in the planned contact posture. However, any such anticipatory motor planning does not, in practice, suffice to cancel out errors in initial force direction because it necessarily involves at the very least an accurate estimate of the time of contact with the surface. As mentioned above, even a 10 ms uncertainty in the estimate of contact time suffices to incur substantial errors in initial force direction of the magnitudes we saw experimentally. This may explain why our healthy and motivated subjects always exhibited a misdirected initial force. After this initial misdirection, musculoskeletal viscoelastic properties and sensory feedback control will undoubtedly take effect in the real finger and cause the observed force oscillations and subsequent refinement of force direction (Fig. 3).

Our experimental design allowed the disambiguation between mechanical, muscular and neural sources of inaccuracies of force production. Comparing across the motion, “preactivated” and “relaxed” initial conditions allowed us to directly identify fluctuations in force direction for the first 65 ms after onset as arising from switching between neural control strategies, as distinct from the effects of premotor planning and muscle activation-contraction dynamics. As previously shown by Valero-Cuevas (2000), the preactivated condition likely only requires scaling of the coordination pattern and is therefore only affected by neuromuscular noise. The relaxed condition, however, is additionally affected by the selection and implementation of the motor program (e.g., premotor planning plus muscle activation-contraction dynamics).

We now discuss the relationships of our findings to past work on anticipatory motor control, and the limitations of our approach. Multiple studies have characterized anticipatory control in the limbs of humans and animals (1) for smooth motion-force tasks for limbs subject to contacting [e.g., manipulanda experiments (Shadmehr and Mussa-Ivaldi, 1994; Lackner and DiZio, 2005)] and noncontacting [e.g., Coriolis force experiments (Lackner and DiZio, 2005)] force fields, (2) during abrupt postural perturbations associated with catching (Lacquaniti and Maioli, 1989; Lacquaniti et al., 1992), and (3) and animal studies of posture vs ground-reaction force control (Lacquaniti and Maioli, 1994) or posture versus movement control (Kurtzer et al., 2005). Our results agree with

their findings and conclusions to the extent that the nervous system can and does effectively anticipate changes in task constraints. In addition, the timing of the onset of anticipatory changes in EMGs of ~ 100 ms are similar to those found previously (Lacquaniti and Maioli, 1989). However, anticipatory control in our task is different from braking to mitigate a collision or from stiffening before catching. We did not observe any anticipatory braking because the goal of our task required a collision so as to be able to ramp up force production as rapidly as possible, as evinced by the spikes in vertical force at contact (Fig. 1a). To our knowledge, this is the first study to record complete muscle coordination patterns and full three-dimensional force vectors while fingertips abruptly contact a surface to produce static force. This enabled us to use careful mathematical analysis and mechanical simulations to (1) uncover the nonlinear nature of the anticipatory transformation of muscle coordination patterns, (2) detect the switch in the underlying neural control strategy, and (3) characterize the consequences of this switch to the accuracy of initial force production. Unlike previous reports, our conclusions are independent of any one specific theory of motor control (e.g., equilibrium point hypothesis, direct cortical control of muscles, etc.). We believe the limitations of our approach do not challenge the validity of our conclusions. Although the use of a custom-molded thimble may appear unnatural, its potential drawbacks are outweighed by the benefits of a well defined contact condition (e.g., fingernail length and shape, skin dryness). This has allowed us to obtain high-fidelity biomechanical recordings that can be well approximated by a model (Valero-Cuevas et al., 1998; Valero-Cuevas, 2000). In addition, the use of the thimble does approximate precision pinch acquisition of small, irregularly shaped or slippery objects. Other considerations point us to future studies such as the effect of lengthy practice on the neural strategy, or the inclusion of specialized populations such as microsurgeons or pianists. Similarly, the torque-driven model of the index finger can be further explored through parameter sensitivity analysis (Santos and Valero-Cuevas, 2006) or extended to include musculature, sophisticated control strategies, and contact collision models.

In conclusion, contacting a surface with the fingertip to produce static force requires (1) accurate prediction of when contact would occur and (2) time-critical switching between underlying neural control strategies. For these reasons, dedicated neural circuits are likely used for representation of motion and force similar to the observation for control of the arm in monkeys (Kurtzer et al., 2005). Interestingly, it is known that in humans direct corticospinal projections to the hand muscles are more prevalent than for the limbs (Scott, 2004). Therefore our results could provide a functional insight into an important evolutionary feature of the human brain: the disproportionately large sensory and motor representations of the hand (Penfield and Boldrey, 1937). If indeed the nervous system faced evolutionary pressures to precisely and anticipatorily control even routine tasks like rapid acquisition of precision pinch, the sensorimotor cortical representations of our fingers would naturally reflect those requirements for careful timing of motor actions and fine independent control of the finger muscles. Finally, our finding of the stringent sensorimotor demands of finger contact transitions might also help understand why precision pinch and finger tapping are skills that take years to develop in young children (Forssberg et al., 1991) and are so vulnerable to neurological degeneration and aging (Cole et al., 1998).

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Supporting Online Material for

Neural control of motion-to-force transitions with the fingertip

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Contents

- S1 Notation
- S2 Joint torques for producing motion and static force are mutually incompatible
- S3 Neuromuscular model of the index finger
 - S3.a Muscle forces and their relation to joint torques
 - S3.b Muscle forces arise from neural control signals and mechanics
 - S3.c Affine approximation
- S4 Proof of switching between mutually incompatible underlying neural control strategies
 - S4.a Validation of simplified affine model
 - S4.b Proof by *reductio ad absurdum*
- S5 Generalizing to include neural and muscle redundancy
 - S5.a Generalization by considering neural redundancy
 - S5.b Consideration of muscle redundancy

List of Figures

- S1 Schematic for a model of index finger tapping.
- S2 Schematic of the main experimental finding.
- S3 Summary of variables used in proof.

S1 Notation

Throughout this supplementary text, underlined variables are vectors and “hatted” variables are unit vectors. For example, $\underline{a}$ is a vector and $\hat{a}$ is its corresponding unit vector, i.e., $\hat{a} = \underline{a} / \|\underline{a}\|$. We use lower case, *italicized* letters for scalars and **boldface** for functions and operators.

S2 Joint torques for producing motion and static force are mutually incompatible

We saw from the main text (equations 1 and 2) how the production of free finger motion and well-directed static force production when in contact with a surface are produced by very different equations. As a consequence, at a given posture, the joint torque patterns for producing motion and static force are different from each other. Not only that, the two joint torque patterns are mutually incompatible, i.e., the torque pattern for producing motion in a specific direction cannot produce well-directed static force in the same direction and *vice versa*. Our experimental observation of starkly different muscle coordination patterns for motion and force is not surprising given that mechanics necessarily dictates different joint torques for motion and force.

S3 Neuromuscular model of the index finger

A dynamical model of the index finger is depicted in Fig. S1. It is necessary for our purposes to separate the various components—neural signals ($\underline{u}(t)$), muscle forces ($\underline{m}(t)$), joint torques ($\underline{\tau}(t)$), finger mechanical condition ($\underline{x}(t)$, a vector of joint angles φ , angular velocities $\dot{\varphi}$ and external forces $\underline{f}$), and external boundary conditions (contact or no-contact). We use a generic model, where the various transformations (e.g., $\underline{g}$ that generates muscle forces) could be as simple as linear functions or as complex as nonlinear differential equations. A simple torque-driven model was used in the main text (equations 1 and 2). Muscle models could be of various complexities. For example, a simple model of muscle could produce muscle

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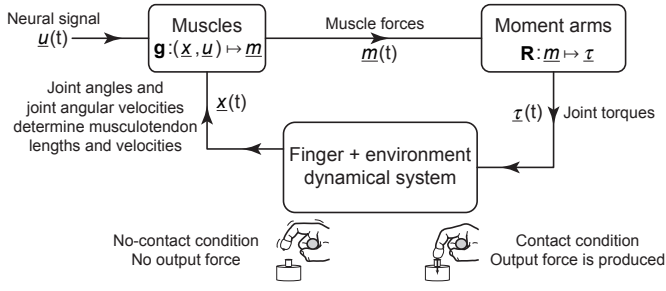


Fig. S1. Schematic for a dynamical model of index finger tapping. The model as shown is fairly generic. Each module ($\mathbf{g}$, $\mathbf{R}$, finger + environment dynamics) is in general a nonlinear dynamical system.

force linearly proportional to the neural signal, but nonlinearly dependent on musculotendon length and velocity (force-length and force-velocity properties of muscle (Zajac, 1989)). In contrast, if the neural signal did not encode muscle forces directly, but something like muscle equilibrium length or neural thresholds (Feldman, 1986, Gribble et al., 1998, Ostry and Feldman, 2003), the function $\mathbf{g}$ will be a relatively complicated and nonlinear function of both the neural signal as well as the musculotendon lengths and velocities.

Redundancy is built-in to typical models at both neural and muscular levels because $\dim(\mathbf{u}(t)) > \dim(\mathbf{m}(t)) > \dim(\boldsymbol{\tau}(t))$. A redundant neural system will allow for a null-space within which “preparatory” or “anticipatory” changes in the neural control signals can happen. For example, changes in the neural control signals would not manifest themselves as changes in muscle forces. Similarly, redundant musculature will allow for changes in muscle forces that will not lead to changes in the net joint torque.

S3.a Muscle forces and their relation to joint torques

Muscle forces are translated into joint torques by the musculotendon moment arms for each muscle about each joint. In general, it could be some nonlinear function of posture.

$$\boldsymbol{\tau}(t) = \mathbf{R}\mathbf{m}(t) \quad (\text{S3.1})$$

where, $\mathbf{R}$ is the moment arm matrix.

S3.b Muscle forces arise from neural control signals and mechanics

Muscle forces are not solely a consequence of either the neural signal or the mechanical condition of the finger ($\mathbf{x}$, i.e., $\varphi, \dot{\varphi}, f$). Rather, it is a function of both. Mathematically stated,

$$\mathbf{m}(t) = \mathbf{g}(\mathbf{x}(t), \mathbf{u}(t)) \quad (\text{S3.2})$$

where, $\mathbf{g}$ is a nonlinear function that can accommodate various types of controllers including direct control of muscle forces or joint torques (e.g., Todorov, 2000), motoneuronal threshold control (e.g., Ostry and Feldman, 2003), etc.

S3.c Affine approximation

We now simplify equation (S3.2) to a linear model. The Taylor series expansion for the function $\mathbf{g}$ about some nominal point ($\mathbf{x}_0, \mathbf{u}_0$) is,

$$\mathbf{g}(\mathbf{x}, \mathbf{u}) \approx \mathbf{g}(\mathbf{x}_0, \mathbf{u}_0) + \left. \frac{\partial \mathbf{g}}{\partial \mathbf{x}} \right|_{(\mathbf{x}_0, \mathbf{u}_0)} (\mathbf{x} - \mathbf{x}_0) + \left. \frac{\partial \mathbf{g}}{\partial \mathbf{u}} \right|_{(\mathbf{x}_0, \mathbf{u}_0)} (\mathbf{u} - \mathbf{u}_0) \quad (\text{S3.3a})$$

Let us consider first the special case where $\mathbf{x} = \mathbf{x}_0$. Then, the Taylor series approximation can be further simplified to,

$$\mathbf{g}(\mathbf{x}, \mathbf{u}) \approx \Psi \mathbf{u} + (\mathbf{g}(\mathbf{x}_0, \mathbf{u}_0) - \Psi \mathbf{u}_0) \quad (\text{S3.3b})$$

where,

$$\Psi = \left. \frac{\partial \mathbf{g}}{\partial \mathbf{u}} \right|_{(\mathbf{x}_0, \mathbf{u}_0)} \quad (\text{S3.3c})$$

Without loss of generality, we can set the constant term (not dependent on $\mathbf{u}$) to 0 in equation (S3.3b). Therefore, we are now left with the following simplified model that, at $\mathbf{x}_0$, maps the neural control signal to muscle forces when the control signal is close to some nominal signal $\mathbf{u}_0$.

$$\mathbf{m} = \Psi(\mathbf{x}_0) \mathbf{u} \quad (\text{S3.4})$$

To emphasize the dependence on mechanical condition, we only show the dependence of Ψ on $\mathbf{x}_0$, although it clearly also depends on $\mathbf{u}_0$.

S4 Proof of switching between mutually incompatible underlying neural control strategies

We show in Fig. S2 an abstraction of the main experimental finding of a switch in muscle coordination pattern before contact occurs. The finger’s mechanical condition is nearly identical

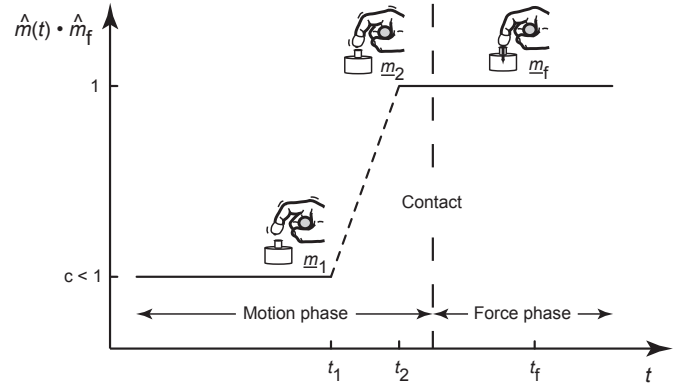


Fig. S2. This figure shows a schematic of the main experimental finding, namely, the muscle coordination pattern vector switches from that for motion to that for static force even before contact occurs. This schematic shows the vector dot product of the unit vector corresponding to the time-varying muscle coordination pattern with the unit vector of the reference muscle coordination pattern. The reference muscle coordination pattern is that which produces static fingertip force. The time-stamps and muscle coordination patterns of interest are indicated using the subscripts 1, 2, and f.

cal between t_1 and t_2 because we found experimentally that the transition happened rapidly (in less than 60ms). Therefore, we make the approximation that $\mathbf{x}_1 \approx \mathbf{x}_2$. Leading to, $\Psi(\mathbf{x}_1) \approx \Psi(\mathbf{x}_2)$. Call these Ψ_m (subscript ‘m’ for motion). Finally, suppose that $\mathbf{m}_1$, $\mathbf{m}_2$ and $\mathbf{m}_f$ are all generated by collinear neural control signals, i.e., there exists $\hat{\mathbf{u}}^*$ and scalars k_1 , k_2 , and k_f such that

$$\mathbf{u}_i = k_i \hat{\mathbf{u}}^*, i = 1, 2, f \quad (\text{S4.5})$$

Substituting these into equation (S3.4) and using appropriate Ψ ,

$$\underline{m}_1 = \Psi_m k_1 \hat{u}^* \quad (\text{S4.6a})$$

$$\underline{m}_2 = \Psi_m k_2 \hat{u}^* \quad (\text{S4.6b})$$

$$\underline{m}_f = \Psi_f k_f \hat{u}^* \quad (\text{S4.6c})$$

These relationships are succinctly summarized in Fig. S3.

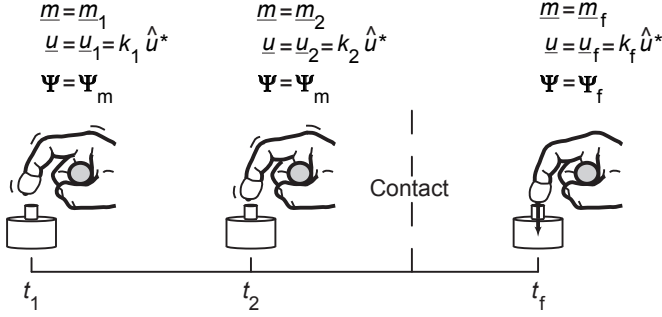


Fig. S3. This figure succinctly summarizes how various relevant variables and mappings change at each snapshot of the finger.

Finally, there are three relationships between muscle coordination patterns that we know to be true based on the experimental results (Fig. S2).

$$\hat{m}_2 \cdot \hat{m}_f = 1 \quad (\text{S4.7a})$$

$$\hat{m}_1 \cdot \hat{m}_2 = c \neq 1 \quad (\text{S4.7b})$$

$$\hat{m}_1 \cdot \hat{m}_f = c \neq 1 \quad (\text{S4.7c})$$

These equalities will be used below to show that the underlying neural control signal had to undergo a rapid switch as well.

S4.a Validation of simplified affine model

We first perform a validation of our simplified model to test whether it allows for a change in muscle coordination pattern without a change in the underlying neural control signal. Namely, whether equation (S4.7c) taken by itself can result from collinear underlying neural control signals (equations (S4.6a) – (S4.6c)).

$$\begin{aligned} \hat{m}_1 \cdot \hat{m}_f \neq 1 &\implies \hat{m}_1 \neq \hat{m}_f \\ \implies \frac{\cancel{k}_1 \Psi_m \hat{u}^*}{\cancel{k}_1 \|\Psi_m \hat{u}^*\|} &\neq \frac{\cancel{k}_f \Psi_f \hat{u}^*}{\cancel{k}_f \|\Psi_f \hat{u}^*\|} \\ \implies \left(\frac{\Psi_m}{\|\Psi_m \hat{u}^*\|} - \frac{\Psi_f}{\|\Psi_f \hat{u}^*\|} \right) \hat{u}^* &\neq 0 \\ \hat{u}^* &\notin \text{null} \left(\frac{\Psi_m}{\|\Psi_m \hat{u}^*\|} - \frac{\Psi_f}{\|\Psi_f \hat{u}^*\|} \right) \end{aligned} \quad (\text{S4.8})$$

It is in general possible to find such a $\hat{u}^*$ that satisfies equation (S4.8) because Ψ_m and Ψ_f are patently different from each other.

S4.b Proof by reductio ad absurdum

Consider the left-hand-side of equation (S4.7b) and substitute for $\hat{m}_1$ and $\hat{m}_2$ from equations (S4.6a) and (S4.6a), respectively. This enforces the assumption that the underlying neural

control signals are collinear (i.e., mutually compatible). This assumption leads to the following result.

$$\hat{m}_1 \cdot \hat{m}_2 = \frac{(\cancel{k}_1 \Psi_m \hat{u}^*) \cdot (\cancel{k}_2 \Psi_m \hat{u}^*)}{\cancel{k}_1 \|\Psi_m \hat{u}^*\| \cancel{k}_2 \|\Psi_m \hat{u}^*\|} = 1 \quad (\text{S4.9})$$

This is in direct contradiction with the experimental fact given in equation (S4.7b). Therefore, we can conclude that the motion and force phases of the task are accomplished by mutually incompatible underlying neural control strategies. $\square$

S5 Generalizing to include neural and muscle redundancy

S5.a Generalization by considering neural redundancy

Neural redundancy permits changes in the underlying neural control signal that do not reflect as changes in muscle coordination pattern, i.e., relaxing the collinearity assumption of Equation (S4.5). Symbolically stated, there exist ϵ_1 , ϵ_2 , and ϵ_f such that,

$$\epsilon_1 \in \text{null}(\Psi_m) \quad (\text{S5.10a})$$

$$\epsilon_2 \in \text{null}(\Psi_m) \quad (\text{S5.10b})$$

$$\epsilon_f \in \text{null}(\Psi_f) \quad (\text{S5.10c})$$

leading to,

$$\underline{u}_i = k_i \hat{u}^* + \epsilon_i, \text{ where } i = 1, 2, f \quad (\text{S5.11})$$

Clearly neural redundancy defined as above has no effect on the proof outlined in Section S4.b so long as ϵ_i are of small enough magnitude for our affine approximation to be reasonable. This is because, by substituting equations (S5.10a) – (S5.10c) in equations (S4.6a) – (S4.6c) it is readily seen that the steps presented in Sections S4.a and S4.b remain exactly unchanged.

S5.b Consideration of muscle redundancy

It remains to be shown that the changes in muscle coordination pattern between t_1 and t_2 were not merely a consequence of muscle redundancy with no effect on joint torques. This result is not immediately apparent because of the following reason. From equation (S3.1) we see that if two muscle coordination patterns $\underline{m}_1$ and $\underline{m}_2$ are such that their difference $\underline{m}_1 - \underline{m}_2 \in \text{null}(\mathbf{R})$, then, $\tau_1 = \tau_2$.

Recall that the moment arm matrix depends only on the posture (Valero-Cuevas et al., 1998, Valero-Cuevas, 2000) and not on the contact with the surface. Therefore the matrix $\mathbf{R}$ at times t_1 , t_2 , and t_f are all nearly identical. This in turn leads to,

$$\hat{m}_2 = \hat{m}_f \implies \hat{\tau}_2 = \hat{\tau}_f \quad (\text{S5.12a})$$

$$\text{Moreover, } \hat{\tau}_1 \neq \hat{\tau}_f \text{ cf. Section S2} \quad (\text{S5.12b})$$

$$\therefore \hat{\tau}_1 \neq \hat{\tau}_2 \text{ from equations (S5.12a) and (S5.12b)}$$

Hence we conclude the joint torques also switched before contact occurred. Therefore, the observed EMG switch does not reflect an anticipatory transition within the null-space of $\mathbf{R}$.

Acknowledgments

We thank Manoj Srinivasan and John Guckenheimer for discussions on the mathematical foundations presented in this note.

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