

Supporting Online Material for

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

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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 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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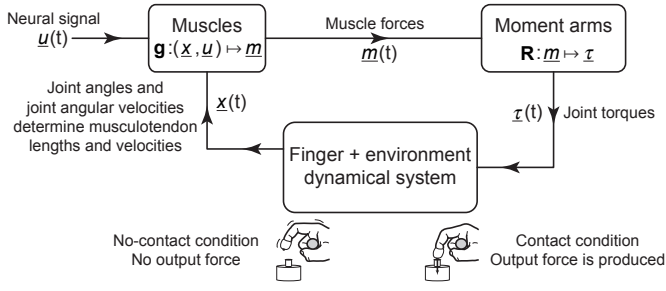


Fig. S1. Schematic for a dynamical model of index finger tapping. The model as shown is fairly generic. Each module (\mathbf{g} , \mathbf{R} , finger + environment dynamics) is in general a nonlinear dynamical system.

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 $\dim(\underline{u}(t)) > \dim(\underline{m}(t)) > \dim(\underline{\tau}(t))$. 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.

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

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 (\underline{x} , i.e., $\underline{\varphi}$, $\underline{\dot{\varphi}}$, \underline{f}). Rather, it is a function of both. Mathematically stated,

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

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 ($\underline{x}_0, \underline{u}_0$) is,

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

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

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

where,

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

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

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

To emphasize the dependence on mechanical condition, we only show the dependence of Ψ on \underline{x}_0 , although it clearly also depends on \underline{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 identi-

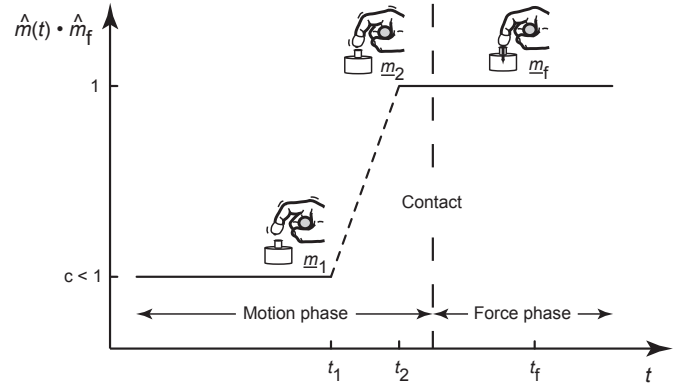


Fig. S2. This figure shows a schematic of the main experimental finding, namely, the muscle coordination pattern vector switches from that for motion to that for static force even before contact occurs. This schematic shows the vector dot product of the unit vector corresponding to the time-varying muscle 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 $\underline{x}_1 \approx \underline{x}_2$. Leading to, $\Psi(\underline{x}_1) \approx \Psi(\underline{x}_2)$. Call these Ψ_m (subscript ‘m’ for motion). Finally, suppose that \underline{m}_1 , \underline{m}_2 and \underline{m}_f are all generated by collinear neural control signals, i.e., there exists \hat{u}^* and scalars k_1 , k_2 , and k_f such that

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

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

$$m_1 = \Psi_m k_1 \hat{u}^* \quad (\text{S4.6a})$$

$$m_2 = \Psi_m k_2 \hat{u}^* \quad (\text{S4.6b})$$

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

These relationships are succinctly summarized in Fig. S3.

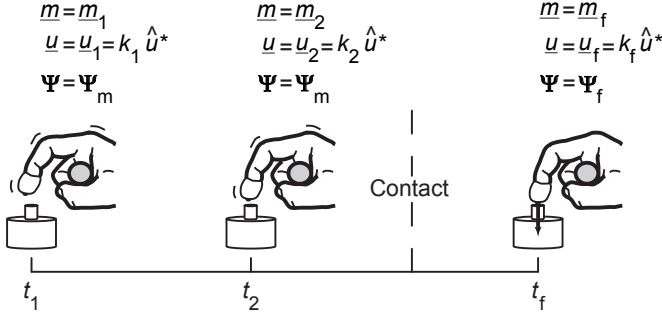


Fig. S3. This figure succinctly summarizes how various relevant variables and mappings change at each snapshot of the finger.

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)).

$$\begin{aligned} \hat{m}_1 \cdot \hat{m}_f \neq 1 &\implies \hat{m}_1 \neq \hat{m}_f \\ \implies \frac{k_1 \Psi_m \hat{u}^*}{k_1 \|\Psi_m \hat{u}^*\|} &\neq \frac{k_f \Psi_f \hat{u}^*}{k_f \|\Psi_f \hat{u}^*\|} \\ \implies \left(\frac{\Psi_m}{\|\Psi_m \hat{u}^*\|} - \frac{\Psi_f}{\|\Psi_f \hat{u}^*\|} \right) \hat{u}^* &\neq 0 \\ \hat{u}^* &\notin \text{null} \left(\frac{\Psi_m}{\|\Psi_m \hat{u}^*\|} - \frac{\Psi_f}{\|\Psi_f \hat{u}^*\|} \right) \end{aligned} \quad (\text{S4.8})$$

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.

$$\hat{m}_1 \cdot \hat{m}_2 = \frac{(k_1 \Psi_m \hat{u}^*) \cdot (k_2 \Psi_m \hat{u}^*)}{k_1 \|\Psi_m \hat{u}^*\| k_2 \|\Psi_m \hat{u}^*\|} = 1 \quad (\text{S4.9})$$

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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