Processes underlying unintentional finger-force changes in the absence of visual feedback

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Abstract

Previous reports show that the forces produced by the fingers of one hand drop exponentially over time in the absence of visual feedback on the forces. We study the force production by the index fingers of both hands with no visual feedback. Subjects produced a specified total force with a specific contribution from each finger by pressing on force sensors. We observed that in the absence of visual feedback: (1) the finger forces dropped with time by an amount proportional to the magnitude of the initial force. For low initial force values (< 7% of MVC of individual finger force), the finger forces showed an increase; (2) The total force (sum of finger forces) evolution showed similar features; (3) Finger forces changed in a way that facilitated more equitable force production by the two fingers; (4) All the force-time changes resemble exponential functions with similar time constants (~ 15 s). We propose that two processes interact to produce these patterns. (1) *RC back-coupling*: The central nervous system defines referent coordinates (RCs) for the digit tips, and the difference between the referent and actual coordinates leads to force production. If actual coordinates are not allowed to move to referent ones, referent coordinates show a slow drift toward the actual ones, leading to a force drop. (2) *Sensory adaptation*: This process, possibly related to sensory receptor characteristics, leads to an increase in finger force. RC back-coupling provides a common account of this and other reported phenomena of hand force or position changes across transient, external perturbations.

Introduction

It is well known that humans are not precise in force production tasks. During accurate force production with continuous visual feedback, there are small deviations of the force from the target level; however, when the visual feedback is removed, subjects show a slow decline of the force despite their attempts to maintain its magnitude (Shapkova et al. 2008; Slifkin et al. 2000; Vaillancourt & Russell, 2002; Vaillancourt et al. 2001). In particular, Vaillancourt and Russell (2002) showed that a specified force produced by the index finger drops exponentially when the visual feedback on the force magnitude is removed. In the present study, we aim to investigate the extent of this phenomenon. We study the force production characteristics of a two-element system under a variety of initial conditions (system state when the visual feedback disappears). Our other aim is to interpret the findings of this study and several previous works, including those of Vaillancourt and colleagues, within the framework of the referent-configuration (RC) hypothesis (Feldman 2009), which is the generalization of the equilibrium-point hypothesis (Feldman 1986) to multiple effectors.

Within the RC hypothesis, observed motor behavior results from the interaction of three factors: (1) the current configuration of the body, (2) the referent (desired) configuration of the body, and (3) the environment. Muscle activations (and thus, forces) emerge as a consequence of and in proportion to the difference between the *referent configuration* of an effector and its (current) *actual configuration*. The RC hypothesis thus views muscle activations as consequences of shifts of referent configurations rather than quantities that are explicitly specified by the central nervous system (See subsection ‘RC back-coupling hypothesis’ in the Discussion for more details). If the RC is attainable, the effector will reach an equilibrium state in that configuration and the muscle activation will be minimal. If the RC is not accessible to the effector because of anatomical and/or external constraints, equilibrium states of the involved effectors are observed with nonzero muscle activations and active forces produced by the effector on the environment. For example, in the task of producing a specified force with an index finger pressing on a sensor, the nervous system specifies a fingertip RC that is below the surface of the sensor (Figure 1A). The environment (sensor surface) provides an external constraint due to which the finger-sensor system achieves equilibrium with non-zero forces at the finger-sensor interface. Similarly, object grasping is achieved by specifying a referent aperture (Figure 1B), while holding a constant hand position against an external load is achieved by specifying a referent hand location displaced from the actual hand posture in a direction opposite to the external force (Figure 1C). An unexpected change in the external conditions, for example removal of the stop in an isometric force production task, would lead to motion of the effector to its referent coordinate (which remains unchanged if the subject is not reacting to the change) while all the muscle activations and forces would change.

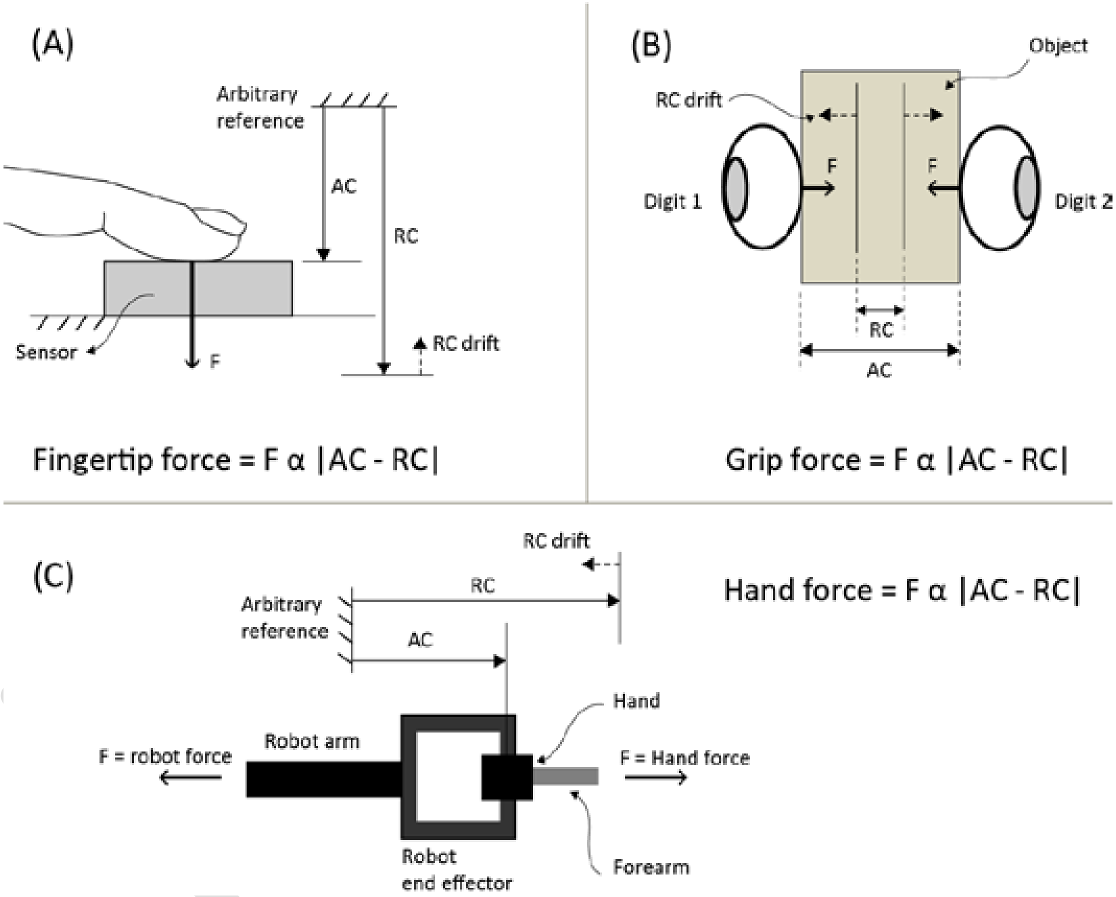

Figure 1. An illustration of the main ideas of the referent configuration (RC) and the RC back-coupling hypotheses. In each panel, force is generated by the effector in proportion to the difference between the nervous-system-defined RC and the effector's actual configuration (AC). The RC back-coupling hypothesis postulates, under certain circumstances (see text), a drift in the RC depicted in each panel. Such a drift will lead to a drop in fingertip forces in panels A and B, and a change in the system's steady-state configuration in panel C. Note that in each panel 'α' is the proportionality sign.

The above description is the traditional version of the RC hypothesis: an animal's intent to produce an action (movement and/or force generation) is transformed into changes in the RCs of relevant body parts. The actual body configuration (AC) is attracted to the changing RCs (coupled to it) with contributions of both reflex-mediated changes in muscle activation and length- and velocity-dependences of muscle forces. For the purpose of the present discussion, we address this process as "direct coupling". More details on the RC hypothesis can be found in Feldman (2009, 2011), Feldman and Latash (2005), and Latash (2010).

The traditional RC hypothesis, by itself, cannot explain the drift in finger forces reported by Vaillancourt and colleagues. In the traditional account, the AC always tracks the RC and never the other way around. Furthermore, in isometric, constant force-production tasks, the body part maintains its configuration, and the resultant force on the environment remains constant since the RC is also time invariant. It follows that if a force drop is recorded in isometric conditions, it must be the RC that shifted. Therefore, we augment the traditional RC hypothesis by proposing a phenomenon of *RC back-coupling*: When an actual effector configuration is obstructed from reaching the specified RC over a period of time, the RC drifts towards the actual configuration. This leads to changes in the steady-state equilibria of the body, which may be manifested as changes in interface forces. For example, in the case of the finger-pressing task illustrated in Figure 1A, the finger AC is prevented from reaching the RC. Therefore, over time, the RC begins to drift towards the finger AC. This leads to a drop in the finger force, since the finger force is assumed to be proportional to the difference between the two configurations. The term "back-coupling" is used to stress the role reversal between the actual and referent configurations of the effector. Note that both direct and back-couplings lead to minimization of the distance between the AC and the RC and, as such, move the system towards its minimal energy state.

Vaillancourt and Russell (2002) propose that the limited temporal capacity of the visuo-motor memory is responsible for the drop in finger force over time in the absence of visual feedback. That hypothesis and the RC back-coupling hypothesis are candidate accounts that could explain the observed force drops. The applicability of those accounts will be re-examined in the Discussion section after the results are reported.

In this paper, we investigate the robustness of the findings of Vaillancourt and colleagues by exploring the force changes in a variety of initial conditions. In particular, we investigate whether the force drops are observed in the case of multi-effector action. Towards these ends, we varied the force magnitude for both the total force and the relative contribution of individual fingers (we call this *force sharing*) at the time of visual feedback removal. The purpose of this manipulation was to explore whether force changes (if any) in an effector are driven by this effector's action or by the combined action of all the effectors as specified by the task. The limited temporal capacity hypothesis has not been previously applied to the case of multiple effectors. However, we make a prediction that the hypothesis applies uniformly to all involved effectors; we see no reason why limited temporal capacity of memory should discriminate between similar effectors. We used two hands instead of two fingers of the same hand to exclude effects of the enslaving between the fingers (Zatsiorsky et al. 1998, 2000). Finally, we explore the explanatory power of the RC back-coupling hypothesis using this experimental paradigm. Previous expositions of this hypothesis (see the 'Related phenomena' section in the Discussion) have always involved a single limb.

Our main hypothesis was that removal of visual feedback would lead to a drop in both the total force and the forces produced by the individual fingers. Based on previous studies, we hypothesized that after visual feedback removal: (H1) the force of each finger would drop in proportion to that finger's initial force. We expected these predictions to be robust to all initial conditions of total force and force sharing. We also explored whether the pattern of changes in the outcome variables is influenced by previous task conditions (history effects on finger forces have been demonstrated by Sun et al. 2011a,b). Therefore, various tasks (i.e. trials with different initial force sharing) in the experiment were performed in both randomized and non-randomized sequences.

Methods

Subjects

Three female and seven male right-handed subjects (mean age = 30.2 years, standard deviation = 3.2 years) participated in this study. All subjects were healthy and had no history of hand injury. All subjects provided informed consent in accordance with the procedures approved by the Office for Research Protection of The Pennsylvania State University.

Apparatus and procedure

Subjects were seated comfortably in a chair with their forearms resting on top of a table. They extended the index fingers of both hands and placed the fleshy part of the distal phalanx facing downwards on two separate sensors (Nano 17, ATI Industrial Automation, Garner, NC) as shown in Figure 2A. The diameter of the sensors was 17 mm, and the distance between the sensors was 30 mm. The mid-point between the sensors was aligned with the midline of the body. Sandpaper (100-grit) was placed on the contact surface of each sensor to increase the friction between the digits and sensors. This was done to prevent any digit-tip slip in the horizontal plane during the experiment. Only the forces exerted vertically downward were analyzed.

Twelve analog signals from the sensors (2 sensors × 6 components) were routed to an analog–digital converter (PCI-6031, National Instruments, Austin, TX). A customized LabVIEW program was used for the data acquisition at 100 Hz with 16-bit resolution and for subject feedback.

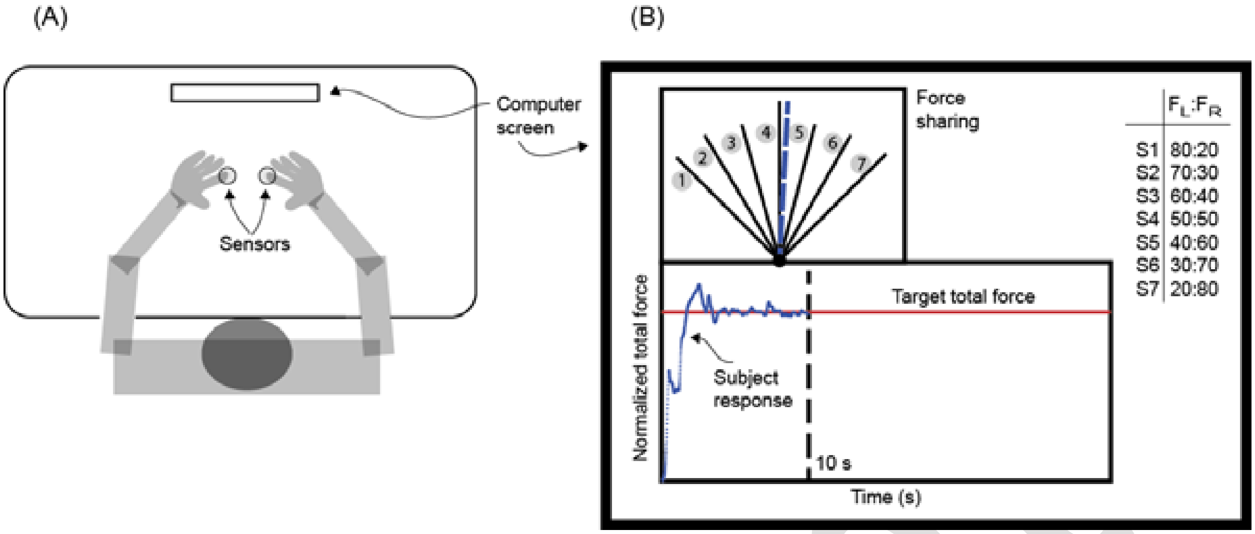

Figure 2. Experimental setup and visual feedback provided to the subject. Figure (A) shows the subject's pose and the force sensors. In Figure (B), $\boldsymbol{F_L}$and $\boldsymbol{F_R}$ represent the left and right finger forces, respectively. In the 'Force sharing' panel, the inclined lines numbered from 1 to 7 correspond to force sharings ($\boldsymbol{F_L}$: $\boldsymbol{F_R}$) from S1 to S7, respectively

First, subjects performed three trials with maximum voluntary contractions (MVC) to produce the highest forces they could manage using both fingers simultaneously. The trials were performed in sequence with 30-s rest intervals. The trial with the maximum total force of the three trials was chosen, and that maximum total force value and the maxima of the individual finger forces during that trial were considered as the MVCs. Visual feedback of the total force was provided using a computer screen placed directly in front of the subjects.

Figure 2B shows the visual feedback provided to the subject during the main task. A horizontal solid line indicated the desired total force level. Also shown was a solid inclined line indicating the desired sharing ratio. As the subject pressed on the two sensors, the total force appeared on the screen as the trace extending to the right over time, and the finger force ratio appeared as a dashed line. This dashed line was vertical when the finger forces were equal (the sharing ratio was 50:50), it tilted towards the left if the left finger force share was larger, and to the right if the right finger share was larger. The subjects had 10 s to match both the total force with the target line, and the desired sharing ratio by matching the dashed and solid inclined lines. The vertical dashed line in the total-force feedback panel indicated the 10-s mark after which the total finger force trace disappeared, and the dashed line representing the subject's sharing ratio froze. So, starting from this instance the subjects had feedback neither on the total force nor on the sharing. The subjects were instructed to 'continue producing the same finger forces' for an additional 20 s.

The left-finger, right-finger, and total forces are denoted as F_L, F_R, and F_T, respectively. Furthermore, we use the term '*Force sharing*' to indicate the force sharing ratio between the two fingers. There were three force levels of F_T (15%, 25%, and 35% MVC) and seven *Force sharings* equally spaced between $F_L\colon F_R = 80\colon 20$ (Force sharing 1, or S1) to $F_L\colon F_R = 20\colon 80$ (Force sharing 7, or S7) (see Figure 2B). The trials were block randomized across subjects for levels of total force. A selected force level remained in effect across two blocks of trials in which the Force sharings were first presented in a non-randomized order and then in a randomized order. For the non-randomized block, the task presentation order was 1-2-3-4-7-6-5-4. The objective was to look for differences in performance of the task with Force sharing S4 ($F_L\colon F_R = 50\colon 50$) when it is approached from the left-heavy (S1) and from the right-heavy (S7) directions (history effects). The non-randomized trials were performed first to avoid the occlusion of history effects by potential effects of learning. Each task lasted 30 s, and each subject performed 45 trials [8 Force sharings × 3 force levels (non-randomized) + 7 Force sharings × 3 Force levels (randomized)]. Subjects were required to ask for rest if they felt fatigued. Ten-minute breaks were enforced after each 35% MVC block.

Data analysis

MATLAB programs were written for data analysis. The vertical finger forces were filtered using a low-pass, zero-lag, fourth order, Butterworth filter with cutoff frequency of 5 Hz. No statistical difference in either the net change in any variable or the rate of that change was observed between the randomized and non-randomized trials (statistical details are provided in the Results section). So, the two (three for task S4) repetitions of each task were averaged. Each subject thus had 21 averaged time series for each force variable, which were subjected to further analysis.

The task variables, total force and force sharing, were computed from the finger forces as

$$F_T = F_R + F_L$$

$$F_S = \frac{F_L}{F_R + F_L}$$

There were 42 finger force traces for each subject (21 conditions × 2 fingers). The time *t* evolution of each finger force normalized by its MVC value (henceforth referred to as *elemental variable*) was modeled using an exponential function of the form

$$F_i(t) = a_i e^{\frac{-t}{\tau_i}} + c_i \qquad (1)$$

where $i = \{L, R\}$. Note that at the time of feedback removal (t = 0), the variable value is given by $F_i(0) = a_i + c_i$, and at the steady state (t = ∞), it is $F_i(\infty) = c_i$. Thus, the coefficients a_i and c_i represent the net change $[F_i(0) - F_i(\infty)]$ and the steady-state value of the modeled variable, respectively, and τ_i is the time constant describing the rate of that change.

A higher value of coefficient a_i implies a greater temporal change in the modeled variable. In the Results section, statistical results for coefficients a_i and τ_i are presented, and those for c_i are not presented because the net drop in the force variables (which is our main outcome variable) is defined only by a_i, not by c_i. For example, according to the postulated hypothesis, a higher value of coefficient a_i is expected when the initial value of the finger force is larger.

Statistics

Most data are presented as means ± standard errors (SE). The coefficients of the exponential fits to the elemental variables, i.e. finger forces normalized by the corresponding MVCs (F_L, F_R), were subject to a three-way, repeated-measures ANOVA with factors *Finger* (two levels: Left and Right), *Force-Level* (three levels of initial total force: 15%, 25%, 35% MVC of F_T) and *Sharing* (seven levels corresponding to the initial force sharings S1 to S7). To investigate the history effects, the coefficients of the exponential fits for the equal-force-sharing task were subjected to a two-way, repeated-measures ANOVA with factors *Task* (three levels: Randomized, Left-heavy, and Right-heavy), and *Force-Level* (three levels). Comparison of the *Task* conditions provides a test for the history effects.

All statistics were performed using an α-level of 0.05. Mauchly's sphericity tests were performed to verify the validity of using repeated-measures ANOVA. The Greenhouse–Geisser adjustment to the degrees of freedom was applied whenever departure from sphericity was observed. Significant effects of ANOVA were further explored using pairwise comparisons with Bonferroni corrections. All statistics were performed with SPSS statistical software.

Results

Temporal changes in the elemental variables (F_L and F_R)

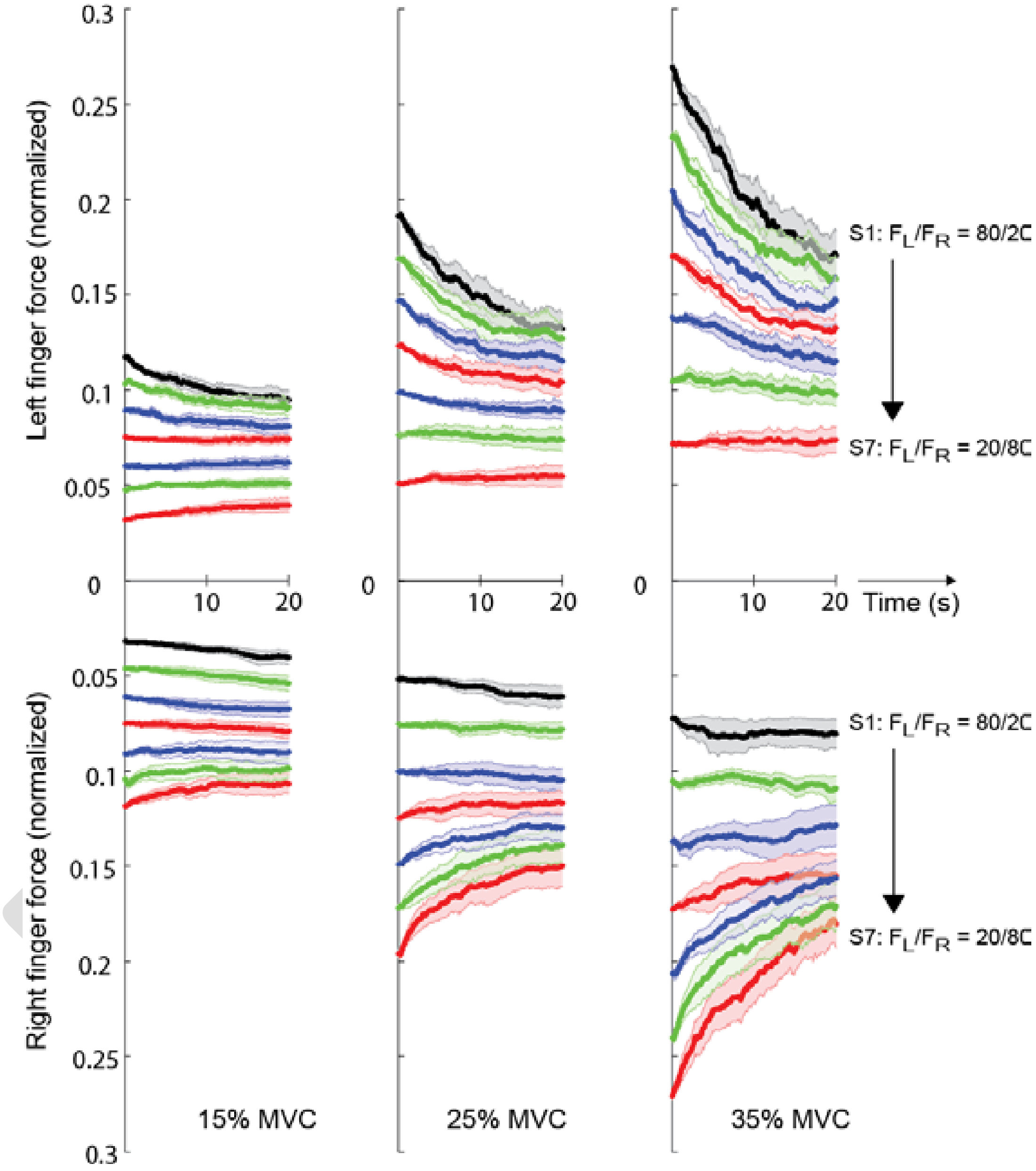

Figure 3. Mean ± SE of the finger forces normalized by the respective finger MVC are plotted on common time axes. The right finger forces are plotted on an inverted Y scale. For a given MVC level, one trace from each panel makes up one task. The traces in each panel start with force sharing S1 on the top and continue to force sharing S7 at the bottom. For example, the top trace for the left-finger 15% MVC level and the top trace for the right-finger 15% MVC level together represent force sharing S1 with sharing ratio $F_L : F_R$ = 80:20. The traces are for the 20 s without visual feedback

After the visual feedback was turned off, the subjects typically showed a drop in the finger forces with time across all *Force-levels* (15%, 25%, and 35% of MVC) and all *Sharings* (from S1 to S7). These results are illustrated in Figure 3, which shows averaged across subjects time profiles of individual finger forces (with standard error bars) over the 20-s time interval during which the subjects had no visual feedback. However, for low initial force magnitudes, the finger force tended to show an increase with time. Such a trend was typically seen for trials with the initial force values up to about 7% of MVC. Low finger force was required for the highly unequal sharings ($F_L : F_R =$ 20:80, 80:20, etc.).

The exponential function ($F_i(t) = a_i e^{\frac{-t}{\tau_i}} + c_i,\ i = \{L, R\}$) approximated the normalized finger force time changes reasonably well. The median of the R^2 values of all fits was 0.91 and the interquartile range was 0.27. The rates of force decay (reflected in τ_i) were invariant across all tasks and across both fingers. The three-way ANOVA on the time constant revealed no significant effects, and so mean ± SE of the time constant is τ = 14.97 ± 1.02 s.

The coefficients a_i (net change in the normalized finger forces) changed in proportion to the *Force-Level* ($F_{(1.285,11.565)} = 55.784$; $p < 0.01$). Overall, there was a net drop in the normalized finger forces ($a_i > 0$), and post-hoc analysis showed that this drop increased with the *Force-Level* ([0.00 ± 0. 005] for 15% MVC < [0.023 ± 0.008] for 25% MVC < [0.052 ± 0.01] for 35% MVC). Coefficient a_i also changed with *Sharing* ($F_{(6,54)} = 3.841$; $p < 0.01$), however pairwise comparisons did not reveal any pair with a significant difference. A significant interaction *Finger* × *Sharing* ($F_{(2.808,25.273)} = 62.022$; $p < 0.01$) reflected the fact that the left finger-force drop decreased as the initial *Sharing* changed from S1 ($F_L : F_R$ = 80:20) to S7 ($F_L : F_R$ = 20:80), and the right finger-force drop showed the exact opposite trend. There was also a significant three-way interaction ($F_{(12,108)} = 16.596$; $p < 0.01$) because the interaction *Finger* × *Sharing* varied across *Force-Level*: As *Force Level* increased, a_i became more positive for all *Sharings* by different amounts for the left and right fingers. Finally, the net force drop in the left finger was significantly greater than that in the right finger ($[a_L = 0.033 \pm 0.0007] > [a_R = 0.018 \pm 0.0083]$) ($F_{(1,9)} = 11.668$; $p < 0.01$).

Temporal changes in the task variables (F_T and F_S)

Figures 4 and 5 show the time evolution of the total force F_T and the sharing ratio F_S. These figures provide two observations worth noting. First, the total force does not show an increase in its magnitude over time for low initial values in contrast to the individual fingers (Figure 4). Second, the sharing ratio tends to converge to a value between 0.5 and 0.4 (Figure 5). This observed convergence of the sharing ratio corresponds well to the sharing ratio computed using the MVC values (F_{S-MVC} = F_{L-MVC} / F_{T-MVC}; mean ± SE = 0.45 ± 0.006). This fits the general idea that a preferred sharing pattern tends to be used as a default across various tasks.

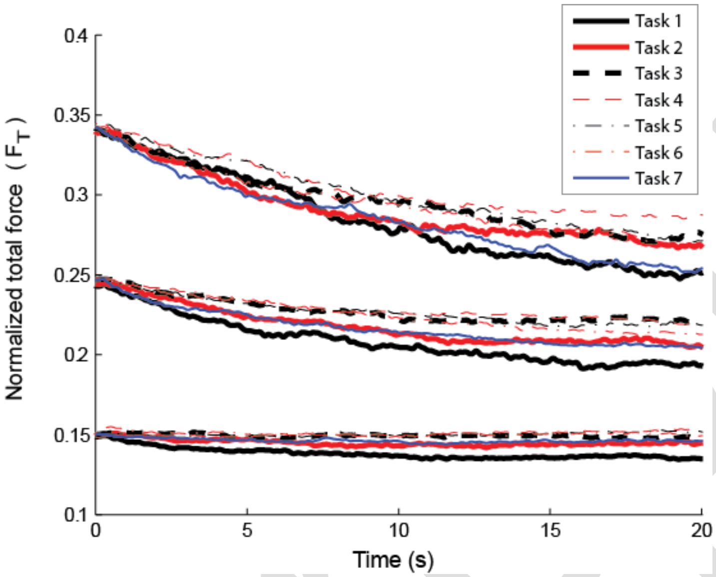

Figure 4. The across-subject mean of the total force F_T. The SE bars for F_T are omitted for clarity. The traces are for the 20 s without visual feedback

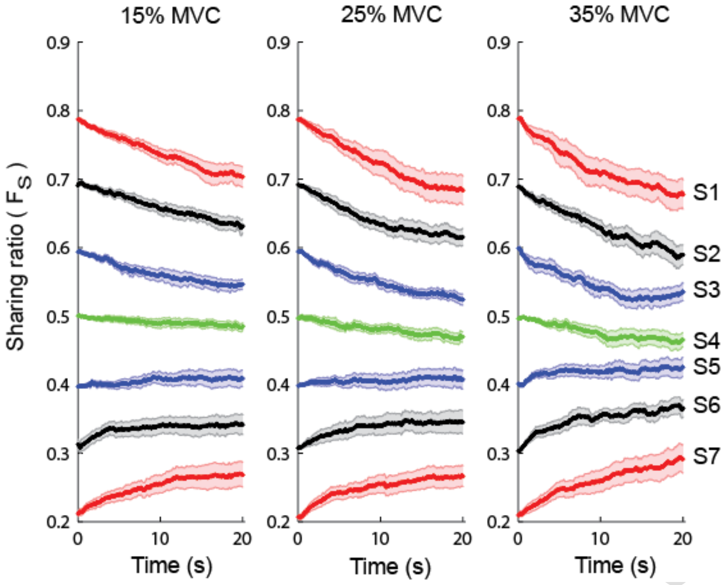

Figure 5. The across-subject mean ± SE of the force sharing ($\boldsymbol{F_S}$) plotted against time. The traces are for the 20 s without visual feedback

Finger-force behavior for the equal-force-sharing task: History effects

The data revealed no history effects in the dynamics of the finger forces for the equal force-sharing task: Both finger forces changed in a similar fashion for this task whether it was part of a random sequence or if it was approached from the left-heavy or right-heavy sharing pattern. The two-way ANOVA revealed no significant main effect of *Task* for any of the coefficients. Particularly, for the net change in the finger forces: left finger (a_L): $F_{(2,18)} = 0.166; p = 0.849$; right finger ($a_R$): $F_{(2,18)} = 0.37; p = 0.696$. For the time constants: left finger (τ_L): $F_{(2,18)} = 0.7; p = 0.509$; right finger ($\tau_R$): $F_{(2,18)} = 0.07; p = 0.932$.

Additionally, there were no significant *Trial* × *Force-Level* interactions for any variable.

Discussion

Our main hypothesis formulated in the Introduction was validated, but only in part. Furthermore, the following findings should be emphasized. (1) In the absence of visual feedback the individual finger forces typically dropped with time, and this drop was proportional to the magnitude of the force produced when the feedback was turned off. However, for low initial force values, the finger forces showed an increase. (2) In contrast, the total force always dropped with time in the absence of visual feedback, and this drop was proportional to the magnitude of the force produced when the feedback was turned off. (3) The sharing ratio changed with time in a way that facilitated more equitable force production by the two fingers. All the force variables showed dynamics that were reasonably well fitted by exponential functions with a time constant of ~ 15 s. The other coefficients of the functions showed systematic variations across task specifications.

Some of these results can be described as a tendency of the two forces towards an arithmetic mean. Our main purpose, however, is to provide explanations to our observations based in physiology and physics. Towards this end, we accepted the framework of the RC hypothesis (Feldman 2009) and complemented it with the idea of RC back-coupling (see Introduction). While the RC back-coupling hypothesis provides explanations for several different experimental observations including the drift in finger and total forces (for most cases) in the present paper, our data suggests that an additional process may be involved.

Based on our results, we hypothesize that there are two distinct processes that interact and influence finger force changes in absence of visual feedback: (1) *RC back-coupling*: A drift of the RC (referent configuration) towards the actual one that tends to decrease the finger force, and (2) *Sensory adaptation*: A process that contributes to an increase in finger force, possibly related to haptic feedback characteristics. Below, we elaborate on each of these processes. We imagine both processes contributing simultaneously to generate the overall trend and variability in the behavior under various initial conditions of force sharing ratio and total force level.

Factors influencing individual finger force evolution

Vaillancourt and Russell (2002) propose that the limited temporal capacity of the visuo-motor memory is responsible for the drop in finger force over time in the absence of visual feedback.

Both increase and decrease in finger force at high and low force levels, respectively, can be explained by this hypothesis. However, we observed a smooth transition from force increase to force decrease as initial force level increased across trials. This suggests that there exists a range of initial forces wherein the change in finger force over time will be close to zero. This can be seen for individual finger forces in Figure 3 for the force levels of about 0.07-0.08 % MVC, and also for the total force in Figure 3 for the 0.15 % MVC task. The hypothetical memory limitation should be applicable irrespective of initial force levels. Indeed, the limited memory explanation, in its current form, fails to explain why the force levels did not change significantly at low initial forces in the data of Vaillancourt and Russell (2002). In addition, one could expect memory limitation to affect forces produced by both fingers in a similar way. This was not the case, however. Individual finger forces could show counter-directional changes or one finger force could stay unchanged while the other would show a large drop. This suggests that mechanisms that define finger force behavior are finger and task specific. To account for our data, the hypothesis must be augmented by positing a “default force level” for which motor memory is more stable compared to all others. Furthermore, the memory limitation must treat effectors differently and be influenced by the task. We see no clear reason, however, why certain force levels or different effectors should be affected differently by memory. These ideas remain largely speculative.

(1) The RC back-coupling hypothesis

An alternative explanation of the finger-force drop is offered by the RC hypothesis (Feldman 2009). The RC hypothesis assumes that the neural control of movement may be adequately described as a time shift of referent values for a set of task-specific variables related to the body configuration. This is achieved by sending sub-threshold depolarization signals to neuronal pools, which effectively change the differential between the membrane potential and the threshold for action potential generation. These neurons also receive excitation related to the discrepancy between the referent and actual values of the task-specific variables. As long as this signal is non-zero, it leads to neuronal activity which drives the hierarchically lower structures. For example, if a task requires hand movement to a point in space, referent hand coordinates will be defined at the task level. Further, they will be transformed into RCs at the joint levels and then into the muscle level where the RCs correspond to thresholds of the tonic stretch reflex (l , as in the classical equilibrium-point hypothesis, Feldman 1986). Each of these transformations is few-to-many (redundant). When actual body configuration reaches the RC, the signal related to the difference in the AC and RC becomes zero, and neuronal activation stops; the system comes to rest in a low-energy state. This scheme leads naturally to inter-trial adjustments of RCs at lower levels organized in a synergic way to stabilize RCs at the task level (Latash 2010).

Within the RC hypothesis, changes in RC drive changes in muscle activations and in the actual body configuration; this may be addressed as *direct coupling* (RC acting as an attractor for actual body configuration) acting at relatively short time delays that are typical of reflex feedback loops. A few recent studies (see the ‘Related phenomena’ section) have suggested back-coupling between the RC and the AC that leads to a drift in RC if it is kept away from the actual body configuration for a relatively long time (Wilhelm et al. 2013; Ambike et al. 2014). We call it *RC back-coupling* (please note that this notion is different from the back-coupling introduced by Latash et al. 2005 and Martin et al. 2009). RC back-coupling is a hypothetical neural mechanism which drives not the AC to the RC (direct coupling) but the RC towards the AC.

The hypothesized RC back-coupling process seems to function over longer time scales. The time constants in this study were larger (~ 15 s) compared to the time scales of spinal reflex loops (on the order of tens of milliseconds). One rationale for RC drift is that when the RC differs from the actual body configuration, and changes in the AC are blocked, net muscle forces are being produced that do not lead to movement. Such isometric force production may be viewed as wasteful, and reducing these forces may be a way to avoid fatigue.

Another feature of the RC back-coupling is that the RC does not move all the way to the actual configuration. In our experiment, this was illustrated by the fact that the force drops were exponential with non-zero saturation values. Perhaps the RC drift stops when the muscle forces reach a sufficiently low value to avoid fatigue accumulation. It is plausible that the RC will drift in different directions under various conditions. For example, it is difficult to predict which way the RC will drift (if at all) when an external perturbation pushes the AC towards the RC.

(2) Sensory adaptation as a possible mechanism of the force-time changes

While RC drift may explain the drop in finger forces at high force magnitudes, it cannot account for the observed force increase at low force levels. These observations suggest the action of another factor leading to an unintentional motion of the RC away from the AC. We suggest that this factor may be related to *sensory adaptation:* a drop in the activity of pressure-sensitive receptors in the fingertip. Note that slowly-adapting receptors (such as Merkel disks and Ruffini corpuscles) show a slow exponential drop in their firing rate during an ongoing, constant deformation. Iggo and Muir (1969) show a two-stage adaptation of the Merkel cell receptor firing rate to a constant external deformation of the fingertip. Stage 1 adaptation has an exponential time constant of about 0.5 s during which the inter-spike interval increases significantly and also becomes more variable. The process continues in Stage 2, but with a longer time constant (10-20 s). Additionally, the firing rates of the Merkel cells may be small for low initial forces to begin with (note that the external deformation is proportional to the force developed at the fingertip). For example, a 0.2 N force exerted on a fingertip with a flat surface (like the sensors used in the present experiment) produces an average firing rate of 2 spikes/s over a period of 2 s (Gardner et al. (2000)). In the present experiment, these processes may lead to a loss of sensation of fingertip pressure at low forces, and the subjects could unintentionally increase the force to restore the expected level of sensory feedback associated with meeting the requirement.

The two hypothetical processes, RC back-coupling that tends to decrease finger force and sensory adaptation that tends to increase it, are active under all conditions and act against each other. At low forces levels, the sensory adaptation process dominates, while RC back-coupling dominates at high force levels. For some optimal initial finger force, the two processes cancel each other, and there is no deviation in the finger forces over time. These hypotheses remain speculative and need experimental confirmation.

Temporal changes in the task variables

Figure 4 shows that the total force drops for high initial values, but remains relatively unchanged for low initial values. This suggests that for these trials, the increase in force of one finger was compensated by the drop in force of the other finger which was initially producing a higher force. An increase in the total force might be seen if both fingers were required to produce low initial forces, but we did not explore such conditions. The distinctive convergent pattern in the sharing ratios evident in Figure 5 is striking. Note that while the task variables are unambiguously related to the elemental variables (finger forces), i.e., the sharing ratio for a given subject is determined by the behavior of her individual fingers, the across-subject behavior of the sharing ratio is non-deterministic. While one subject may show the patterns seen in Figure 5, other subjects may possess finger characteristics (the parameters a_i and t_i, for example) that define a different evolution pattern for the sharing ratio. Therefore, this across-subject regularity may reflect a drive to equalize the moment about a horizontal axis along the anterior-posterior direction passing through the center of the body. This is a version of the idea of minimization of secondary moments (i.e., moments not constrained by the task requirements) for bilateral force production tasks. The principle states that there exists a drive that tends to equalize the moment of force with respect to a horizontal axis in a sagittal plane (Li et al. 1998). This has been confirmed for two-hand tasks (Li et al. 2001).

Related phenomena

We believe that the RC back-coupling hypothesis has a wider applicability than isometric force production. Phenomena similar to the finger-force drifts in the absence of visual feedback were observed in a series of force–production and position-holding experiments that used transient perturbations, suggesting that RC back-coupling may be accentuated by external perturbations. First, Wilhelm et al. (2013) asked subjects to produce a specified total force by pressing with four fingers of the right hand. The authors removed visual feedback on total force, and then perturbed one finger by smoothly raising and then lowering it to its initial position. They observed a larger drop in the total force at the end of the perturbed trials compared to the drop observed in unperturbed control trials. Second, Ambike et al. (2014) imposed smooth, transient perturbations of the grip aperture while subjects “naturally” grasped an object using the prismatic grasp (the thumb opposing the four fingers). The grip aperture was smoothly increased and then decreased to the initial configuration. The grip force after the perturbation was significantly lower than that before the perturbation. Finally, Zhou et al. (2014) used a robot to impose transient perturbations on the position of the subject’s hand. In the initial steady state, the hand was maintained at a constant position against a robot-applied, constant bias force. The robot then applied a smooth force perturbation (increase-hold-decrease), such that the robot force returned to its initial bias value. At the end of the perturbation, the hand came to a final steady-state position that undershot the initial steady-state position.

Within the RC hypothesis, producing fingertip force is achieved by specifying a referent fingertip position (Figure 1A), object grasping is achieved by specifying a referent aperture (Figure 1B), while holding a constant hand position against an external load is achieved by specifying a referent hand location displaced from the actual hand posture in a direction opposite to the external force (Figure 1C). In all three cases, the effectors cannot reach their RCs due to either the external constraints and/or the task requirement (e.g., to hold a position). The resulting equilibrium states of the fingertips and the hand involve non-zero forces being exerted on the environment. In all three cases the AC was driven further from the RC by the external perturbation which led to an RC drift.

Two characteristics of RC-back coupling observed in the present study were also observed by Zhou et al. (2014): the slow nature of the drift (time constant ~ 1 s) compared to the typical time scale of spinal reflex loops, and a partial drift of the RC - up to 50% of the total hand excursion caused by the change in the external load. In these experiments, the hand was held by a robot in a perturbed position, and when the perturbation was removed, the hand moved only partly towards its original, unperturbed location, presumably due to a RC drift during the perturbation dwell time. However, this RC drift was limited, and the hand always moved towards the original position even after being held in the perturbed position for several seconds (up to 9 s). Partial drifts in the RC were also observed by Wilhelm et al. (2013) and Ambike et al. (2014).

Reinkensmeyer and colleagues (Reinkensmeyer et al., 2009; Secoli et al., 2011) suggested the concept of ‘*slacking*’ as the property of the human motor system to continuously decrease levels of muscle activation when movement error is small. Slacking was observed while practicing arm and gait movements with robotic assistance after neurologic injury when subjects sometimes reduced their effort in response to external assistance. Wolbrecht et al. (2008) have altered rehabilitation strategies based on these observations. Slacking and RC back-coupling seem to be related; perhaps slacking is a manifestation of RC back-coupling in the robot-assisted-rehabilitation setting. A better understanding of the phenomenon of RC back-coupling in the healthy population may potentially assist in the assessment of recovery during rehabilitation.

Concluding Comments

We have shown that the phenomenon of finger-force drift in the absence of visual feedback is robust to variation in the initial conditions, and it generalizes to a case of multi-effector action. While we did not observe history effects in the finger-force drifts: the behavior is unaffected by previous tasks, we have shown that the phenomenon is more complex than previously thought. The results have led us to propose the two-factor hypothesis to explain finger-force drifts in the absence of visual feedback of those forces: RC back-coupling + sensory adaptation. This two-factor hypothesis may apply across a few different phenomena: the drifts in isometric finger forces (Shapkova et al. 2008; Slifkin et al. 2000; Vaillancourt & Russell, 2002; Vaillancourt et al. 2001) as well as changes in the grip force (Ambike at al. 2014) and hand position (Zhou et al. 2014) when exposed to relatively long-lasting transient perturbations. While the cited studies have reported phenomena explained by the RC back-coupling phenomenon (see Figure 1), the effects of sensory adaptation have not been examined in those studies. We are currently working on these issues.

Finally, we acknowledge a few shortcomings of the present study. First, the hypothesis on the role of sensory system remains speculative. Second, because we used a limited set of conditions, the generalization of the conclusions is limited. It remains unknown whether similar temporal patterns will be observed in other force production tasks, e.g. with the fingers of the same hand or by different effectors, such as two elbows or two knees, or asymmetrical tasks (force generation with elbow + finger). The potential role of fatigue also remains unclear. We tried to limit our tasks to those that were not expected to lead to fatigue. Earlier fatigue studies (Singh et al. 2012) suggest that much higher forces are needed to produce measurable fatigue of flexor muscles that contribute to the fingertip force. Additionally, there was no observable fatigue effect across trials: The force change over twenty seconds did not show any pattern across trial number for any subject (data not provided). We conclude that muscle fatigue plays little or no part in the emergence of all relevant temporal patterns in various variables seen in this study.

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