Published in final edited form as:

Neuroscience. 2017 May 14; 350: 94–109. doi:10.1016/j.neuroscience.2017.03.022.

Unintentional force changes in cyclical tasks performed by an abundant system: Empirical observations and a dynamical model

Sasha Reschechtko¹, Fariba Hasanbarani^{1,6}, Vladimir M. Akulin^{2,3,4}, and Mark L. Latash^{1,5}

¹Pennsylvania State University, University Park PA 16802, USA

²Laboratoire Aimé Cotton, 91405 Orsay, France

³Laboratoire Jean-Victor Poncelet, CNRS, Moscow, 119002, Russia

⁴Institute for Problems of Information Transmission, Moscow, 127994, Russia

⁵Moscow Institute of Physics and Technology, Dolgoprudny, 141700, Russia

⁶University of Tehran, Tehran, Iran

Abstract

The study explored unintentional force changes elicited by removing visual feedback during cyclical, two-finger isometric force production tasks. Subjects performed two types of tasks at 1 Hz, paced by an auditory metronome. One – Force task – required cyclical changes in total force while maintaining the sharing, defined as relative contribution of a finger to total force. The other task – Share task – required cyclical changes in sharing while keeping total force unchanged. Each trial started under full visual feedback on both force and sharing; subsequently, feedback on the variable that was instructed to stay constant was frozen, and finally feedback on the other variable was also removed. In both tasks, turning off visual feedback on total force elicited a drop in the mid-point of the force cycle and an increase in the peak-to-peak force amplitude. Turning off visual feedback on sharing led to a drift of mean share toward 50:50 across both tasks. Without visual feedback there was consistent deviation of the two force time series from the in-phase pattern (typical of the Force task) and from the out-of-phase pattern (typical of the Share task). This finding is in contrast to most earlier studies that demonstrated only two stable patterns, in-phase and out-of-phase. We interpret the results as consequences of drifts of parameters in a dynamical system leading in particular to drifts in the referent finger coordinates toward their actual coordinates. The relative phase desynchronization is caused by the right-left differences in the hypothesized drift processes, consistent with the dynamic dominance hypothesis.

Address for correspondence: Mark Latash, Department of Kinesiology, Rec.Hall-267, The Pennsylvania State University, University Park, PA 16802, USA, tel: (814) 863-5374, fax: (814) 863-4424, mll11@psu.edu.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

Keywords

force drift; cyclical action; relative phase; hand dominance

Introduction

Unintentional changes in motor behavior have been documented over a range of actions including unperturbed continuous force-production trials (Slifkin et al., 2000; Vaillancourt and Russell, 2002), in response to transient force perturbations (Wilhelm et al., 2013; Zhou et al., 2014), and over repeated trials (Heijnen et al., 2012, 2014). In this context, we use the expression “unintentional movement” for consistent drifts in characteristics of motor action, not limited to increased motor variability, that supposedly use the same neural mechanisms as intentional voluntary actions (see below and Latash 2016). For example, when a person is asked to maintain accurate constant force by a fingertip under visual feedback and then the feedback is removed, a slow drift in force (typically decreasing) is observed (Vaillancourt and Russell, 2002). A similar, but much faster, drift is observed when the fingertip is subjected to a transient mechanical perturbation (Wilhelm et al., 2013; Reschechtko et al., 2014). During rhythmical force production tasks, turning visual feedback off results in a quick increase in the force peak-to-peak amplitude superimposed on a slower drift in the mid-point of the force cycle toward lower magnitudes (Ambike et al., 2016a).

Most of the aforementioned studies explored tasks performed by a single effector, e.g., pressing by a single finger. In contrast to such experiments, natural actions involve large (abundant, Latash, 2012) sets of effectors, which may be characterized by their overall output (such as total force) and the sharing pattern of the output among the effectors (such as fraction of total force produced by each effector, Li et al., 1998). In multi-finger tasks, the drift in the overall performance is accompanied by a drift in the sharing toward a preferred pattern (Ambike et al. 2015), possibly reflecting an optimization principle (Parsa et al., 2016b).

These observations have been interpreted within the idea of the neural control of movements with time changes in referent coordinates (RCs) for salient variables (reviewed in Latash, 2010; Feldman, 2015). According to this scheme, a sequence of few-to-many transformations converts a relatively low-dimensional set of spatial RCs at the task-specific level into a higher-dimensional set of RCs for the involved elements such as digits, joints, and muscles. Physiologically, the concept of RC reflects subthreshold depolarization of a corresponding neuronal pool. For a single muscle, this corresponds to depolarization of the alpha-motoneuronal pool, which defines threshold of the tonic stretch reflex, as in the classical equilibrium-point hypothesis (Feldman, 1966, 1986, 2015). Within this scheme, the drift in performance during an isometric finger-pressing task is a consequence of a drift of RC for the fingertip toward its actual coordinate (which is unchanged in isometric conditions), possibly with a contribution from a drift in the apparent stiffness (Latash and Zatsiorsky, 1993). This hypothetical mechanism, addressed as RC-back-coupling (Zhou et al., 2014; Ambike et al., 2015), has received experimental support in recent studies of performance drifts in multi-finger force-moment production tasks (Parsa et al., 2016a,b).

The present paper both reports the results of several experiments involving two-finger tasks and suggests a dynamical model for finger RC (and consequently force) drift during two-finger cyclical force-production tasks. The model, described in detail in a later section, represents changes in RC for each finger as the output of a non-linear oscillator. RC-back-coupling is assumed to attract the RC value – associated with setting the midpoint of the force cycle – toward a preferred value, typically closer to the actual fingertip coordinate. The amplitude of the cyclical process is assumed to be attracted to a preferred magnitude. When visual feedback is available, the effects of these drifts are corrected; however, they can be observed when the visual feedback is turned off. In cyclical tasks in which a metronome imposes rhythmicity, we assume that there are phase adjustments to synchronize points of force reversal with metronome beats. We also assume that the dynamics of the hypothesized processes differ for each finger; this supposition reflects the dynamic dominance hypothesis (Sainburg, 2002), which predicts better stability of steady-state actions in the non-dominant hand compared to the dominant hand (confirmed in Park et al., 2012; Parsa et al., 2016a,b).

A large body of literature has addressed unintentional changes in the relative phase during actions by two effectors, which could be observed with a slow increase in the action frequency (reviewed in Schöner and Kelso, 1988; Kelso, 1997). Models with coupled non-linear oscillators have been used to describe these phenomena as well as some other salient features of behavior. In contrast, the purpose of our model is to describe *unintentional* changes in behavior that can be seen in the absence of changes in action frequency. Moreover, the model and the data show phase desynchronization between the two finger forces in the absence of vision-based corrections.

We asked the subjects to perform two types of cyclical tasks in isometric conditions while paced by the metronome. All tasks involved pressing with the two index fingers, which were selected because they are the most accurately controlled fingers (Li et al., 1998; Gorniak et al., 2008). The main tasks were the *Force* task and the *Share* task. During the *Force* task, the subjects were required to produce cyclical changes in total force (F_{TOT}) while keeping the sharing (S , relative amount of F_{TOT} produced by a finger) within a narrow range. During the *Share* task, the subjects were asked to produce cyclical changes in S while keeping the magnitude of F_{TOT} within a narrow range. As a result, the *Force* task required the subjects to change finger forces in-phase, while the *Share* task encouraged them to change finger forces out-of-phase. After the subjects stabilized their performance under visual feedback on both variables (S and F_{TOT}), visual feedback was turned off for the variable that was instructed to remain constant (S for *Force* task and F_{TOT} for the *Share* task) and then, after some time, visual feedback on the other variables was also turned off. The subjects were always instructed to “continue doing what you have been doing” throughout the trial.

Based on earlier studies, we predicted that turning off visual feedback for F_{TOT} would lead to an increase in the F_{TOT} amplitude and a drop in the mid-point of the F_{TOT} cycle (Hypothesis 1, cf. Ambike et al., 2016a). We also expected that turning off visual feedback for S would lead to a drift in S toward a preferred sharing pattern (expected to be nearly 50:50; Ambike et al., 2015; Hypothesis 2). No previous studies have explored changes in S during cyclical tasks. However, given that changes in S are a reflection of changes in individual finger forces and that the peak-to-peak ranges of the forces were expected to

increase, an increase in the peak-to-peak S was predicted (Hypothesis 3). The model predicted a possibility of phase desynchronization between the two fingers; based on this prediction, we expected to see development of elliptical trajectories on the force-force plane after visual feedback was completely turned off (Hypothesis 4).

Experimental Methods

Subjects

Ten healthy young adult subjects (5 female; 25 – 32 years of age) participated in the present study. All subjects self-identified as right-handed based on their hand use during eating and writing, and had no history of hand injuries or neurological disorders that would interfere with the hand function. All subjects provided informed consent in accordance with procedures approved by the Office of Research Protections at The Pennsylvania State University.

Apparatus

For the experimental procedure, subjects used both of their index fingers to press on two multi-axis force/torque transducers (Nano 17, ATI Industrial Automation, Apex, NC). Each sensor operated in a networked force/torque system (Net F/T, ATI Industrial Automation), which transmitted force and torque values to the data collection computer at a rate of 1000 samples per second. Depending on the experimental condition (see the next section), subjects were provided with visual feedback on total force (F_{TOT}) produced by both fingers and/or the fraction of force produced by one finger (share, S). Subjects produced cyclical F_{TOT} or S profiles while being paced by an auditory metronome. The surface of each sensor was covered with 320-grit sandpaper to provide high friction. The experimental setup is illustrated in the left panel of Figure 1.

A custom application developed in the LabVIEW programming environment (National Instruments, Austin, TX) displayed feedback and logged data for subsequent offline analysis.

Experimental procedure

Subjects performed two types of tasks: *Force* tasks and *Share* tasks. These tasks refer to whether subjects were instructed to vary the amount of F_{TOT} produced by both fingers (Force task) while keeping S constant, or to vary S while maintaining the same level of F_{TOT} (Share task). We define F_{TOT} as $F_L + F_R$ (where F_L and F_R are forces produced by left and right index fingers, respectively) and S as F_R/F_{TOT} . On the feedback provided to the subjects, changes in F_{TOT} moved the cursor vertically on the screen (upward indicated larger magnitude of F_{TOT}), while changes in S moved the cursor horizontally (left or right according to which finger was producing a greater proportion of F_{TOT}). For the Force (Share) tasks, the vertical (horizontal) line served as a static template (see Fig. 1). The rectangle surrounding this template indicated an acceptable boundary of performance error, i.e., permissible deviation of the non-instructed variable, S in the Force task and F_{TOT} in the Share task. We chose to center the task at all times due to pilot studies in which the horizontal position of the cursor on the screen appeared to bias sharing pattern. During ideal

cyclical F_{TOT} force production, the cursor would move vertically in the center of the screen while during ideal cyclical S production, the cursor would move horizontally in the center of the screen.

During the Force task, subjects were instructed to produce a cyclical profile of F_{TOT} ranging from 8 N to 16 N for male subjects and 7 N to 13 N for female subjects. These levels of force were chosen based on pilot trials to avoid fatigue across different conditions. In the Force tasks, three S conditions were used: 0.33, 0.5, and 0.67. For each of these conditions, the feedback on the screen during task performance was unchanged: centering the feedback constituted the required S condition. The middle panel of Figure 1 shows a schematic of visual feedback for the Force task with three hashed circles at the bottom of the screen, each representing the starting point for one of the three sharing conditions. For the first 8 s of each trial, subjects were given feedback on both F_{TOT} and S ; for the next 15 s (8–23 s after trial onset), subjects received feedback only on F_{TOT} because feedback on S was frozen at the ideal performance level. Finally, for the last 15 s of the trial (23–38 s), subjects received no visual feedback on both F_{TOT} and S because the cursor disappeared.

During the Share task, subjects followed a similar instruction to that in the Force task, except they were required to change S in a cyclic fashion while maintaining F_{TOT} levels of 12 N or 10 N (for male and female subjects, respectively). The amplitude of the instructed cyclical S pattern was 0.3, and, as in the Force task, there were three initial sharing conditions around which subjects produced this cyclical profile: 0.33, 0.5, and 0.67 (where each fraction refers to the quotient F_L/F_{TOT}). Feedback was centered on the screen for all initial S conditions by translating the starting point horizontally. The right panel of Figure 1 presents a schematic of visual feedback in the Share task illustrating the three possible starting points for the cursor. As in the Force task, feedback was provided on both F_{TOT} and S for the first 8 s, only on S for the next 15 s (by freezing the cursor's vertical movement at the level of desired performance), and no feedback was provided for the last 15 s. During all tasks and conditions, the subjects were instructed to continue producing the same finger force time profiles at all times: "Continue doing what you have been doing".

In all tasks, subjects were paced by an auditory metronome set at 2 Hz, such that subjects would produce maximal and minimal values of F_{TOT} or S on consecutive beats, for a cycle frequency of 1 Hz. The metronome remained on throughout each trial. Subjects performed blocks of 5 trials for each condition, for a total of 15 trials in the Force task and 15 trials in the Share task. The order of initial S conditions within a task was randomized, while the order of tasks themselves (Force and Share) was balanced across subjects. Subjects were provided with 10–30 s rest intervals between trials (as requested), and 120 s rest intervals were imposed between conditions and tasks. Prior to the analyzed trials for each task and each condition, subjects performed 5 practice trials. These practice trials were 30 s long and performed with continuous visual feedback on both F_{TOT} and S for the entire duration of the trial. The primary objective of this procedure was to familiarize the subjects with the force manipulations required to move the cursor in the prescribed direction; during pilot testing, we were surprised by the difficulty subjects had performing these seemingly easy tasks. This practice may also have conditioned the subjects to rely on the visual feedback; this issue is addressed in more detail in Discussion.

Data analysis

Data processing was performed offline using MATLAB (The MathWorks Inc., Natick MA). Before further analysis, all data were low-pass filtered using a zero-lag 4th-order Butterworth filter at 10 Hz. Further quantitative analyses were performed on pairs of complete cycles in each of three time windows: 5.5–8 s (before any feedback was removed), 20.5–23 s (when only non-task feedback was removed), and 33.5–36 s (when no feedback was available) after trials began. These time windows will subsequently be called Phase-1, Phase-2, and Phase-3, respectively. Phase-3 was slightly before end of the trial (33.5–36 s instead of 35.5–38 s) because subjects occasionally stopped force production early in anticipation of the end of the trial. Cycles were defined by identifying every other time that the demeaned value of F_L crossed 0. For each subject and each *Task* (Force, Share) $\times$ *Initial Sharing* (0.33, 0.5, 0.67) combination of conditions, the following quantities were calculated in each phase.

Root-mean-square error (RMS) was computed as a metric of how well the subjects followed the prescribed F_{TOT} or S pattern. Two cycles of a template F_{TOT} or S sinusoid were generated with appropriate amplitude and period, and the RMS difference between the actual signal and this reference was computed. Sometimes subjects did not precisely follow the metronome – and, as such, the two identified cycles took somewhat more or less than 2 s. In such a case, the signal was compared to the template over the actual signal duration only. For example, performance of a subject performing two cycles in 1.9 s was compared to 1.9 s of the 1 Hz template, whereas a subject producing two cycles in 2.1 s would be compared to 2.1 s of the 1 Hz template signal.

In addition to computing RMS for three Phases in the test trials, we compared Phase-1 RMS in the test trials to the RMS computed for the same time period in the practice trials for each subject. During Phase-1, comparison between test and practice trials is straightforward because subjects had equivalent feedback (on both F_{TOT} and S) during this time in both practice and test trials. This comparison was carried out to investigate the effect of practice on subjects' ability to perform the task with full feedback.

Mean F_{TOT} and S was computed for both Force and Share tasks, yielding the outcome variables F_M and S_M , respectively. The peak-to-peak amplitude of both F_{TOT} and S were also computed and are subsequently referred to as F_A and S_A .

Similar analysis was performed with respect to the individual finger forces, F_R and F_L . For both tasks, average mean and peak-to-peak force values were computed over the three phases.

We also analyzed the phase relation between F_R and F_L using two methods. First, we computed the eccentricity of the ellipse drawn by the finger forces on the $\{F_R; F_L\}$ plane. On that plane, two directions can be identified corresponding to the two tasks. The Force task required no change in S , which corresponded to motion along a line with positive slope corresponding to in-phase changes in F_R and F_L , while the Share task required no change in F_{TOT} , which corresponded to motion along a line with negative slope of 45° corresponding to anti-phase changes in F_R and F_L . Hence, we quantified peak-to-peak deviations along those two directions over the cycles selected within the three Phase (Phase-1, Phase-2, and

Phase-3). The eccentricity index was computed as the ratio of the mean peak-to-peak deviation along the prescribed direction (normalized by its instructed magnitude) to the mean peak-to-peak deviation along the non-prescribed direction (normalized by the magnitude instructed when it was the prescribed direction). This was done for both the Force task (E_F) and Share task (E_S).

We computed the phase lag between the $F_R(t)$ and $F_L(t)$ over the cycles in Phase-1, Phase-2, and Phase-3 separately. This was done by computing the cross-correlation function between the two finger force time series, $F_R(t)$ and $F_L(t)$, at each of the three windows of analysis, and expressing the time delay corresponding to the peak of this function in phase units.

While we performed statistical analysis on phase lag between fingers during a few cycles as described above, we also computed continuous relative phase to observe the general changes in phase relation over the course of the trial. We computed continuous relative phase according to the methods suggested by Lamb and Stöckl (2014). Briefly, for each trial, each finger's phase portrait (from 2.5–35 s after trial initiation) was centered and relative phase was subsequently computed for each trial by subtracting the phase angle – obtained by finding the Hilbert transform of the centered data – of the right hand from that of the left hand. For each trial, relative phase values were averaged in 1-s bins; these bins were then averaged across all trials of a given task/initial sharing condition.

Statistics

Unless otherwise stated, all data are presented in the text and figures as means $\pm$ standard errors. To test the first three specific hypotheses, ANOVAs with repeated measures (using a mixed-model approach) were used to explore changes in the main characteristics of F_{TOT} and S (F_A , F_M , S_A , and S_M) across the phases and as functions of the initial sharing conditions. The main factors were *Task* (Force and Share), *Phase* (1, 2, and 3), and *Initial Sharing* (1:1, 2:1, and 1:2). We also explored the differences between the right and left finger force changes with the factor *Finger* (right and left). To address the fourth hypothesis, cross-correlation was used to quantify the phase lag between the two finger forces, followed by ANOVA on the time delay of the peak of the cross-correlation function. After running ANOVAs, significant effects of factors with more than two levels were further explored with pairwise contrasts with Bonferroni corrections. All statistical tests were run in SAS 9.4 (The SAS Institute Inc, Cary, NC). We assume statistical significance when $p < 0.05$.

Results

General patterns of performance

After five practice trials, subjects were able to perform the tasks with acceptable accuracy. RMS deviations during the last two cycles before turning off visual feedback were not affected by the initial sharing condition for either task while under full visual feedback. Across all task and sharing conditions, these deviations averaged $34.56 \pm 3.27\%$ of the task magnitude (6 or 8 N in the Force task or 0.3 in the Share task) by the end of practice.

Visual feedback was turned off in two steps in each trial. The first step (turning off feedback on F_{TOT} in the Share task and on S in the Force task) resulted in a consistent drift in the

variable deprived of the feedback. In the Share task, the midpoint of the F_{TOT} drifted to lower values, while the amplitude of the force cyclic changes increased. In the Force task, S drifted toward 0.5 when the initial sharing conditions differed from 0.5 (0.33 and 0.67). Turning off the feedback on the task-related variable (S in the Share task and F_{TOT} in the Force task) caused drift in both variables. Across conditions, the midpoint of the force cycle drifted to lower values while its amplitude increased; S drifted toward 0.5, while the peak-to-peak amplitude of changes in S increased.

Figure 2 illustrates typical performance by a representative subject using time series of $F_{TOT}(t)$ and $S(t)$ (solid gray and dashed black lines, respectively). The times when visual feedback was manipulated are shown with dashed vertical lines. Note the visible drifts in both $F_{TOT}(t)$ and $S(t)$ compatible with the described pattern.

Figure 3 illustrates the same data in the force-force space (x-axis: left finger force; y-axis: right finger force). The task is shown by a black bar with a circle in the middle corresponding to the required midpoint values of F_{TOT} and S . The blue trajectory shows the performance during the initial time interval (Phase-1) when full visual feedback was available. The dashed green line shows the performance after turning one of the feedbacks off, and the red line shows the performance after both feedbacks were turned off. Note that the described trends in the two performance variables were associated with the emergence of elliptical trajectories on the force-force plane suggesting a consistent phase lag between the individual finger force time functions. When individual finger forces approached zero, the elliptical trajectories became distorted and started to resemble triangles.

Analysis of drifts in task variables, F_{TOT} and S

To explore the drifts in the two task-related variables, F_{TOT} and S , we quantified these variables with two parameters, the mean value over a cycle (F_M and S_M) and the peak-to-peak amplitude over a cycle (F_A and S_A). Figure 4 shows averaged across subjects magnitudes of these four parameters at the end of Phase-1 (full visual feedback), at the end of Phase-2 (feedback on S only in the Share task and on F_{TOT} only in the Force task), and at the end of Phase-3 (no visual feedback).

In the Share task, there was an increase in F_A by an average of 3.26 ± 0.56 N (effect of *Phase*, $F_{[2,72]} = 96.04$; $p < 0.001$) and a drop in F_M , on average by 3.46 ± 0.56 N (effect of *Phase*, $F_{[2,72]} = 91.07$; $p < 0.001$) following removal of feedback on F_{TOT} . Relevant post-hoc tests indicated that F_A continued to increase after the removal of feedback on S in Phase-3, while F_M stayed at about the same level. The two sharing characteristics, S_M and S_A , showed no significant changes from Phase-1 to Phase-2 when feedback on S was available. After turning the S feedback off, S_M showed minimal changes in the 1:1 sharing task. In the other two tasks (2:1 and 1:2), it changed toward the 1:1 patterns, as reflected in a significant *Phase* $\times$ *Initial Sharing* interaction ($F_{[4,72]} = 13.89$; $p < 0.001$). As a result, by the end of Phase-3, S_M was, on average 0.62 ± 0.02 (significantly smaller than the required 0.67) in the 1:2 task, and 0.42 ± 0.02 (significantly larger than the required 0.33) in the 2:1 task. At the same time, S_A increased by an average of 0.36 ± 0.04 following the removal of feedback on S (effect of *Phase*, $F_{[2,72]} = 222.4$; $p < 0.001$).

In the Force task, removing feedback on S led to its drift toward the 1:1 pattern in conditions where the initial sharing pattern was not 1:1 already, as indicated by a significant *Phase* $\times$ *Initial Sharing* interaction for S_M ($F_{[4,72]} = 4.71$; $p < 0.01$). Post-hoc tests showed that S_M continued to drift toward the 1:1 pattern when F_{TOT} feedback was also removed in Phase-3. As a result, by the end of Phase-3, S_M was, on average, 0.62 ± 0.05 in the 1:2 task (significantly smaller than the required 0.67), and 0.48 ± 0.03 in the 2:1 task (significantly larger than the required 0.33). Compared to Phase-1, S_A increased by 0.31 ± 0.06 in Phase-3 when no feedback was available (effect of *Phase*, $F_{[2,72]} = 71.1$; $p < 0.001$). There were no significant changes in F_{TOT} characteristics between Phases-1 and -2 in the Force task. However, after the F_{TOT} feedback was removed, there was an increase in F_A of 5.2 ± 0.89 N (effect of *Phase*, $F_{[2,72]} = 117.8$; $p < 0.001$) and a drop in F_M of 1.85 ± 0.50 N (effect of *Phase*, $F_{[2,72]} = 43.32$; $p < 0.001$).

Analysis of drifts in individual finger forces, F_R and F_L

Individual finger forces showed drifts compatible with the described patterns of F_{TOT} and S. Time series $F_R(t)$ and $F_L(t)$ for a representative subject are presented in Figure 5, with F_L represented as a solid gray line and F_R as a dashed black line, while the average values of F_M and F_A for each finger and for each of the three phases are shown in Figure 6. Note the consistent increase in F_A and a drop in F_M from Phase-1 to Phase-3 for both force time series confirmed by the main effect of *Phase* in the *Initial Share* $\times$ *Phase* $\times$ *Finger* ANOVA for both Share task and Force task ($F_{[2,153]} > 32.3$; $p < 0.001$). Because the outcome variables used in Force and Share tasks were neither commensurate nor straightforwardly transformable into commensurate units, we ran separate ANOVAs for the two tasks.

There were significant differences between the behaviors of the right and left fingers. In particular, the left finger showed smaller drop in F_M from Phase-1 to Phase-3 in both tasks. In the Share task, the left F_M dropped from 5.34 ± 0.52 N to 3.95 ± 0.48 N, while the right F_M dropped from a comparable initial value of 5.45 ± 0.52 N to 3.37 ± 0.36 N, significantly smaller than that of the left F_M (confirmed by the significant interaction *Finger* $\times$ *Phase*; $F_{[2,153]} = 4.59$; $p < 0.05$). Similarly, in the Force task, the left F_M dropped to 4.81 ± 0.32 N, while the right F_M dropped to 4.24 ± 0.33 N, significantly smaller than that of the left F_M (confirmed by the significant interaction *Finger* $\times$ *Phase*; $F_{[2,153]} = 3.28$; $p < 0.05$).

In contrast, the changes in F_A from Phase-1 to Phase-3 were larger in the left hand. In the Force task, F_A in the left hand increased from 4.95 ± 0.39 N to 8.38 ± 0.53 N. This increase was smaller in the right hand, on average from 4.83 ± 0.41 N to 7.29 ± 0.77 N (*Finger* $\times$ *Phase*, $F_{[2,153]} = 3.10$; $p < 0.05$). In the Share task, F_A in the left hand increased from 4.14 ± 0.33 N to 6.72 ± 0.74 N. This increase was smaller in the right hand, on average from 4.13 ± 0.26 N to 5.79 ± 0.63 N. This effect was just below the level of significance ($F_{[2,153]} = 3.03$; $p = 0.051$).

Other significant effects were either trivial (e.g., differences in F_M across tasks with different initial sharing) or reflected the described drifts of S toward 0.5 in tasks with 1:2 and 2:1 initial sharing. We are not presenting them here for brevity.

Analysis of the relative phase

When the Force task was performed under full visual feedback, the two finger forces changed mostly in-phase (see Fig. 5). In contrast, the Phase-1 performance of the Share task was characterized by close to out-of-phase changes in the two finger forces. When feedback on both variables was removed, the performance on the force-force plane (Fig. 3) showed consistent deviations from straight lines expected from the in-phase and out-of-phase regimes. These changes were quantified using two methods. First, we quantified the ratio of force change in the direction required by the task to force change in the orthogonal direction (which had to be close to zero). For a perfect ellipse, this ratio corresponds to the ellipse eccentricity.

Figure 7 illustrates the changes in the eccentricity index over the three phases in the Force task (left panel) and Share task (right panel). Analysis of this index confirmed its drop after visual feedback had been removed in both Force and Share tasks: this was indicated by a significant effect of *Phase* ($F_{[2,72]} = 86.81$; $p < 0.001$) and significant *Phase* $\times$ *Initial Sharing* interaction ($F_{[4,72]} = 4.04$; $p < 0.01$) in the Force task, while a significant main effect of *Phase* without interactions was observed in the Share task ($F_{[2,72]} = 4.34$; $p < 0.05$).

We also quantified the relative phase between the two finger force signals within the time intervals at the end of Phase-1, Phase-2, and Phase-3. The across-subjects results are illustrated in Figure 8. They confirm significant deviation of the relative phase from 0 (Force task, inphase) and 3.12 (Share task, out-of-phase). The magnitude of the phase drift by the end of Phase-3 was, on average, 0.27 ± 0.04 rad for the Force task and 0.31 ± 0.09 rad for the Share task. One-sided t-tests indicated that these values were significantly different from zero. Typically (28 of 30 observations in the Share task and 29 of 30 observations in the Force task; $p < 0.001$ according to the sign test), the observed phase shift reflected the right finger moving *ahead* of the left finger.

Plots of binned continuous relative phase data in Force and Share tasks (for all initial sharing patterns), averaged across subjects with standard error bars, are presented in Figure 9. For each task/initial sharing condition, we fit a single-term exponential decay to the observed phase shift. All the regressions were significant at $p < 0.01$. In the Force task, the time constants of the exponential regressions were: 27.5 s ($R^2 = 0.93$); 28.6 s ($R^2 = 0.92$); and 21.2 s ($R^2 = 0.81$) for the 1:1, 1:2, and 2:1 initial sharing patterns, respectively. In contrast, time constants were approximately an order of magnitude larger in the Share task: 245.1 s ($R^2 = 0.87$); 415.4 s ($R^2 = 0.71$); and 262.0 s ($R^2 = 0.86$) for the 1:1, 1:2, and 2:1 initial sharing patterns, respectively.

Model

Basic concepts

Within the idea of control with spatial referent coordinates, we assume that the neural control of finger force production along a coordinate X can be described with two variables, referent coordinate along X (X_{RC}) and apparent stiffness (k) (cf. Pilon et al., 2007; Ambike et al., 2016b). We assume that the conditions are isometric and there are no changes in the actual finger coordinate, $X_{AC} = 0$. Hence, $F = -kX_{RC}$.

During practice, the subjects were assumed to develop a task-specific function that serves as an input into a non-linear system that displays limit cycle behavior and generates X_{RC} . This input is assumed to be a constant for constant force production tasks and a sinusoidal function of time in the cyclical force production tasks. We chose a damped driven nonlinear oscillator as a proof-of-concept toy-model of such a system. We use the term *toy-model* because, while the model is able to account for some salient features of behavior, it lacks clear links to the physical and physiological features of the behaving system. Parameters of the oscillator are assumed to show slow drift resulting in drifts in X_{RC} and performance. Based on a recent study (Ambike et al., 2016b), we limited the model to a drift in X_{RC} , without a drift in k ; this also reduces the number of parameters. During cyclical tasks, k is assumed to change at twice the frequency of X_{RC} changes with peaks at about the maximal rates of X_{RC} (Latash, 1992). We explored a range of parameters for $k(t)$ and found only minor effects on salient characteristics of the model output. Visual feedback, when available, is used to compensate for the drifts. Here we limit the model to conditions with full visual feedback and with no visual feedback only (corresponding to Phase-1 and Phase-3 in the experiment).

Since the metronome was on throughout the experiment, we assume no change in the input frequency. We assume that the subjects used the metronome to synchronize their F_{TOT} pattern with the beats across all cyclical tasks.

General structure of the model

We assume that each $X_{RC}(t)$ is produced by a dynamic process, which is a limit cycle, from a mathematical point of view. The two oscillators were coupled by feedback information only: auditory at all times and visual when it was available (see below). We have chosen a driven, damped solid pendulum model as a standard dynamic system manifesting the limit cycle. For simplicity, we use x and y for the oscillator's coordinate and momentum, respectively.

To ensure finger forces are only positive (we assume non-sticking contact that allows only pushing, not pulling forces), we introduce repulsive potentials and local damping when force values approach zero. As a result, our system of equations for one finger is:

$$\dot{y}(t) = -\sin(x(t) - \bar{x}(t) - x_0) - \gamma y(t) + P(\bar{u}(t)) \sin(\pi h + t + \bar{\tau}(t)) - V_1 \exp(-x(t)^3) \quad (1)$$

$$\dot{x}(t) = y(t) - V_2 \exp(-x(t)^3) \text{sign}(y(t)) \quad (2)$$

This system describes a limit cycle with a friction-like term, $V_2 \exp(-x(t)^3) \cdot \text{sign}(y(t))$ directed always opposite to the rate of change due to the factor $\text{sign}(y(t))$. The first two right-hand terms of Eq. (1) have been selected as typical for a limit cycle attractor. The third term in the right side of Eq. (1) represents the time-varying drive adjusted by a factor P , which is a function of a parameter $\bar{u}$. It is important that P is a monotonically increasing function of $\bar{u}$; we assume $P = 0.1 e^{0.1 \bar{u}}$. Other parameters are: γ – damping coefficient; x_0 – preferred

midpoint for the oscillator; $\bar{x}$ – required vision-based correction of the midpoint to match the task; $\bar{\tau}$ – phase adjustment (the product of time delay and frequency) of the drive to match the task-defined phase (it is driven by the auditory metronome). The term $V_1 \exp(-x(t)^3)$ prevents the system from generating negative force values. In these and following equations, we use bars for slowly changing parameters. The phase parameter πh is introduced to distinguish between the Force task and Share task. For the Force task, $h = 0$ for both fingers (in-phase action), while for the Share task, $h = 0$ for one finger and $h = 1$ for the other finger (out-of-phase action).

The following equation has been chosen to define adjustments ($\bar{\tau}$) of the phase to synchronize the performance with the metronome. This equation is based on the idea that, when two oscillations are perfectly in-phase, the derivative of one of the oscillations has minimal overlap with the other oscillation (as sine and cosine functions):

$$\dot{\bar{\tau}}(t) + \lambda_{\sigma} \bar{\tau}(t) = -\sigma [(x(t) - \bar{x}(t) - x_0) \cos(\pi h + t)]^2 \quad (3)$$

In Eq. (3), λ_{σ} stands for the rate of phase relaxation; and σ is a parameter that defines sensitivity to phase deviation from the one specified by the metronome.

The following equations have been chosen to describe drift of the midpoint of x toward a preferred value and corresponding vision-based corrections:

$$\dot{\bar{x}}(t) + \lambda \bar{x}(t) = -\lambda_1 P_0(t) (\bar{s}(t) - S) \quad (4)$$

$$\dot{\bar{s}}(t) + \mu \bar{s}(t) = \mu x(t) \quad (5)$$

In these equations, λ and λ_1 are parameters (λ defines the speed of relaxation of $\bar{x}$, while λ_1 defines sensitivity to vision-based corrections). Visual feedback is assumed to estimate average value of force ($\bar{s}$) over a typical time interval $1/\mu$. In these equations, for simplicity, we equate force with x , although in the simulations (see later), force was estimated as the product $-kx$. S is the value of $\bar{s}$ defined by the task. $P_0(t)$ reflects a condition when visual feedback is turned off at time zero: $P_0(t) = 1$ when visual feedback is available, $P_0(t) = 0$ when there is no visual feedback.

The next two equations define drift of $\bar{d}$ that causes changes in the amplitude of x toward a preferred value, and corresponding vision-based corrections:

$$\dot{\bar{d}}(t) + \delta \bar{d}(t) = -\kappa [(x(t) - \bar{x}(t) - x_0)^2 - U_g] - \mu_1 P_0(t) (\bar{d}(t) - U) \quad (6)$$

$$\bar{d}'(t) + \mu \bar{d}(t) = \mu (x(t) - \bar{s}(t))^2 \quad (7)$$

In these equations, δ defines speed of relaxation of $\bar{d}$; U_g stands for the preferred amplitude of action; U is a parameter that defines vision-based correction toward the amplitude defined by the task; $\bar{d}$ is average of squared deviations of x from $\bar{s}$ over a characteristic time $1/\mu$; and κ is a parameter that defines rate of change of $\bar{d}$ toward U_g .

Figure 10 illustrates the performance of the model in the Force task (top panels) and Share task (bottom panels). The two simulations differed only by parameter h : For the Force task, $h = 0$ for both fingers, while for the Share task, $h = 0$ for the right finger and $h = 1$ for the left finger. The values of all other parameters were considered identical for the two fingers with the exception of the following: $x_0 = 1.55$ for the right finger and 1.05 for the left finger; $S = 3$ for the right finger and 3.3 for the left finger; $U_g = 6.9$ for the right finger and 4.83 for the left finger. The values of other parameters, common for the two fingers, are: $\gamma = 0.11$; $\lambda = 0.02$; $\lambda_1 = 0.09$; $\mu = 0.05$; $\mu_1 = 0.3$; $\mu_2 = 2.7$; $\delta = 0.1$; $\kappa = 0.4$; $U = 0.15$; $\sigma = 0.3$; $V_1 = 0.3$; $V_2 = 0.105$; $\lambda\sigma = 0.1$.

The left panels of Fig. 10 show the time profiles of F_{TOT} and S . Note the similarity of the simulation to the data illustrated in Fig. 2, in particular, the changes in F_{TOT} peak-to-peak amplitude. The middle panels of Fig. 10 show the force-force time series that can be compared to the plots in Fig. 3. Note the emergence of elliptical trajectories in the Force task and of the distorted triangular-shape trajectories in the Share task. The right panels of Fig. 10 show the time series of individual finger forces (similar to Fig. 5).

Discussion

The results of the experiment support all four hypotheses formulated in the Introduction. In particular, turning off visual feedback on F_{TOT} led to a drop in the mid-point of the F_{TOT} cycle in the Force task and to a drop in the mean F_{TOT} during S tasks. At the same time, an increase in the peak-to-peak amplitude of the cyclical F_{TOT} changes was observed. These results confirm Hypothesis 1 and are consistent with an earlier study of cyclical F_{TOT} production by a single finger (Ambike et al., 2016a). Turning off visual feedback on S led to a drift of mean S toward a preferred sharing pattern (closer to 50:50; cf. Ambike et al., 2015) across both Force and Share tasks. These observations confirm Hypothesis 2. We also observed an increase in the peak-to-peak S amplitude consistent with Hypothesis 3. One of the less expected results was the deviation of the two force time series from the in-phase pattern (typical of the Force task) and from the out-of-phase pattern (typical of the Share task). To our knowledge, no earlier studies predicted this result; moreover, most earlier studies of two-finger cyclical actions demonstrated only two stable patterns, in-phase (more stable) and out-of-phase (somewhat less stable) across both movement and force production tasks (Haken et al., 1985; Schöner and Kelso, 1988; Carson, 1995; reviewed in Kelso, 1995).

To account for the main observations, we developed a dynamical model, which at this time may be viewed as a *toy-model* because its functional form and parameters are not mapped

on physiological processes within the human body. The model predicts a possibility of phase desynchronization between the two fingers following withdrawal of visual feedback (Hypothesis 4), and this prediction has indeed been confirmed in the experiment. In the following sections we address a range of implications of our study with respect to such hotly debated issues as the nature of unintentional changes in performance, control with referent spatial coordinates, stability of salient performance variables, and changes in the relative phase of individual effector trajectories.

Unintentional movements as consequences of drifts in referent coordinates

Recently, a number of studies have explored the phenomenon of unintentional finger force drop during accurate force production tasks, which is commonly seen after visual feedback has been turned off (Slifkin et al., 2000; Vaillancourt and Russell, 2002; Shapkova et al., 2008; Ambike et al., 2015). Similar effects were observed in grasping studies following a slow transient change in the aperture (Ambike et al., 2014). Faster unintentional changes in finger forces were observed in experiments with transient perturbations applied to the effectors (Wilhelm et al., 2014; Reschechtko et al., 2015), and similar findings have also been reported in arm position tasks (Zhou et al., 2014, 2015).

Some of the earlier studies invoked the notion of working memory limitation as the primary cause for the unintentional force drop (Vaillancourt et al., 2001; Vaillancourt and Russell, 2002). Potential involvement of working memory in these phenomena was based on a series of studies documenting connections between prefrontal and premotor cortices with the dorsolateral prefrontal cortex and posterior parietal cortex during tasks requiring memory in nonhuman primates (Goldman-Rakic, 1988; Selemon and Goldman-Rakic, 1988). The role of working memory has also been supported by studies of cortical activation using MRI-based methods (Vaillancourt et al., 2003) as well as by EEG studies (Poon et al., 2012). On the other hand, involvement of working memory has been challenged in some recent studies (Jo et al., 2016; Parsa et al., 2016a,b) based on the observations that resting for a comparable time interval led to no consistent force drift and that, in some conditions, a consistent and reproducible drift toward higher finger force magnitudes can be observed.

A conceptually different interpretation has been suggested which views unintentional changes in performance as consequences of natural relaxation processes in the motor system (Ambike et al., 2015; Latash, 2016a,b). According to the hypothesis that movements are controlled via changes in referent coordinates (RCs) for the effectors (Feldman, 2015), unintentional actions may be viewed as consequences of a drift of the RC toward the actual location of the effector (actual coordinate: AC). Such drifts move the system toward a state with lowest potential energy and higher stability, which would be hypothetically achieved when RC and AC are identical. This process has been addressed as *RC back-coupling* (Zhou et al., 2014). RC back-coupling can predict some of our present observations, in particular: the drop in the mean force value (F_M) and an increase in the peak-to-peak force amplitude (F_A). Other results, however, do not lend themselves to predictions based on the concept of RC back-coupling, in particular the loss of the original in-phase and out-of-phase relation between the two finger force time profiles.

The task studied in our experiment may be viewed as *marginally redundant* (cf. Latash et al., 2001). This means that the number of effectors equals the number of constraints (formally, the system is non-redundant) but the constraints are not absolute and allow a margin of error such that an infinite number of solutions are *good enough* (cf. Simon, 1956; Loeb, 1999). The subjects had to manipulate two elemental variables (finger forces) to satisfy tasks that prescribed a certain pattern of changes in two performance variables, F_{TOT} and S . So, perfect task performance could be viewed as a sinusoidal motion along a fixed straight line in the force-force space (shown by the black lines in Figure 3). Subjects deviated from the line of perfect performance, even when full visual feedback was available (see the blue lines on the plots in Figure 3). As such, the tasks allowed variability in the performance to a degree, which was viewed as acceptable by the subjects and experimenters.

In earlier studies (Vaillancourt and Russell, 2002; Wilhelm et al., 2013; Zhou et al., 2014; Ambike et al., 2016a), two types of drifts were described, fast (typical times of 1–2 s) and slow (typical times of 10–20 s). Fast drifts were observed in experiments with external perturbations and also in experiments when the subjects were asked to change a salient performance variable quickly. Slow drifts were typically seen in steady-state tasks or task components in the absence of changes in external force field. The two types of drifts were associated with processes within the space where the salient performance variable did not change (uncontrolled manifold, UCM, Scholz and Schöner, 1999) and within the orthogonal to the UCM space (ORT). The movement of the system within the UCM is expected to be less stable, and therefore correspond to relatively slow processes, while in ORT the system is more stable and typical processes are faster. We did not quantitatively assess the drift timing in our experiment, but the records (e.g., Figures 2 and 5) suggest that, across conditions, the drift to a new steady state process took about 2–3 cycles after the visual feedback had been turned off, i.e., it was fast (cf. Ambike et al. 2016a). This could be due to the fact that, in our marginally redundant task, the UCMs for F_{TOT} and S were orthogonal. As a result, drift in any direction had a large ORT component corresponding to relatively fast processes.

Drifts in performance, referent coordinates, and dynamic system parameters

Within literature hypothesizing that neural control of movement is carried out with time patterns of RCs for effectors, the origin of these RC patterns is rarely discussed. An important exception is a theoretical paper by Martin, Scholz, and Schöner (Martin et al., 2009), which viewed RC time profiles as outcome of a higher-level dynamical system. Our model was inspired by that study: We assumed that the time profiles of RCs for the individual fingers were produced by a dynamical system with several parameters; changes in the parameters caused drifts in the performance. As such, this study makes a step to include hierarchically higher levels of control as compared to previous studies within the RC control hypothesis (Latash, 2010, 2016, 2017; Feldman, 2015).

We emphasize that the current version of our dynamical model should only be viewed as a toy-model designed to account for the experimental observations, and so its parameters have no clear relation to physiological processes within the body. We believe, however, that this model is an important step toward inclusion of higher-order processes into the current schemes of motor control and may be seen as proof of concept that the observed complex

patterns of unintentional force changes may result from drifts of parameters within a dynamical system. In future, we hope that such a model can be refined to provide links to neurophysiology.

Within the present model, we assumed three factors: (1) Drift of model parameters to values corresponding to preferred mid-point and preferred amplitude of action (cf. Ambike et al., 2015); (2) Different drift characteristics in parameters of the right and left hands (cf. the dynamic dominance hypothesis, Sainburg, 2002, 2005; Parsa et al., 2016a,b); and (3) Vision-based adjustments of the parameters leading to corrections of the drifts in performance and of the phase drift. The first factor allowed accounting for the main observations such as the drifts of force-time characteristics to lower F_M and larger F_A . The second factor was introduced to account for the phase drift observed consistently across subjects and conditions. The first two factors were assumed to act at all times. To account for accurate performance under unchanged visual feedback, we introduced the third factor.

A number of further simplifications were introduced. In particular, we assumed no changes in muscle length in the isometric conditions. This is of course a simplification because active force production in isometric conditions implies that the sum of the muscle fiber length and tendon length remains constant, while muscle fiber length can change during force changes (e.g., shorten during force increase). This factor, together with changes in the activation of the system of gamma-motoneurons, could lead to modulation of the reflex contribution to muscle activation. Another simplification is the assumption that unintentional finger force changes are associated with drifts in the finger RC but not in its apparent stiffness (cf. Latash and Zatsiorsky, 1993). This assumption is based on a recent study of the unintentional force drift during steady force production by a finger that documented consistent RC drifts but inconsistent changes in the apparent stiffness (Ambike et al., 2016b).

Phase desynchronization: Possible causes

A large number of studies of cyclical motion produced by pairs of effectors – including those of the cyclical finger motion – have reported in-phase and out-of-phase actions as the only stable ones (Schöner and Kelso, 1988; reviewed in Kelso, 1995). During cyclical motion under natural visual feedback, out-of-phase motion was less stable and commonly switched to an in-phase pattern under an increase in the movement frequency. A dynamical model was developed to account for the salient features of these behavioral observations, the so-called Haken-Kelso-Bunz model (Haken et al., 1985); this model has received support in a number of recent studies (e.g., Avitabile et al., 2016; Russell et al., 2016).

Other phase relations among moving effectors can be observed during natural actions, for example during canter gait in horses (Robilliard et al., 2007). Consistent phase shifts during bilateral human actions are seen with asymmetrical loading of the moving effectors, e.g. during natural swinging of two pendulums with different natural frequencies (Sternad et al., 1995, 1999). However, during two-finger action only stable in-phase and out-of-phase have been reported so far. If visual feedback was manipulated, out-of-phase pattern could become more stable (Mechsner et al., 2001), and stable polyrhythm patterns have also been observed with appropriately organized visual feedback, as well as 1:1 patterns with a relative phase shift (Kovacs et al., 2009, 2010).

Consistent phase drifts in our study were observed after turning visual feedback off. It is feasible that the formulation of the task and practice schedule conditioned our subjects to depend on the visual feedback for accurate performance. In such conditions, turning salient visual feedback off is known to cause major deterioration of performance (Kovacs et al., 2010), while it has also been found that using a fading schedule of visual feedback reduces or eliminates such performance deficits (Kovacs and Shea, 2011). Several studies have suggested that if the participant is not provided with salient information on the phase relationship between the limbs and cannot detect the shifts in relative phase because of other constraints or inadequate perceptual information, he or she may not be able to correct errors when they occur (Wilson et al., 2003, 2010; Wilson and Bingham, 2008). Since in our experiment the task was formulated in terms of F_{TOT} and S , we did not provide explicit information on relative phase, and never even mentioned it while instructing the subjects, these issues may be highly relevant. The task used in our study may be viewed as relatively complex because the subjects were required to produce not only in-phase or out-of-phase force changes, encoded via required changes in F_{TOT} and S , but also to produce coordinated peak-to-peak magnitudes of those changes. To explore possible causes of the phase drift, it would be highly desirable to have a control condition when the subjects initiate performance without visual feedback. While we did not have such a condition in the present study, the inclusion of control condition is in our immediate plans for follow-up studies.

The different phase regimes observed in our experiment with and without visual feedback could reflect the different neurophysiological structures involved in the production of externally and intrinsically triggered actions. The different involvement of brain structures in the two types of actions has been documented in both animal studies (Mushiakhe et al., 1991; Schieber 1999) and brain imaging studies in humans (Debaere et al, 2001, 2003).

Note that the importance of visual feedback for stability of in-phase and out-of-phase coordination has also been demonstrated in isometric force production tasks (Lafe et al., 2016a,b). However, to our knowledge, our experiment is the first report on spontaneous phase desynchronization from both in-phase (Force task) and out-of-phase (Share task) regimes in symmetrical conditions and without changes in the action frequency. The phase drift caused by turning visual feedback off was on the order of 0.5 rad with the left finger consistently trailing the right finger.

A number of studies have shown that stability of in-phase and anti-phase actions can depend strongly on the action direction, action magnitude, and external loading conditions. Experiments with finger motion synchronization with the metronome showed a loss of anti-phase stability when the finger extended instead of flexed with a metronome beat (Kelso et al. 1990). Changes in movement amplitude were shown to cause loss of anti-phase regime during bimanual circle drawing (Carson et al. 1997; Ryu and Buchanan 2004). During isometric cyclical force production task, anti-phase action was less stable than the in-phase pattern, but no switch to the in-phase pattern was observed with an increase in the action frequency (Carson, 1995). Asymmetrical loading of the legs during locomotion has been shown to lead to deviations of phase from 3.14 rad, with the loaded leg lagging behind the other leg (Russell et al., 2016).

We believe that our observation of phase desynchronization between the two finger forces caused by turning salient visual feedback off in the absence of changes in the frequency of action is unique. In contrast to the aforementioned studies, we observed a phase drift not to one of the traditionally stable regimes, in-phase or anti-phase, but to regimes with a relative phase that differed from in-phase or anti-phase by about 0.5 rad over the trial duration and, according to the exponential regressions, this drift could be expected to continue. Within our model, these effects are due to the right-left differences in the assumed preferred values for the model parameters leading to the drift in the mean force and force amplitude. This assumption is based on earlier observations of faster force drifts in the right hand of right-handers during steady-state force production tasks (Parsa et al., 2016a,b). This assumption is also compatible with recent observations of changes in ongoing cyclical actions performed by a limb in the 1:2 bimanual force coordination task, which could be attributed to the production of force by the contralateral limb (Kennedy et al., 2016).

While the mean force (F_M) in our experiment showed a larger drop in the right finger (similar to the cited earlier reports), the peak-to-peak force amplitude (F_A) increase was smaller in the right finger. To interpret these observations, we invoke the dynamic dominance hypothesis, which assumes that the two hands (and the corresponding cortical hemispheres) are specialized for different tasks (reviewed in Sainburg, 2005). The dominant hemisphere is specialized for the control of fast actions, while the non-dominant one – for the control of steady states. As a result, steady-state task components are expected to show higher stability in the non-dominant hand (left finger in our study) and, correspondingly, a smaller unintentional force drift after turning visual feedback off. In contrast, the fast-changing task components are expected to show higher stability in the dominant hand (right finger) leading to the smaller drift in the peak-to-peak force amplitude. Of course, these are preliminary, qualitative considerations that have to be explored in detail in future studies.

At least one of the results resembles the so-called “assimilation effect” in two-limb tasks with the bias toward the movements of dominant limb, limb with the faster frequency or greater force (e.g., Sherwood, 1994; Kovacs and Shea, 2010). Namely, in trials that started with an uneven sharing of F_{TOT} between the two fingers (0.33 and 0.67) we observed a drift toward more equal sharing (0.5). The sharing drift was, however, at least as strong (typically stronger) in trials that started with higher force produced by the right (dominant) finger. This observation is not readily compatible with the mentioned bias of the assimilation effects. It is, however, readily compatible with the larger force drifts in the dominant hand corresponding to lower stability of its performance of steady-state task components (Parsa et al., 2016a,b). We would also like to note that similar force drifts and effects on relative phase were observed when both fingers were required to produce the same force patterns ($S = 0.5$) at the beginning of the trial.

Concluding comments

Our study demonstrates complex patterns of changes in performance caused by turning visual feedback off. Note that the subjects were unaware of these changes and were consistently under the impression that they followed the instruction and continued performing the task without distortions. This happened despite the very large errors in

performance characteristics such as the peak-to-peak changes in the instructed variables (F_{TOT} and S) and their average magnitudes. The apparent inability of memory and somatosensory information to detect these deviations of performance and correct them is striking and needs to be explored in more detail. Another unexpected result is the consistent deviations of performance from the prescribed in-phase and out-of-phase regimes. While we were able to simulate the main findings using a dynamical model, we are the first to admit that the model is only a toy-model with no clear links to physiology. The number of parameters in the model is large as compared to earlier dynamical models in the field; however, most earlier models simulated only general characteristics of behavior such as frequency and relative phase, while our model simulates more specific changes including drifts in quantitative characteristics of finger forces. Additionally, some of the model parameters are task specific – like those introduced to account for presence or absence of visual feedback and for the unidirectional forces produced in the experiment. The purpose of the model has been to show how complex patterns of unintentional force drifts could result from drift of salient parameters within a dynamical system. It is notable that the time constants of the relative phase drift were larger than those expected from the drift characteristics of the individual finger force time profiles, particularly for the Share task. Typical unintentional slow force drifts in one-finger tasks were on the order of 10–20 s (Ambike et al. 2015, 2016a); these values are not far from those computed for the Force task, but they are an order of magnitude smaller than those computed for the Share task. Overall, we think that this study poses more questions than it answers, and we see this feature as a major asset of the study.

In the context of research in cyclical actions and dynamical systems, some features of our experimental design are atypical and, in this context, may indeed be seen as suboptimal. For example, during training we emphasized reliance on visual display, which could lead to some of the observed effects of turning the visual feedback off. Using a metronome in our study may be viewed as another useful or disruptive manipulation (e.g., Kovacs et al., 2009); it is therefore possible that alternative methods of frequency instruction would have altered subjects' performance. However, we chose to use a metronome to avoid complicating the design with another changing parameter of performance. Further, many of the response variables we planned to analyze were tied to the cyclical nature of the task (e.g. mid-cycle magnitude of force production) – so being less restrictive with frequency might have additionally complicated the interpretation of these responses. While acknowledging these potential shortcomings, we would like to emphasize that the design of our experiment was driven by our primary goal: to explore the effects of removal of visual feedback on force characteristics.

Acknowledgments

The study was in part supported by a grant R01 NS035032 from the National Institutes of Health.

References

- Ambike S, Mattos D, Zatsiorsky VM, Latash ML. The nature of constant and cyclic force production: Unintentional force-drift characteristics. *Exp Brain Res*. 2016a; 234:197–208. [PubMed: 26419663]

- Ambike S, Mattos D, Zatsiorsky VM, Latash ML. Synergies in the space of control variables within the equilibrium-point hypothesis. *Neuroscience*. 2016b; 315:150–161. [PubMed: 26701299]
- Ambike S, Zatsiorsky VM, Latash ML. Processes underlying unintentional finger force changes in the absence of visual feedback. *Exp Brain Res*. 2015; 233:711–721. [PubMed: 25417192]
- Avitabile D, Słowiński P, Bardy B, Tsaneva-Atanasova K. Beyond in-phase and anti-phase coordination in a model of joint action. *Biol Cybern*. 2016; 110:201–216. [PubMed: 27278609]
- Carson RG. The dynamics of isometric bimanual coordination. *Exp Brain Res*. 1995; 105:465–476. [PubMed: 7498400]
- Carson RG, Thomas J, Summers JJ, Walters MR, Semjen A. The dynamics of bimanual circle drawing. *Q J Exp Psychol A*. 1997; 50:664–683. [PubMed: 9314729]
- Debaere F, Van Assche D, Kiekens C, Verschueren SM, Swinnen SP. Coordination of upper and lower limb segments: deficits on the ipsilesional side after unilateral stroke. *Exp Brain Res*. 2001; 141:519–529. [PubMed: 11810145]
- Debaere F, Wenderoth N, Sunaert S, Van Hecke P, Swinnen SP. Internal vs external generation of movements: differential neural pathways involved in bimanual coordination performed in the presence or absence of augmented visual feedback. *Neuroimage*. 2003; 19:764–776. [PubMed: 12880805]
- Feldman AG. Functional tuning of the nervous system with control of movement or maintenance of a steady posture. II. Controllable parameters of the muscle. *Biophysics*. 1966; 11:565–578.
- Feldman AG. Once more on the equilibrium-point hypothesis (λ -model) for motor control. *J Mot Behav*. 1986; 18:17–54. [PubMed: 15136283]
- Feldman AG. Referent control of action and perception: Challenging conventional theories in behavioral science. Springer; NY: 2015.
- Goldman-Rakic PS. Topography of cognition: parallel distributed networks in primate association cortex. *Ann Rev Neurosci*. 1988; 11:137–156. [PubMed: 3284439]
- Gorniak SL, Duarte M, Latash ML. Do synergies improve accuracy? A study of speed-accuracy trade-offs during finger force production. *Motor Control*. 2008; 12:151–172. [PubMed: 18483449]
- Haken H, Kelso JAS, Bunz H. A theoretical model of phase transitions in human hand movements. *Biol Cybern*. 1985; 51:347–356. [PubMed: 3978150]
- Heijnen MJ, Muir BC, Rietdyk S. Factors leading to obstacle contact during adaptive locomotion. *Exp Brain Res*. 2012; 223:219–231. [PubMed: 22972450]
- Heijnen MJ, Romine NL, Stumpf DM, Rietdyk S. Memory-guided obstacle crossing: more failures were observed for the trail limb versus lead limb. *Exp Brain Res*. 2014; 232:2131–2142. [PubMed: 24838551]
- Jo HJ, Ambike S, Lewis MM, Huang X, Latash ML. Finger force changes in the absence of visual feedback in patients with Parkinson's disease. *Clin Neurophysiol*. 2016; 127:684–692. [PubMed: 26072437]
- Kelso, JAS. Dynamic patterns: The self-organization of brain and behavior. Cambridge: MIT Press; 1995.
- Kelso JAS, DelColle JD, Schöner G. Action-perception as a pattern formation process. *Attention and performance XIII*. 1990; 5:139–169.
- Kennedy D, Rhee J, Shea CH. Symmetrical and asymmetrical influences on force production in 1:2 and 2:1 bimanual force coordination tasks. *Exp Brain Res*. 2016; 234:287–300. [PubMed: 26466827]
- Kovacs AJ, Buchanan JJ, Shea CH. Bimanual 1:1 with 90 degrees continuous relative phase: difficult or easy. *Exp Brain Res*. 2009; 193:129–136. [PubMed: 19093104]
- Kovacs AJ, Buchanan JJ, Shea CH. Impossible is nothing: 5:3 and 4:3 multi-frequency bimanual coordination. *Exp Brain Res*. 2010; 201:249–259. [PubMed: 19798488]
- Kovacs AJ, Shea CH. The learning of 90° continuous relative phase with and without Lissajous feedback: external and internally generated bimanual coordination. *Acta Psychol*. 2011; 136:311–320.

- Lafe CW, Pacheco MM, Newell KM. Adapting relative phase of bimanual isometric force coordination through scaling visual information intermittency. *Hum Mov Sci.* 2016a; 47:186–196. [PubMed: 27017544]
- Lafe CW, Pacheco MM, Newell KM. Bimanual coordination and the intermittency of visual information in isometric force tracking. *Exp Brain Res.* 2016b; 234:2025–2034. [PubMed: 26960740]
- Lamb PF, Stöckl M. On the use of continuous relative phase: Review of current approaches and outline for a new standard. *Clin Biomech.* 2014; 29:484–493.
- Latash ML. Virtual trajectories, joint stiffness, and changes in natural frequency during single-joint oscillatory movements. *Neuroscience.* 1992; 49:209–220. [PubMed: 1407547]
- Latash ML. Motor synergies and the equilibrium-point hypothesis. *Motor Control.* 2010; 14:294–322. [PubMed: 20702893]
- Latash ML. The bliss (not the problem) of motor abundance (not redundancy). *Exp Brain Res.* 2012; 217:1–5. [PubMed: 22246105]
- Latash ML. Towards physics of neural processes and behavior. *Neurosci Biobehav Rev.* 2016; 69:136–146. [PubMed: 27497717]
- Latash ML. Biological movement and laws of physics. *Motor Control.* 2017 (in press).
- Latash ML, Scholz JP, Schöner G. Toward a new theory of motor synergies. *Motor Control.* 2007; 11:276–308. [PubMed: 17715460]
- Latash, ML., Zatsiorsky, VM. *Biomechanics and Motor Control: Defining Central Concepts.* Academic Press; New York, NY: 2016.
- Li ZM, Latash ML, Zatsiorsky VM. Force sharing among fingers as a model of the redundancy problem. *Exp Brain Res.* 1998; 119:276–286. [PubMed: 9551828]
- Loeb GE. What might the brain know about muscles, limbs and spinal circuits? *Prog Brain Res.* 1999; 123:405–409. [PubMed: 10635735]
- Martin V, Scholz JP, Schöner G. Redundancy, self-motion, and motor control. *Neural Comput.* 2009; 21:1371–1414. [PubMed: 19718817]
- Mechsner F, Kerzel D, Knoblich G, Prinz W. Perceptual basis of bimanual coordination. *Nature.* 2001; 414:69–73. [PubMed: 11689944]
- Mushiake H, Inase M, Tanji J. Neuronal activity in the primate premotor, supplementary, and precentral motor cortex during visually guided and internally determined sequential movements. *J Neurophysiol.* 1991; 66:705–718. [PubMed: 1753282]
- Park J, Wu Y-H, Lewis MM, Huang X, Latash ML. Changes in multi-finger interaction and coordination in Parkinson's disease. *J Neurophysiol.* 2012; 108:915–924. [PubMed: 22552184]
- Parsa B, O'Shea DJ, Zatsiorsky VM, Latash ML. On the nature of unintentional action: A study of force/moment drifts during multi-finger tasks. *J Neurophysiol.* 2016a; 116:698–708. [PubMed: 27193319]
- Parsa B, Terekhov A, Zatsiorsky VM, Latash ML. Optimality and stability of intentional and unintentional actions: I. Origins of drifts in performance. *Exp Brain Res.* 2016b (in press).
- Pilon J-F, De Serres SJ, Feldman AG. Threshold position control of arm movement with anticipatory increase in grip force. *Exp Brain Res.* 2007; 181:49–67. [PubMed: 17340124]
- Poon C, Chin-Cottongim LG, Coombes SA, Corcos DM, Vaillancourt DE. Spatiotemporal dynamics of brain activity during the transition from visually guided to memory-guided force control. *J Neurophysiol.* 2012; 108:1335–1348. [PubMed: 22696535]
- Reschechtko S, Zatsiorsky VM, Latash ML. Stability of multifinger action in different state spaces. *J Neurophysiol.* 2014; 112:3209–3218. [PubMed: 25253478]
- Reschechtko S, Zatsiorsky VM, Latash ML. Task-specific stability of multi-finger steady-state action. *Journal of Motor Behavior.* 2015; 47:365–377. [PubMed: 25565327]
- Robilliard JJ, Pfau T, Wilson AM. Gait characterisation and classification in horses. *J Exp Biol.* 2007; 210:187–197. [PubMed: 17210956]
- Russell DM, Haworth JL, Martinez-Garza C. Coordination dynamics of (a)symmetrically loaded gait. *Exp Brain Res.* 2016; 234:867–881. [PubMed: 26661338]

- Ryu YU, Buchanan J. Amplitude scaling in a bimanual circle-drawing task: pattern switching and end-effector variability. *J Mot Behav.* 2004; 36:265–279. [PubMed: 15262623]
- Sainburg RL. Evidence for a dynamic-dominance hypothesis of handedness. *Exp Brain Res.* 2002; 142:241–258. [PubMed: 11807578]
- Sainburg RL. Handedness: differential specializations for control of trajectory and position. *Exerc Sport Sci Rev.* 2005; 33:206–213. [PubMed: 16239839]
- Schieber, MH. Voluntary descending control. In: Zigmond, MJ.Bloom, FE.Landis, SC.Roberts, JL., Squire, LR., editors. *Fundamental Neuroscience.* Academic Press; San Diego etc: 1999. p. 931-949.
- Scholz JP, Schöner G. The uncontrolled manifold concept: Identifying control variables for a functional task. *Exp Brain Res.* 1999; 126:289–306. [PubMed: 10382616]
- Schoner G, Kelso JAS. Dynamic pattern generation in behavioral and neural systems. *Science.* 1988; 239:1513–1520. [PubMed: 3281253]
- Selemon LD, Goldman-Rakic PS. Common cortical and subcortical targets of the dorsolateral prefrontal and posterior parietal cortices in the rhesus monkey: evidence for a distributed neural network subserving spatially guided behavior. *J Neurosci.* 1988; 8:4049–4068. [PubMed: 2846794]
- Yu, Shapkova E., Shapkova, AL., Goodman, SR., Zatsiorsky, VM., Latash, ML. Do synergies decrease force variability? A study of single-finger and multi-finger force production. *Exp Brain Res.* 2008; 188:411–425. [PubMed: 18425506]
- Sherwood DE. Hand preference, practice order, and spatial assimilations in rapid bimanual movement. *J Mot Behav.* 1994; 26:123–143. [PubMed: 15753065]
- Simon HA. Rational choice and the structure of the environment. *Psychol Rev.* 1956; 63:129–138. [PubMed: 13310708]
- Slifkin AB, Vaillancourt DE, Newell KM. Intermittency in the control of continuous force production. *J Neurophysiol.* 2000; 84:1708–1718. [PubMed: 11024063]
- Sternad D, Collins D, Turvey MT. The detuning factor in the dynamics of interlimb rhythmic coordination. *Biol Cybern.* 1995; 73:27–35. [PubMed: 7654847]
- Sternad D, Turvey MT, Saltzman EL. Dynamics of 1:2 coordination: Sources of symmetry breaking. *J Mot Behav.* 1999; 31:224–235. [PubMed: 11177633]
- Vaillancourt DE, Russell DM. Temporal capacity of short-term visuomotor memory in continuous force production. *Exp Brain Res.* 2002; 145:275–285. [PubMed: 12136377]
- Vaillancourt DE, Slifkin AB, Newell KM. Visual control of isometric force in Parkinson's disease. *Neurophysiologia.* 2001; 39:1410–1418.
- Vaillancourt DE, Thulborn KR, Corcos DM. Neural basis for the processes that underlie visually guided and internally guided force control in humans. *J Neurophysiol.* 2003; 90:3330–3340. [PubMed: 12840082]
- Wilhelm L, Zatsiorsky VM, Latash ML. Equifinality and its violations in a redundant system: Multi-finger accurate force production. *J Neurophysiol.* 2013; 110:1965–1973. [PubMed: 23904497]
- Wilson AD, Bingham GP. Identifying the information for the visual perception of relative phase. *Percept Psychophys.* 2008; 70:465–476. [PubMed: 18459257]
- Wilson AD, Bingham GP, Craig JC. Proprioceptive perception of phase variability. *J Exp Psychol Hum Percept Perform.* 2003; 29:1179–1190. [PubMed: 14640837]
- Wilson AD, Snapp-Childs W, Coats R, Bingham GP. Learning a coordinated rhythmic movement with task-appropriate coordination feedback. *Exp Brain Res.* 2010; 205:513–520. [PubMed: 20703872]
- Zhou T, Solnik S, Wu Y-H, Latash ML. Equifinality and its violations in a redundant system: Control with referent configurations in a multi-joint positional task. *Motor Control.* 2014; 18:405–424. [PubMed: 24717213]
- Zhou T, Zhang L, Latash ML. Intentional and unintentional multi-joint movements: their nature and structure of variance. *Neuroscience.* 2015b; 289:181–193. [PubMed: 25596318]

Highlights

- Turning visual feedback off causes drifts in the midpoint and amplitude of force cycle;
- Typically, midpoint drifts to lower values while amplitude increases;
- In two-finger tasks, this is accompanied by desynchronization of finger force cycles;
- A dynamical model with parameter drift is able to reproduce these features;
- The results fit the scheme of control with referent effector coordinates.

Figure 1.

An illustration of the setup (left panel) and the feedback during the Force task (middle panel) and Share task (right panel). The three dots on the bottom of the screen in the middle and right panels show the shifts of the share axis that ensured that, for each share (1:2, 1:1, and 2:1), ideal task performance corresponded to the same picture of the screen.

Figure 2.

Performance of a representative male subject in the Force task (top row) and Share task (bottom row) under various initial sharing conditions (from left to right: 1:2, 1:1, and 2:1). Total force is represented by the solid gray line (corresponding values on the left Y-axis), while Share is represented by the dashed black line (values on the right Y-axis). Red dashed lines represent the target maximum and minimum levels of force in each task, while blue dashed lines represent the target maximum and minimum share levels required. Note that only one force target line is visible in Share tasks because force is supposed to remain constant; similarly, only one share target is visible in Force tasks because share should be held constant. Vertical dashed lines show when elements of visual feedback were removed.

Figure 3.

Typical performance of a representative subject (same data as in Figure 2) on the force-force plane. Y-axis shows right finger force (F_R), while X-axis shows left finger force (F_L). Progression of time is illustrated by line color and style: the first 8 s are shown with solid blue lines; 8–23 s are shown with dashed green lines; 23–35 s are shown with red lines. The black line represents ideal performance (perfect modulation of F_{TOT} or S), while the circle represents the center of this ideal performance line.

Figure 4.

Across-subject averaged magnitudes of mean total force level (F_M) and amplitude (F_A) and mean share level (S_M) and amplitude (S_A). Different phases are represented by different fill styles (open: Phase 1; diagonal stripes: Phase 2; filled bars: Phase 3). Note the consistent increase in F_A and S_A , while F_M showed a consistent drop over the phases.

Figure 5.

Individual finger forces (F_L : solid line; F_R : dashed line) for each initial sharing pattern (columns) and task (rows) are shown for typical performance of the male subject shown in Figures 2 and 3. The instructed minima and maxima for individual finger force production are illustrated with solid red (F_R) and dashed blue (F_L) horizontal lines. Dashed vertical lines correspond to the times at which elements of visual feedback were removed.

Figure 6.

Across-subject averaged magnitudes of Force amplitude (F_A) and mean force level (F_M) for individual fingers in the Force task (left panels) and Share task (right panels). Note the increase in F_A and a drop in F_M throughout the conditions.

Figure 7.

Average magnitude of the eccentricity index (ratio of force change in the task direction vs. force change in the orthogonal direction) for both Force and Share tasks. Note the consistent drop in the index, particularly pronounced in the Force task.

Figure 8.

Across-subject average values of relative phase between left and right finger force changes in the Force task (in Phase 1 force changes are approximately *in phase*) and Share task (in Phase 1 force changes are approximately *out of phase*). Note the consistent phase drift across phases.

Figure 9.

Relative phase of the right hand force with respect to the left hand force is plotted as a time function for both Force task (top) and Share task (bottom). Individual data points are averages across subjects with standard error bars. Lines represent exponential regression fits; for each regression, $R^2 = 0.71$ ($p < 0.01$). Data for different initial sharing conditions are shown with black symbols (1:1), blue symbols (1:2), and red symbols (2:1). Note that data are jittered slightly on the time axis; for each sharing pattern, binned averages were computed at the same time points.

Figure 10.

Results of simulation using the model. Top panel: Force task; bottom panels: Share task. The left panels (A and D) show the time series of total force (F_{TOT}) and sharing (S). The dashed vertical line shows the time when visual feedback was turned off. Compare the results with Figure 2. The middle panels (B and E) show the same data as a plot of left finger force (F_L) as a function of right finger force (F_R). Compare the results to those in Figure 3. The right panels (C and F) show the time series of individual finger forces, F_L and F_R . Compare the results to those in Figure 5. Since this is a simulation, all units are normalized. Parameter values used in the simulation are presented in the text.