The nature of constant and cyclic force production: Unintentional force-drift characteristics

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ABSTRACT

We explored unintentional changes in forces during performance of constant and cyclic force production tasks (F-tasks) after visual feedback removal. Based on earlier studies, we expected all force parameters to drop exponentially with time. We also explored possible role of working memory in the force drop phenomena. Healthy subjects performed constant or cyclic isometric F-tasks with the index finger under visual feedback. The cyclic task was paced by a metronome. Removing visual feedback resulted in a consistent force drop in constant F-tasks and a qualitatively similar drift in the mean force in the cyclic F-task; both were slow with characteristic times of about 10-20 s. In contrast, force amplitude in the cyclic F-task increased quickly (within 1-2 s). When the subjects were asked to stop producing force for 5 s after the visual feedback disappeared and then resume force production, no downward force drift was seen in constant F-tasks, while in cyclic F-tasks, the drift of the mean force was present and an exaggerated increase in force amplitude was also observed. We conclude that while working memory limitations may influence cyclic F-tasks, their role in determining the force drift in constant F-tasks is limited. The results of both experiments are interpreted within the referent configuration hypothesis supplemented with an idea of unintentional drift of referent coordinates (RC-back-coupling) induced by differences between the referent and actual body configurations.

INTRODUCTION

Human movements result from the interplay of neural commands and forces external to the body. Within the reference configuration (RC) hypothesis (Feldman and Levin 1995; Feldman 2009), the former are associated with neural processes that establish values (time profiles) of referent spatial coordinates for task-specific performance variables. We will refer to movements produced by RC shifts as '*voluntary*'. In isometric conditions, shifts lead to force production instead of movement, since the actual effector coordinate is not allowed to move to the RC. Movements can also be produced by changes in external forces without a change in RC, and these will be addressed as '*involuntary*'. For example, pressing with a finger against a stop is associated with setting a value of finger referent coordinate (equivalent to RC) along the direction of force production (Pilon et al. 2007; Latash et al. 2010). The pressing force reflects the difference between the actual finger coordinate and its RC. If, however, the actual fingertip coordinate is moved by external forces, an involuntary force change takes place (Martin et al. 2009).

Recently, an intermediate example of force change has been documented, namely a drift in force not purposefully executed by the subject and not associated with changes in external forces. For example, if a person is asked to produce a constant initial pressing force with a fingertip under visual force feedback and then the feedback is turned off, a slow drop in the force is typically observed, while the subject is unaware of the force change (Slifkin et al. 2000; Vaillancourt et al. 2001; Vaillancourt and Russell 2002; Shapkova et al. 2008). This force drift was interpreted in the cited early studies as a consequence of a working memory limitation. In more recent studies, this hypothesis has been challenged. In particular, a consistent force increase was documented at low initial force levels, while a force decrease was observed at higher initial force levels, and there was no force change at intermediate initial force levels (Ambike et al. 2015). An alternative hypothesis has been offered that force drift resulted from an unintentional drift in the finger RC towards the actual configuration, while the force increase could result from adaptation of pressure-sensitive receptors. The former hypothesis suggests that these unintentional force changes were mediated by the same mechanism as voluntary force production (Ambike et al. 2015; Zhou et al. 2015). All the force changes above were well approximated with exponential functions with a time constant of about 10-15 s.

Similar unintentional movements, but with much shorter time constants (about 1 s), have been documented in experiments with relatively short-lasting, transient perturbations (Wilhelm et al. 2013; Zhou et al. 2014; Reschechtko et al. 2014). When the perturbation was over, major changes in both kinematic and kinetic variables were observed despite the instruction to the subject not to react to the perturbations (“do not interfere voluntarily”, Feldman 1966; Latash 1994). Hence, two types of unintentional force changes can occur: slow (during steady-state tasks) and fast (during quick changes). Our main assumption is that both are associated with unintentional drifts in the memorized, task-specific RC time profiles.

There are two main goals of this paper. First, we explored more thoroughly the role of working memory in the unintentional finger force drift when the task is performed without visual feedback. Specifically, we compared performance of subjects in a *continuous task* (similar to previous studies) and in a task where, after turning the visual feedback off, the subject relaxed and waited for a certain time interval before resuming the performance. Memory limitations were expected to be at least as strong in such *discontinuous tasks*. The logic was that, if the memory limitation is responsible for the RC drift leading to force drop during continuous force production, a similar or a stronger one is expected over a comparable time interval of rest, since the subject was forced to rely exclusively on memory during the rest period. However, since we did not expect memory limitations to cause the force drift (Ambike et al. 2015), our first Hypothesis was: Discontinuous trials will lead to no consistent force drift while continuous trials will.

Second, we studied isometric, cyclic finger-force production (cyclic F-task) paced by a metronome in addition to constant-force-production tasks (constant F-task). We assume that cyclic F-task at a given frequency involves two implicit components: specification of the mean RC value (reflected in the mean force) and the peak-to-peak RC amplitude (reflected in the force amplitude). We expected the force changes to reflect the earlier reported force drift characteristics observed in constant F-tasks. Hence, our second Hypothesis was: There will be a drop in the mean force during the cyclic F-task similar in time course and magnitude to the force drop in constant F-tasks. With regard to peak-to-peak force amplitude, since (1) the amplitude is computed as the difference in the consecutive maximum and minimum force values and (2) the rate of force drop is independent of the force magnitude (Vaillancourt and Russell 2002; Ambike et al. 2015), our third Hypothesis states that the force amplitude will drop with the same time constant as the mean force.

METHODS

Subjects

Ten healthy subjects voluntarily participated in this study (6 males and 4 females; age: 25.7 ± 5.53 yr., height: 176.33 ± 6.12 cm, weight: 77.15 ± 11.53 kg; mean ± SD). All subjects were right-hand dominant by self-report and had no history of discomfort or injury in the upper arm for the past six months. All subjects provided informed consent in accordance with the procedures approved by the Office for Research Protection of the Pennsylvania State University.

Equipment and procedures

Subjects sat comfortably in a chair with the forearms resting on top of a table. Each subject was allowed to choose a comfortable hand posture such that the index finger was comfortably extended and the other fingers were curled into a fist. The hand posture was consistent across trials. The subjects placed the volar aspect of the distal phalanx of the index finger on a force sensor (PCB model 208C01, PCB Piezotronics, Depew, NY) as shown in Figure 1A. The diameter of the sensor was 17 mm. Sandpaper (100-grit) was placed on the contact surface of the sensor to increase the friction between the digits and sensor. The signals from the transducer were sent to a PCB 484B11 signal conditioner and then digitized at 200 Hz using a 16-bit National Instruments PCI-6052E analog-to-digital card (National Instruments, Austin, TX). The sensor reading was zeroed with the subject's finger resting on the sensor with the hand relaxed just before data collection so that the finger's weight was not included in the force measured by the sensors. A customized LabVIEW program was used for the data acquisition and for subject feedback. Visual feedback was provided using a 19-inch monitor placed at 0.8 m in front of the subject.

Both hands were tested, and the order of testing the left and right hands was randomized across subjects. For each hand, subjects first performed maximum voluntary contractions (MVC). In the MVC trials, the subject was instructed to press on the sensor as hard as possible, achieve maximal force level within 6 s, and relax immediately after reaching maximal force. The finger force feedback was provided to the subjects. Each subject performed two consecutive trials, and the trial with the higher MVC was selected to set the main task. The two trials were performed in sequence with a 30-s rest interval.

The main task of the experiment had three conditions. In **Condition-1** (the *continuous, constant-F task*), the subject was required to press with the index finger and match the target set at 20% of the MVC value and shown as a horizontal line on the computer screen (Figure 1B). In **Condition-2** (the *continuous, cyclic F-task*), the subject produced a cyclic pattern of finger force between 25% and 15% of the MVC value (shown as two horizontal lines, Figure 1B). The subjects were paced by an auditory metronome set at a frequency of 2 Hz. Visual feedback on the index finger force was provided during the first 8 s as a trace moving from left to right with time. In the cyclic task, subjects were required to modulate their finger force and touch each of the target lines at the metronome beeps, so that the force-production frequency was 1 Hz. After the first 8 s, the visual feedback was removed, and subjects were instructed to keep producing either the constant force (Condition-1) or the cyclic force pattern (Condition-2) until the end of the trial. The metronome was kept on for the entire duration of the trials. Conditions-1 and -2 and the tested hand were block randomized across subjects.

Condition-3 was performed last. It was designed to test the effect of memory on the force production. In contrast to the continuous trials of Conditions 1 and 2, this condition included *discontinuous trials*: After the first 8 s of force production (constant F-task or cyclic F-task), visual feedback on the force disappeared, and the word "STOP" appeared on the screen indicating to the subject to stop pressing on the sensor without lifting the finger. After another 5 s, the word "PRESS" appeared on the screen, following which the subject resumed the force-production task without any visual feedback and tried to match the force profile before the feedback disappeared and continued that performance until the end of the trial. The discontinuous, constant F-task and cyclic F-task, and the tested hands within Condition-3 were block randomized across subjects.

All the trials were 22-s long. Each condition was repeated six times in a row. Each subject performed 4 MVC trials (2 repetitions × 2 hands), and 48 experimental trials (2 types of tasks – constant F-task and cyclic F-task × 2 types of trials – continuous and discontinuous × 2 hands × 6 repetitions). A 20-s interval was enforced between trials, and 1-min breaks were enforced after every 6 trials. Subjects were instructed to ask for additional rest if they felt tired. However, no subject reported fatigue during the experiment. Before the data collection began, practice trials were performed to familiarize the subject with the tasks and the experimental protocol. During these trials, subjects received full visual feedback on the finger force. At least six practice trials were performed for the cyclic F-task, whereas one practice trial was sufficient for all subjects to successfully accomplish the constant F-task.

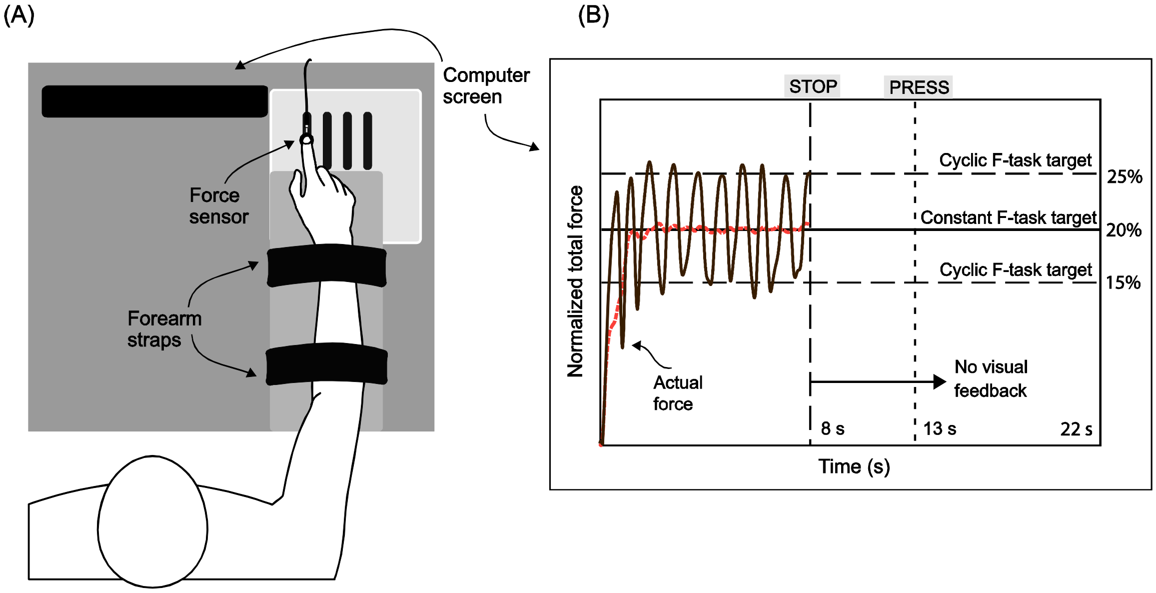

Figure 1. Experimental setup. Panel (A) shows the subject seated in a chair and pressing on the force sensor with the index finger. The computer monitor provides visual feedback. Panel (B) shows the visual feedback provided during the actual trials. Two horizontal lines at 25% and 15% of the finger-force MVC were displayed for the cyclic force task, and a single line at 20% MVC was displayed for the constant-force-production force-production task. The actual finger force was also displayed as a trace moving from the left to the right with time for the first 8 s of each trial, after which subjects continued with the task without visual feedback. The solid trace depicts a typical cyclic task performance, and the dashed trace depicts a typical constant-force-production force production trial. For the memory tasks, the feedback is identical as that for the main tasks. However, subjects stop the task for a period of about 5 s before resuming the task without visual feedback. The instructions 'STOP' and 'PRESS' were displayed on the screen at 8 s and 13 s time points

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 10 Hz. All force trajectories were normalized by the corresponding hand’s MVC value, and further analysis was conducted on the normalized forces.

Analysis of the continuous tasks

Subject performance of the continuous tasks was analyzed for differences across task types, movement phases, and hands. The normalized force trajectories of typical subject performance for the continuous cyclic F-task and constant F-task trials are depicted in Figures 2A and 2B, respectively. For the cyclic F-task, the phase of the force oscillation at the 8-s instant (when the visual feedback was turned off) varied across trials. Therefore, instead of averaging the six repetitions for a subject, the mean force and the force amplitude were computed for each oscillation as the mean force value of the consecutive extrema, and the absolute difference between the consecutive extrema, respectively. These values were assigned to the middle of the time interval between the two extrema (Figure 2A). The mean force and force amplitude values were pooled across trials and then binned along the time axis. Three bins were chosen to represent the response values just before (7 to 7.5 s), just after (9 to 9.5 s), and a long time after (15 to 15.5 s) the visual feedback was turned off (which occurred at 8 s). These time intervals are referred to as Phase I, Phase II and Phase III from here on. The mean of the data in these bins provided estimates of the force values, i.e. mean force and peak-to-peak force change, for Phase I, Phase II and Phase III, respectively. For the constant-F trials, the same time bins were used, and force values from all repetitions within the bins were averaged to obtain an estimate of the mean force.

For various quantities (means and amplitudes for the cyclic F-task, and mean force for the continuous F-task), exponential functions of the form $F(t) = a \times \mathrm{e}^{-t/\mathrm{t}} + c$ were fit to the data, where t is time, and t is the time constant (seconds) of the exponential change in F. This particular functional form was motivated by earlier studies (e.g., Ambike et al. 2015; Jo et al. 2015) as well as by the typical exponential forms of relaxation processes in physical systems. Note that at the time of feedback removal ($t = 0$), the variable value is given by $F(0) = a + c$, and at the steady state ($t = \infty$), it is $F(\infty) = c$. Thus, a estimates the net drop in F. These fits were performed for data averaged across subjects.

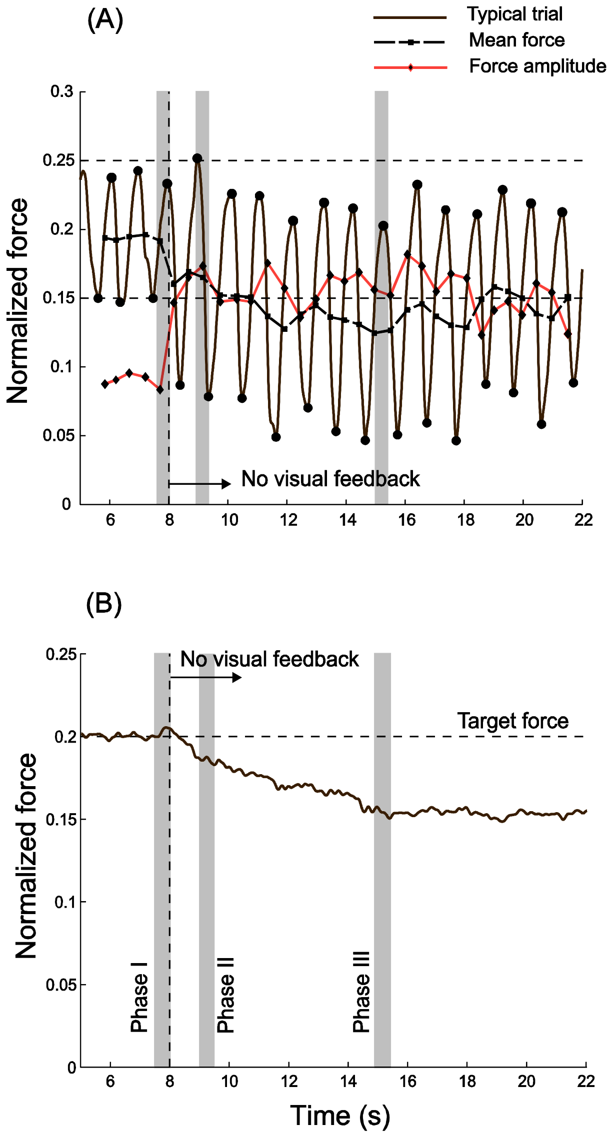

Figure 2. Typical subject response in the main cyclic and constant F-tasks. Panel (A) depicts the cyclic trial response as the solid oscillating line. The mean force is computed as the mean of the successive force extrema, and the force amplitude is computed as the difference between the successive extrema. Panel (B) shows the finger force as a function of time. Forces are normalized by the corresponding MVC values. Visual feedback of the force is removed after the 8 s mark. The vertical gray rectangles denote the time bins the data within which was pooled to obtain the estimates of force variables just before, just after, and much after visual feedback removal. These locations are called Phase I, Phase II and Phase III

Analysis of the discontinuous task

The main goal was to compare the performance of the discontinuous tasks with that of the corresponding continuous tasks. Typical subject performances for the discontinuous and continuous cyclic F-task tasks are depicted in Figures 3A and 3B, respectively. Three phases (Phase I, Phase II and Phase III) were defined differently here than for the continuous cyclic F-task vs. constant F-task analysis. In the discontinuous trial (Figure 3A), the last cycle before the 8-s mark, the first cycle after the first peak on task resumption, and the first cycle after the 20-s mark were used to compute the mean (solid lines with dots) and instantaneous amplitudes (dashed lines) at Phase I, Phase II and Phase III of the trial. In the continuous trial (Figure 3B), the amplitude and mean force estimates were obtained by using the cycles in 2-s windows from 6-8 s (Phase I), 14-16 s (Phase II) and the 20-22 s (Phase III). For each subject, the means and amplitudes computed from all repetitions for each condition were averaged and used as the estimates of finger-force behavior for that condition. Note that for the continuous trial, a 2-s window is used to estimate the force mean and amplitude after the 13-s mark (when task was resumed in the corresponding discontinuous trial) since it was not possible to pinpoint the precise time when the chosen cycles in the discontinuous tasks occurred.

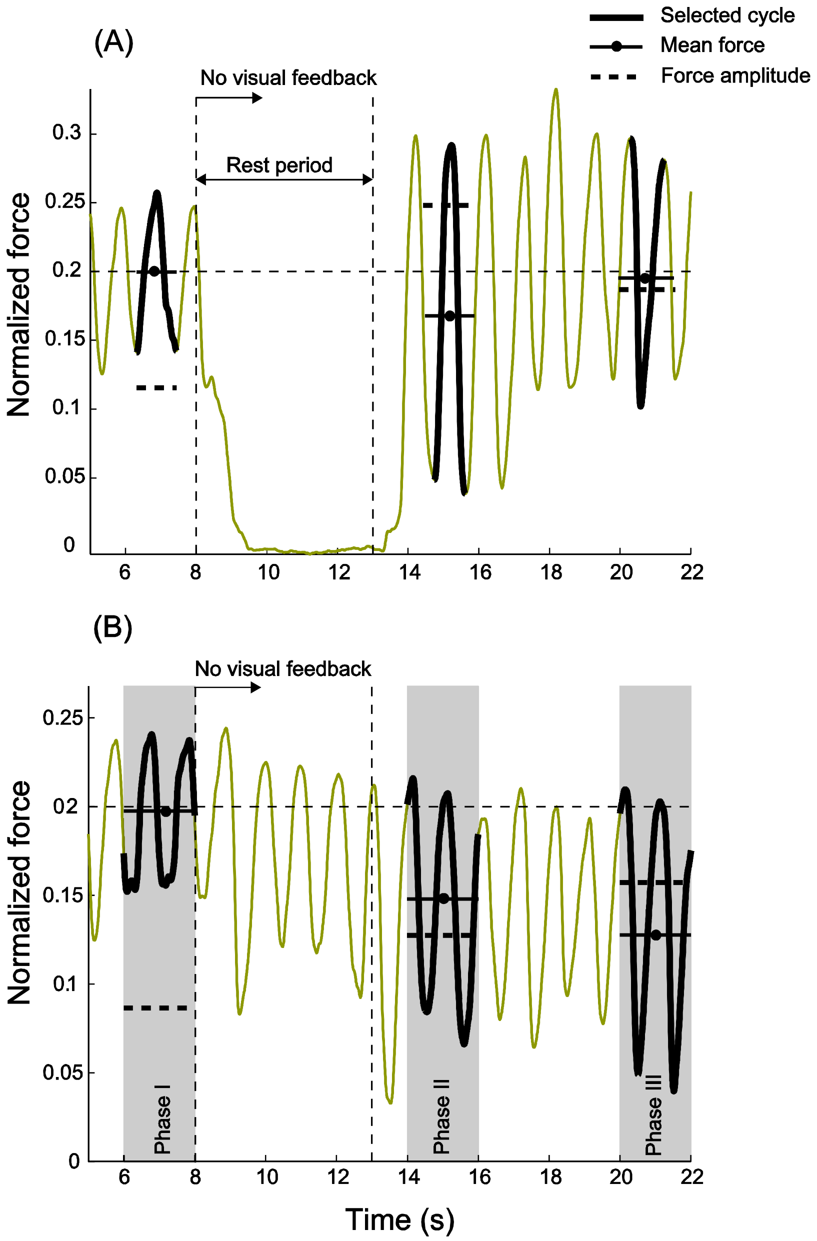

Figure 3. Panel (A) shows a typical response for the discontinuous task. The last cycle before the 8-s mark, the first cycle after the first peak on task resumption, and the first cycle after the 20-s mark are used to compute the mean (line with dot) and instantaneous amplitudes (dashed black lines) at Phase I, Phase II and Phase III. Panel (B) shows the continuous trial. The amplitude and mean force estimates are obtained by using the cycles in 2-s windows placed at the 6 s (Phase I), 14 s (Phase II) and the 20 s (Phase III)

For the discontinuous, constant F-task, the finger forces were quantified over three PHASES as the mean value of the data in three bins: 7.5 - 8 s (Phase I), a 0.5 s bin centered at the first peak of the force after the resumption of the task (Phase II) and 20-20.5 s (Phase III). For the continuous, constant F-task, the Phase I and Phase III bins were obtained similarly. However, the bin for the Phase II force was centered at a different time for each subject. This bin center was the mean of the times of the bin centers for that subject's discontinuous, constant F-task. For each subject, the mean of all repetitions for each condition was used as the estimate of the finger force for that condition.

Statistics

Most data are presented as means and standard errors (SE). To test possible effects of working memory (Hypothesis-1), a three-way, repeated-measures ANOVA on mean force values with factors TASK (2 levels: Continuous and Discontinuous), HAND (Left and Right), and PHASE (3 levels) was performed. To test the effects of removing visual feedback on mean force level (Hypothesis-2), the mean force was subjected to three-way, repeated measures ANOVA with factors HAND (Left and Right), TASK (Cyclic F-task, Constant F-task), and PHASE (three levels). To test Hypothesis-3, the force amplitude was subjected to a two-way, repeated-measures ANOVA with factors HAND (Left and Right), and PHASE (3 levels). 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

Continuous tasks

Removing visual feedback led to an exponential drop in force during the continuous, constant F-task. A similar trend was seen for the mean force for the continuous, cyclic F-tasks. However, the drop in mean force was greater for the cyclic F-task than the constant F-task. Additionally, the force amplitude *increased* after visual feedback removal for the continuous, cyclic F-task. These trends were evident for both the left and right index fingers, as seen in Figures 4A, C and 4B, D, respectively. For the continuous, constant F-task, the data were averaged across subjects. For the continuous, cyclic F-task, the mean force and force amplitudes were computed for all trials and subjects within 0.5-s bins (see Methods). The means ± SE of those data are presented in Figure 4 with the exponential regression lines fitted to the averaged data.

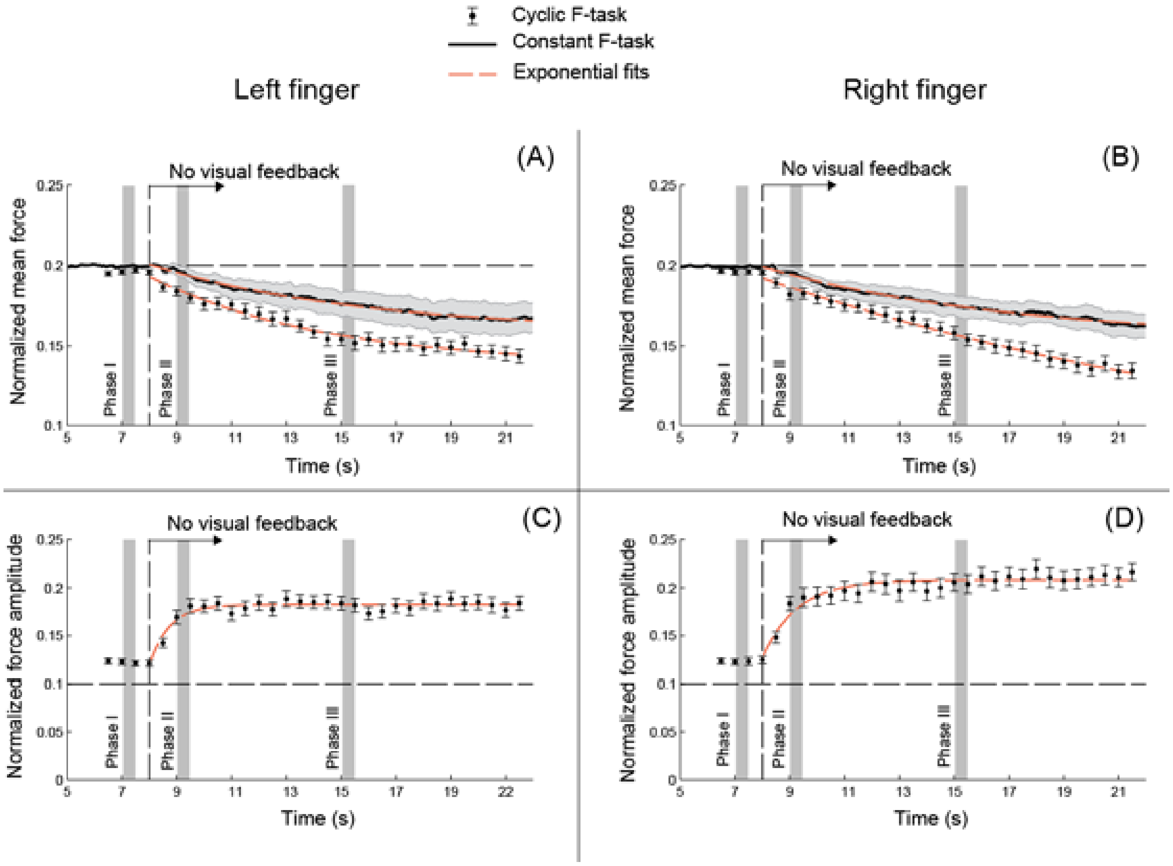

Figure 4. The across-subject mean ± SE for the mean forces and the force amplitudes of both hands are shown. Panels (A) and (B) show the mean finger forces normalized by their respective MVC values. The forces for the constant F-task ± SE appear as thick lines and gray bands. The mean force for the cyclic F-task is binned and the mean ± SE of the binned data is depicted. Panels (C) and (D) show the mean± SE of the binned force amplitudes. The dashed lines passing through the data after the 8 s point in all panels are the exponential fits to the mean values. These lines are sometimes close to the mean traces, and therefore, hard to notice

In the continuous, cyclic F-task, subjects achieved a mean force of about 20% of MVC with full visual feedback. After feedback removal, the drop in mean force was relatively slow with the time constants of 6.4 s and 24.4 s (R^2 = 0.97 and 0.99) for the left and right hands, respectively. During the continuous, constant F-task, force also showed a drop after the visual feedback disappearance. The time constants for the force drop were 7.7 s and 8.9 s ($R^2 = 0.99$ and 0.98) for the left and right hands, respectively. Figures 4A and 4B also show that the net drop in finger force over 14 s after the visual feedback removal was greater for the cyclic than the constant F-task. The force drop magnitude (estimated with the exponential fits) was 9% MVC (Left) and 15% MVC (Right) for the cyclic F-task, while it was about 6% MVC for both hands in the constant F-task.

Statistical analysis validated all the observations above. The mean force for the continuous, constant F-task was greater than that for the continuous, cyclic F-task (0.194 ± 0.003 vs. 0.175 ± 0.05; $F_{(1,9)} = 20.151$; $p < 0.01$). The mean forces also showed an effect of PHASE ($F_{(2,18)} = 38.508$; $p < 0.01$). Pair-wise comparisons revealed that the force prior to visual feedback removal (Phase I; 0.198 ± 0.001) and about 1 s after feedback removal (Phase II; 0.189 ± 0.004) were significantly greater than that about 7 s after feedback removal (Phase III; 0.165 ± 0.005). There was no significant difference between the force values in Phase I and Phase II. The ANOVA also revealed a TASK × PHASE interaction ($F_{(2,18)} = 6.601$; $p < 0.01$) reflecting the fact that the force drop was larger for the continuous, cyclic F-task compared to the continuous, constant F-task (Figure 5A).

During the continuous, cyclic F-task, the force amplitude increased following removal of the visual feedback at a much faster rate than those for the mean force drops (Figure 4C and 4D). The time constants of these changes were 0.5 s and 1.6 s ($R^2 = 0.89$ and 0.91) for the left and right hands, respectively. The two-way ANOVA revealed a main effect of PHASE ($F_{(2,18)} = 18.344$; $p < 0.01$) without an effect of HAND and without an interaction. Pair-wise comparisons showed that the amplitude at Phase I (0.122 ± 0.005) was significantly smaller than at Phase II (0.187 ± 0.017) and at Phase III (0.194 ± 0.018). There was no significant difference in the force amplitudes between Phase II and Phase III (Figure 5B).

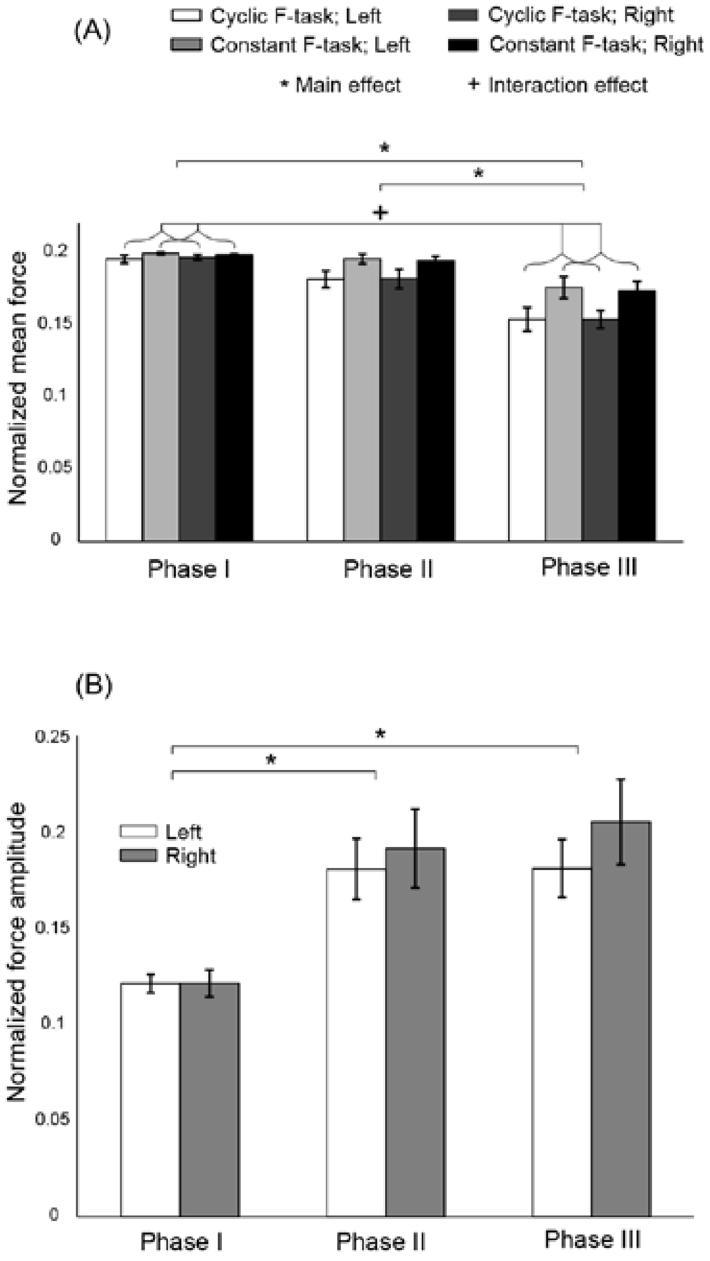

Figure 5. The mean ± SE of the mean forces and the force amplitudes normalized by the MVC values are shown. Data are for the continuous, constant F-tasks and cyclic F-tasks. The stars indicate significant main effects, and '+' indicates interaction effects. See text for more detail

Discontinuous tasks

Cyclic F-task

For the discontinuous, cyclic F-task, the 5-s time interval of rest following the visual feedback removal resulted in an exaggerated increase in the force amplitude (Figure 6A) and a smaller drop in the mean force level (Figure 6B) compared to the force changes seen in continuous, cyclic F-tasks. In particular, force amplitude for the discontinuous, cyclic F-tasks was greater than for the continuous, cyclic F-tasks (0.204 ± 0.016 vs. 0.168 ± 0.011; $F_{(1,9)} = 9.348$; $p < 0.05$). Furthermore, PHASE had a significant effect on amplitude ($F_{(2,18)} = 36.259$; $p < 0.01$); pair-wise comparisons revealed that amplitude for Phase I (0.122 ± 0.004) < amplitude for Phase II and Phase III (0.22 ± 0.018 and 0.216 ± 0.017) without a difference between Phase II and Phase III. There was also a TASK x PHASE interaction ($F_{(1.163,10.471)} = 9.079$; $p < 0.01$) reflecting the fact that the amplitude increase from Phase I to Phase II and from Phase I to Phase III was larger for the discontinuous task as compared to the continuous task.

The mean force across all Phases for the discontinuous, cyclic F-task was significantly greater than that for the continuous, cyclic F-task (0.175 ± 0.006 vs. 0.166 ± 0.004; $F_{(1,9)} = 7.191$; $p < 0.05$). Furthermore, the mean force showed an effect of PHASE ($F_{(2,18)} = 24.942$; $p <0.01$); Phase I (0.195 ± 0.001) > Phase II (0.164 ± 0.007) > Phase III (0.153 ± 0.007). Finally, there was a

TASK x PHASE interaction effect ($F_{(2,18)} = 5.118$; $p < 0.05$). The interaction reflected the fact that the mean force dropped from Phase I to Phase II to Phase III faster for the continuous trials than for the discontinuous trials (Figure 6B).

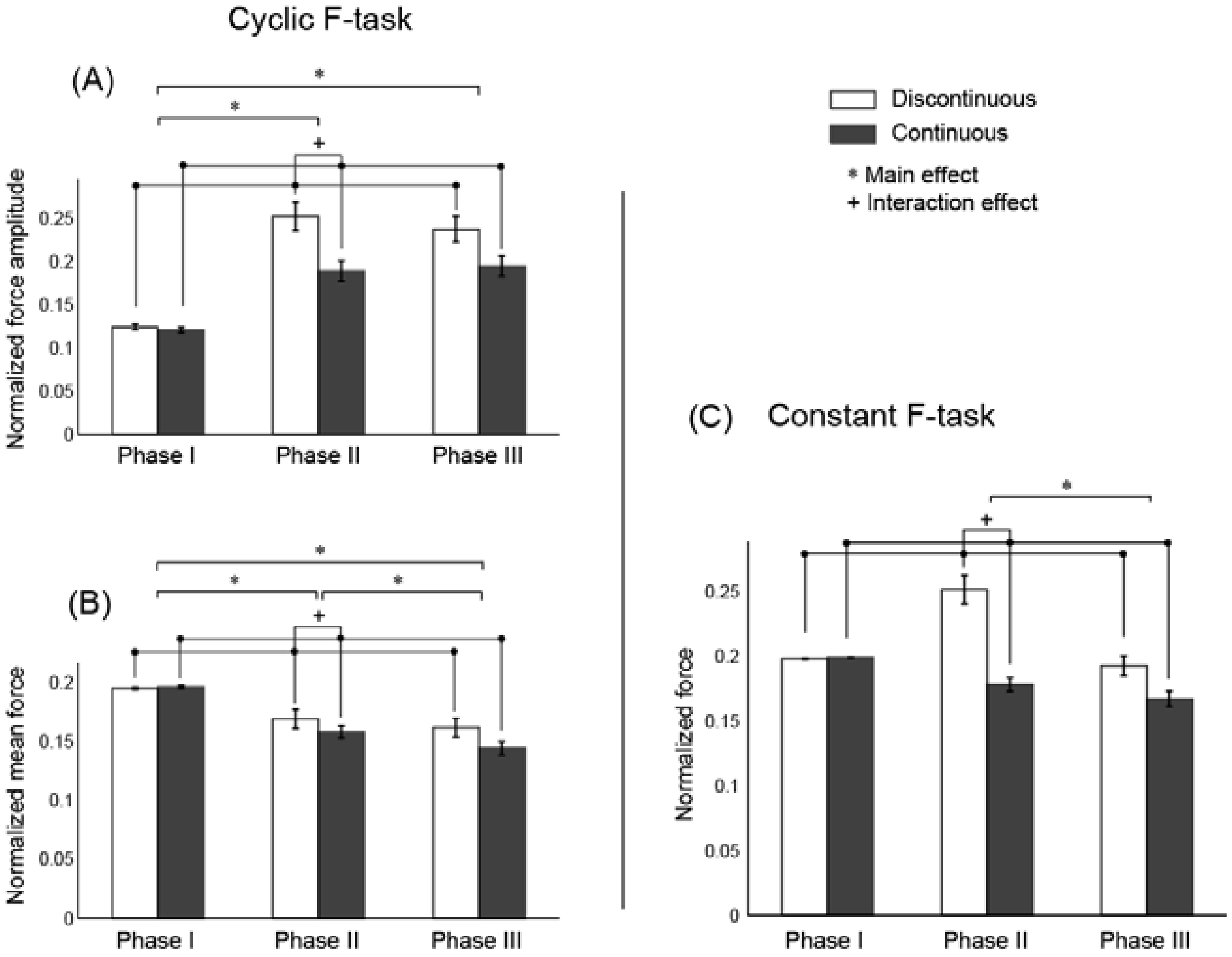

Figure 6. The mean ± SE of the mean forces and the force amplitudes normalized by the MVC values for the cyclic F-task are shown in Panels (A) and (B). Mean ± SE for the constant F-task are shown in Panel (C). Data are for the discontinuous tasks. The stars indicate significant main effects, and '+' indicates interaction effects. See text for more detail

Constant F-task

The means and SEs of the performance of all subjects in the discontinuous, constant F-task and the corresponding continuous trials for the left and right hands are depicted in Figures 7A and 7B, respectively. (Approximate location of Phase II in both panels of Figure 7 is shown).

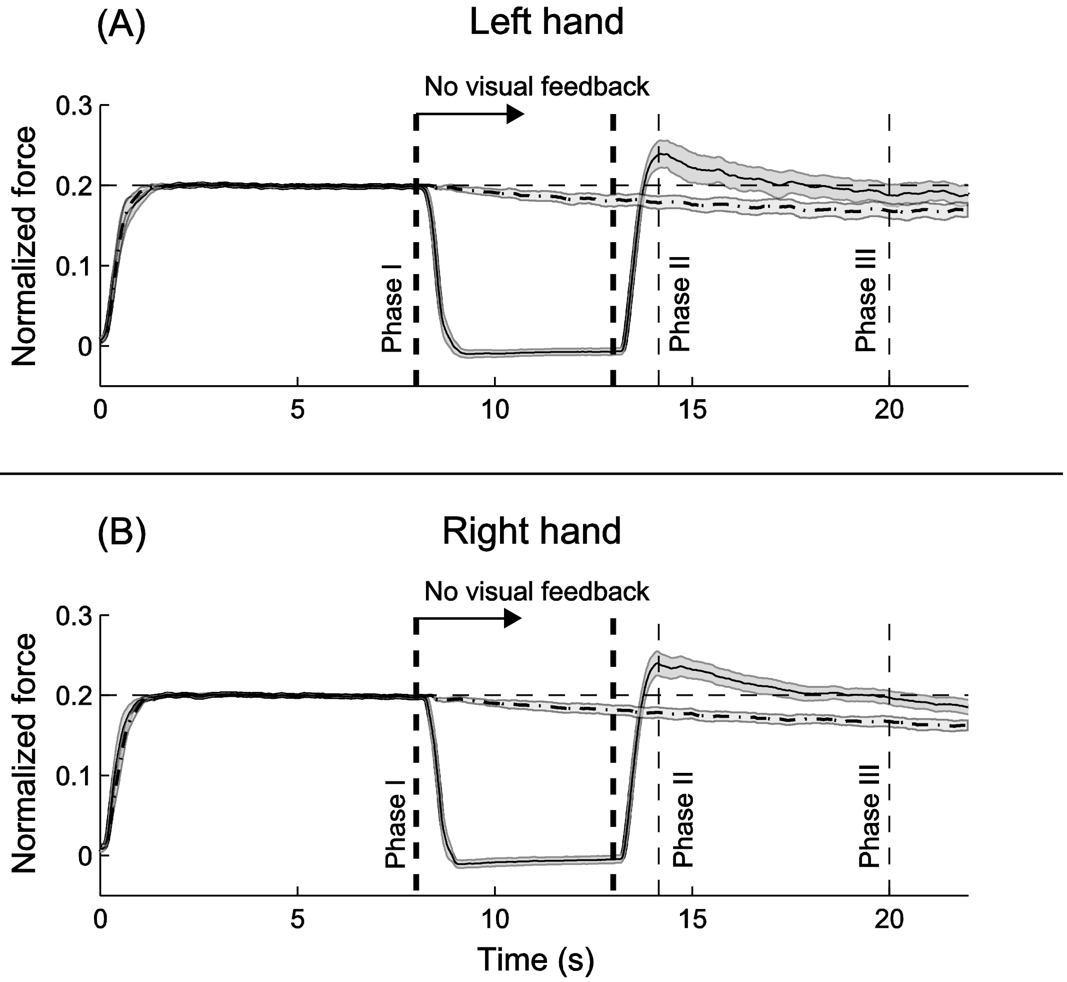

Figure 7. The normalized finger forces for all subjects and repetitions of the constant F-tasks are plotted against time for the left hand in Panel (A) and the right hand in Panel (B). The dash-dot traces are the mean ± SE for the continuous task with visual feedback removal after 8s. The solid traces are

the mean ± SE of the discontinuous task that have a 5s rest between 8s and 13s. The period of rest is indicated by the vertical dashed lines. For the statistical analysis, the forces at 8s and 20s representing Phase I and Phase III, respectively are sampled. Phase II is also represented in the panels as a vertical dash-dot line only qualitatively. See text for details

The finger force produced during the discontinuous, constant F-task was greater than that produced in the continuous task (0.21 ± 0.007 > 0.182 ± 0.005; $F_{(1,9)} = 27.848$; $p < 0.01$). Furthermore, force produced at Phase II was greater than that at Phase III (0.215 ± 0.008 > 0.18 ± 0.008; $F_{(2,18)} = 12.64$; $p < 0.01$). Finally, there was a TASK x PHASE interaction ($F_{(2,18)} = 30.187$; $p < 0.01$). The interaction reflected the fact that the force increased from Phase I to Phase II for the discontinuous task, but dropped for the continuous task (Figure 6C).

DISCUSSION

The experiments provided support for some of the specific hypotheses, but not for others. Our first specific Hypothesis stated that discontinuous trials would lead to no consistent force drift while continuous trials will. For the constant F-task, we observed no downward deviation of force immediately after the rest period in discontinuous tasks while such a deviation was significant at a comparable temporal location in continuous tasks (similar to the data in Vaillancourt and Russell 2002; Ambike et al 2015). So, the hypothesis has been confirmed for constant F-task. In contrast, Hypothesis-1 has been falsified for the cyclic F-task: Indeed, there was a decrease in the mean force and an increase in the peak-to-peak force amplitude after the rest period that were similar in magnitude or even larger than the changes observed in the corresponding continuous tasks.

Our second specific Hypothesis stated that there would be a drop in the mean force during the cyclic F-task similar in time course and magnitude to the force drop in constant F-tasks. This hypothesis was supported in part by the data. Indeed, after the visual feedback was turned off, a relatively slow drift of force was observed during the constant F-task and a similar downward drift of mean force was observed during the cyclic F-task. While the timing constants in the exponential fits varied between hands and tasks, making them difficult to compare across tasks, they were not far from the expected range of 10-15 s (cf. Vaillancourt and Russell 2002; Ambike et al 2015). However, the magnitude of the drift was larger for the cyclic F-task compared to the constant F-task.

The third specific hypothesis, which predicted that the force amplitude would drop with the same time constant as the mean force during the cyclic F-task, has been falsified. There was a much quicker change in the force peak-to-peak amplitude during the cyclic F-task after the visual feedback disappeared as compared to the drift in the mean force and in the force level in constant F-tasks. The characteristic time of the force amplitude increase was, in fact, similar to the times reported for experiments with perturbations (Wilhelm et al. 2013; Zhou et al. 2014; Reschechtko et al. 2014). Moreover, the change in the force amplitude was in the opposite direction (an increase) as compared to the prediction of Hypothesis-3.

These results provide insights into mechanisms underlying constant and cyclic force production. We believe that the results are most compatible with the idea of RC-back-coupling (Ambike et al. 2014; Zhou et al. 2015) described further in this section. Some of the results, however, have no straightforward explanation: They raise more questions than they answer.

Unintentional force drift: Possible causes

While the phenomenon of unintentional drop in force without visual feedback has been known over at least 15 years (Slifkin et al. 2000), it has not drawn sufficient attention. Indeed, after the original publication, only a few studies explored this phenomenon (Vaillancourt et al. 2001, Vaillancourt and Russell 2002, Shapkova et al. 2008), and it was also invoked in studies of “slacking”, a phenomenon observed in stroke survivors who show a drop in effort when helped by an external device (Reinkensmaier et al. 2009). The original interpretation that the phenomenon reflected a limitation in the working memory was indirectly supported by a study of patients with Parkinson's disease (Vaillancourt et al. 2001) and has not been challenged until recently (Ambike et al. 2015; Jo et al. 2015).

In the current experiment, we used a short rest period (discontinuous tasks) to test possible effects of working memory. The logic was that, if the memory limitation indeed was responsible for the force drop during continuous force production, a similar force drop or even a stronger one could be expected over a comparable time interval of rest, since the subject was forced to rely exclusively on memory during the rest period. This prediction was falsified for the constant F-task. Indeed, immediately following the rest period, there was an increase in the force, which then showed an exponential drop similar to the one observed in the continuous, constant F-task. At all times, however, force levels during the discontinuous, constant F- task were higher than during the continuous, constant F-task (see Figure 7).

To our surprise, however, the "memory hypothesis" has been at least partly supported for the cyclic F-task. After the rest period in discontinuous, cyclic F-tasks, there was a drop in the mean force level and an increase in the peak-to-peak force amplitude that were qualitatively similar to the effects observed in the continuous, cyclic F-tasks (Figure 6). The effect of visual feedback removal + rest period on the mean force was smaller and the force amplitude was larger than the effects of visual feedback removal alone had on those quantities.

It is possible that the increase in the force level in the discontinuous, constant F-tasks and in the force amplitude in the discontinuous, cyclic F-task reflected the quick increase in force after the rest period leading to an overshoot of the desired force level. Such an overshoot is expected from an underdamped system; note that the available estimates of the apparent stiffness and apparent damping of fingers suggest that the system is indeed underdamped (Park et al. 2014).

Fatigue was an unlikely contributor to the observed unintentional force changes. The force levels in the experiment were relatively low and not expected to lead to fatigue. Force drift phenomena started within a few seconds after the visual feedback was turned off (within 10-12 s after the trial initiation), which is too short to induce visible fatigue effects. Hence, in the next subsection we turn to the only remaining hypothesis on the nature of unintentional force changes, the RC-back-coupling hypothesis.

The increase in the force amplitude during the cyclic F-task remains without an explanation. We can only speculate at this time that this force amplitude increase reflected a drift to a potentially frequency-dependent optimal magnitude of RC change within a cycle. This could result from involvement of non-linear oscillatory processes as assumed in many studies starting from the classical works of Schöner and Kelso (1988; see also Schöner 1990).

RC-back-coupling hypothesis on unintentional actions

The idea of control with referent body configurations (RCs) is a generalization of the classical equilibrium-point hypothesis (Feldman 1966, 1986) to multi-muscle actions. The RC hypothesis, in its most recent form (Latash 2010; Feldman 2011, 2015), assumes that neural signals at the hierarchically highest control level encode spatial referent coordinates for a few task-specific, salient performance variables. Further, a sequence of few-to-many mappings results in referent coordinates for variables at lower levels of the hierarchy, e.g., those related to actions by individual effectors, joints, muscles, etc. The difference between the referent and actual coordinates for the salient variables drives the actual coordinates to their corresponding referent values, if such motion is unimpeded. If external conditions keep the actual body configuration from moving to its RC, the effectors generate net forces on the environment. We emphasize that control variables within the RC-hypothesis are spatial, while peripheral consequences of their shifts may be expressed in different physical variables, such as force (as in our study).

The RC hypothesis is naturally compatible with the principle of abundance (Gelfand and Latash 1998; Latash 2012) and the idea of synergies as neural organizations stabilizing values or time profiles of salient performance variables (reviewed in Latash 2010). Movement of actual body configuration to RC may be addressed as direct coupling within the scheme; it is supposed to proceed quickly with typical times of about 0.1 s (conduction time delays plus the electromechanical delay; cf. Corcos et al. 1992). A series of recent observations have suggested that, if body motion towards RC is impossible, RC may drift towards the current actual configuration – a phenomenon addressed as RC-back-coupling (Wilhelm et al. 2013; Zhou et al. 2014; Ambike et al. 2014). The notion of RC-back-coupling has been introduced to account for unintentional drifts of performance in kinetic and kinematic variables observed when subjects, who began an action with the assistance of visual feedback, were instructed to continue to produce the action after the visual feedback was removed.

Two types of RC-back-coupling have been suggested to account for relatively fast (with characteristic times of about 1 s; Zhou et al. 2014; Reschechtko et al. 2014) and relatively slow (with characteristic times of 10-15 s; Ambike et al. 2015) unintentional drifts in performance. The former is observed in tasks with quick force changes, for example those induced by transient perturbations, while the latter is seen in steady-state tasks. If one assumes that the observed drifts in performance reflect natural relaxation processes in the physical-physiological system, the two time constants, 1 s and 10 s, point to the existence of two separate processes. We suggest that the two time constants reflect typical relaxation times within the uncontrolled manifold (UCM) and the manifold orthogonal to the UCM (ORT) as defined within the UCM hypothesis (Scholz and Schoner 1999). The UCM and the ORT are manifolds in the (redundant) space of elemental variables for the task. In our study, the single-finger force production task is redundant at a number of hidden levels involved in the force production, e.g., the level of muscle involvement and motor unit recruitment. The task may also be conceived within the space of control variables, such as the r-command and c-command (Feldman 1980), or in the space of thresholds of the tonic stretch reflex (l) for the involved muscles (Feldman 1966, 1986, 2009). The analysis within the RC hypothesis assumes that elemental variables are spatial (referent coordinates) while performance variables may have different measurement units. In particular, one can formally compute in the space of r- and c-commands (or in the space of l values) a manifold corresponding to no changes in finger force in isometric conditions – the UCM for this analysis. Any deviation along the UCM, by definition, does not affect the salient performance variables (the fingertip force). Hence, as assumed in the original study of Scholz and Schöner (1999), processes within UCM show low stability, which naturally corresponds to slower relaxation processes. In contrast, deviations along ORT are resisted vigorously since they affect the performance variable, and therefore, relaxations along ORT are presumably fast.

The force drifts in the constant F-task and in the mean of the cyclic F-task were slow. These drifts present a puzzle, since they occur along the ORT manifold for the performance variable (force), whereas drifts along ORT are supposed to be fast. The contradiction can be resolved by positing that the UCM and ORT are coupled (in contrast to what has been assumed thus far in the literature), and the observed ORT drifts are, in-fact, reflections of slow processes in the UCM that leak into the ORT via the coupling. Note that the two manifolds, UCM and ORT, are defined with respect to stability of a performance variable. Although they are mathematically orthogonal, we are discovering new underlying processes that produce correlated changes in the two manifolds. Therefore, empirically, these manifolds are not independent. The suggested coupling is an initial step to model the effect of the new process on the measured data. This is a purely speculative view, and we are currently working on providing experimental support.

In contrast to the UCM-triggered slow drifts along ORT, the fast drift of the peak-to-peak amplitude in the cyclic F-task (Figures 4C, 4D, 5B) suggests another process within the ORT manifold. Note that its timing is similar to the time characteristics reported in earlier studies with external perturbations of constant-force-production kinematic and kinetic actions (Wilhelm et al. 2013; Zhou et al. 2014; Reschechtko et al. 2014). These observations suggest that both externally driven and intentional processes can trigger a relatively quick motion of RC along ORT.

The RC-back-coupling hypothesis predicts that, given enough time, RC will approach the actual finger coordinate, and the force will vanish. However, this is not observed: In all the cited studies, the force dropped by a substantial amount, but saturated at levels far from zero (on the order of 50% of the initial force). Other factors, such as somatosensory feedback, may be responsible for curtailing the RC-back-coupling drift, despite the explicit instruction to the subjects “not to correct” the ongoing action. Involvement of such factors has been assumed in studies of similar phenomena during multi-joint positional tasks (Zhou et al. 2015). This is another speculative explanation in need of experimental exploration.

Concluding Comments

A rather old discussion on the nature of discrete versus cyclic actions views cyclic actions as a concatenation of discrete components and discrete actions as half-a-cycle of a cyclic action stopped in an appropriate phase (reviewed in Schöner 1990; Hogan and Sternad 2007). Our results suggest a somewhat different dichotomy, between a constant action and a cyclic action. Indeed, a constant force-production action may be viewed as a special case of a cyclic action given the presence of physiological tremor. On the other hand, a constant action under visual (or other modality) feedback may be viewed as an action involving a sequence of corrections that represent small discrete actions.

Our results reflect differences in constant and cyclic actions. First, while the constant F-task showed a slow decay in force, the force drift in the cyclic F-task had two distinct characteristics: The mean force level decayed similarly to that of the constant F-task, although to a greater extent, but the peak-to-peak amplitude changed much faster and in the opposite direction. Second, the effects of the 5-s rest period seen in the discontinuous tasks were qualitatively different. No drift of force was seen in the constant F-task. In contrast, the cyclic F-task showed effects on both mean force level and peak-to-peak amplitude similar to those observed in the continuous tasks. These observations suggest qualitative differences in the neural control of constant and cyclic actions. On the one hand, this view is supported by recent imaging work: Neely et al (2013) showed that static precision grip force production was associated with unique blood-oxygen-level-dependent (BOLD) activity in a right-lateralized cortical network, and, in contrast, dynamic precision grip force was associated with unique BOLD activity in left-lateralized and midline cortical regions of the cortex. On the other hand, we are still searching for physical-physiological explanations as to why the RCs for the cyclic F-task have different back-coupling drift characteristics as compared to the constant F-task.

Finally, we mention limitations of the present study. First, we did not explicitly test the effect of fatigue on the force production. However, the force levels observed in this study are lower than those required to produce measurable fatigue (Singh et al. 2012). Second, we utilized a 5-s rest period during the discontinuous tasks. It remains to be seen whether larger rest periods will alter memory effects. Finally, although the two hands show some differences on average (see Figure 4), we did not observe any statistically significant differences in the task performance of the two hands while such differences could be expected, for example, from the dynamic dominance hypothesis (Sainburg 2002). This may be because the tasks employed in the study were relatively easy.

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Author conflict of interest

None.

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