



Repetitive finger force production in predictable environments

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ABSTRACT

Previous research suggests that removal of visual feedback of force output in a sequential force production task results in a continuous escalation of the force magnitudes produced. Central predictive mechanisms involving reafference result in self-generated forces being perceived as weaker, thus leading to a systematic over-production of force. While this effect has been widely examined with respect to sensation of self-produced stimuli, its role in the sequential production of discrete forces has not been extensively studied. The objective of the present experiment was to further investigate the force escalation effect by examining the sequential force production task in two predictable environments where force targets progressively changed between 8 and 16 N. In one environment target force magnitudes continually increased at a predictable rate, while in the second target force magnitudes decreased at the same rate. Eight healthy participants produced a series of repetitive pinch grip forces in time to a metronome at a frequency of 2 Hz. Visual feedback of force output was removed 10 s in to the trial, with participants performing continued responses for the remaining 20 s. Following removal of visual feedback participants rapidly accrued errors in force magnitude, but slopes of the peak force series did not differ from those of the target series. Errors in magnitude were bi-directional, showing dependence on the increasing or decreasing environment in which the task was performed. The observed escalation and de-escalation effect can both be attributed to central predictive mechanisms and the force salience effect in reafference.

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All interactions between an organism and its environment are dependent on the ability to distinguish self-generated sensory information from that which has an external source. It has been reliably shown that self-generated tactile stimuli are perceived as weaker than external stimuli of the same magnitude [1–3,13,16]. Many researchers have proposed that information from the motor command is used to distinguish the consequences of self-produced actions from externally sourced stimuli [13,16]. Specifically, a predictive mechanism where a forward model (constructed from the efference copy of a motor command) anticipates the sensory consequences of an action has been proposed [1]. The predicted component is thought to be subtracted from the incoming sensory information, effectively attenuating the self-generated feedback [1–3,13,16].

Sensory attenuation with self-produced stimuli has been documented in discrete and isometric force production tasks [1,13,16], but this effect has not been extensively studied in sequential force production. Previous work by Therrien and Balasubramaniam sug-

gested that removal of visual feedback of force output during sequential force production task results in an increase in the force magnitude responses over time. This effect was interpreted in the context of predictive mechanisms involving reafference. Self-generated forces were perceived as weaker leading to a systematic compensatory over-production of the force magnitudes required [13,14,16]. In the previously noted experiment, target force magnitudes remained constant throughout the trial. However, in most natural force production settings, such as when hammering a nail or playing the piano, we often have to scale the produced forces to target requirements. Said differently, one has to adjust the relationship between successive forces in order to produce forces of equal, less or greater magnitude. The slope of any given force time series (the rate of change) is a good indicator of how two adjacent forces are scaled within a time series.

The objective of the present experiment was to further investigate the force escalation effect [14] by examining the sequential force production task in two predictable environments where force targets progressively changed between 8 and 16 N. To set up the experimental conditions, we modified the repetitive force production task used by Therrien and Balasubramaniam. In the present experiment, pinch grip forces were rhythmically produced in two target force ramp conditions. In two conditions the target force levels increased or decreased at a constant rate throughout the

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trial. Consistent with the mechanism proposed in earlier results [13,14,16] we predicted that regardless of the target force ramp condition, following removal of visual feedback of force output, the magnitude of the forces produced would change. If the force output is perceived to be lower than the target (due to reafference) and the target force required on the next iteration is higher, the participant would produce an even larger force that leads to escalation. In the downward ramp, the expectation task dictates that the force produced in a subsequent iteration is less than the previous one. If the force produced in the previous iteration is perceived to be less than it actually is, the level of force produced in the subsequent iteration will be even less thus leading to a reduction in force magnitudes (de-escalation).

In experimental terms, we made the following predictions. In the condition where the target force level was increasing throughout the trial, we predicted that the removal of visual feedback would result in a further increase in the force production levels from the target (escalation effect). Conversely, in the decreasing ramp condition, we predicted that the magnitude of forces produced will be lower than those required by the target (de-escalation effect). As we did not expect visual feedback to play a role in the relative scaling between forces, we did not expect to see any changes in the slope of the force series produced by the participants and the target force series.

Eight healthy participants (six male, two female) volunteered for this experiment. All were students from McMaster University and were right handed according to both self-report as well as the Edinburgh Handedness Inventory [10]. Participants were free of any known neurological impairment or musculoskeletal impairments to the upper extremities and had normal or corrected normal vision. In keeping with the Declaration of Helsinki, prior to participation, volunteers gave their informed consent in accordance with McMaster Research Ethics Board regulations.

Similar to the apparatus used in Therrien and Balasubramaniam, force data were collected using a 6-DOF load cell (ATI Nano 17) mounted on a stainless steel stand so that forces were applied on the horizontal (z axis). The apparatus was fixed to a table with a computer monitor placed behind for subject's feedback. Force data were sampled at 1000 Hz with data acquisition hardware (National Instruments DAQ-card-6024E) using custom software written with Labview (Labview 8.2, National Instruments). This software was customized to provide visual feedback to the subjects on a Viewsonic 19 in. flat panel display with a refresh rate of 60 Hz. The force transducers were calibrated with a 6×6 matrix that describes the relation of voltage gain to resolved force. The factory-generated calibration matrix allowed for correction of crosstalk between each measured force and moment axis. Furthermore, signals were amplified with the packaged AMTI amplifier, and signals digitized with the National Instruments PCI-6220 DAQ. This combination of voltage amplification and 16-bit resolution of a DAQ lead to an ultimate resolution of $1/320$ N in the z axis. There was no hysteresis in the zero level of the resolved forces ensuring that there was no significant drift or offset in the force data due to ongoing use of the apparatus. The gain was set so that a change in force output of 1 N corresponded to a 1 cm change in amplitude.

Participants were seated in a comfortable, non-rotating chair with their right forearm resting on a table. They were positioned so that they could comfortably reach the force transducer and successfully perform the pinch grip (between the thumb and index finger) motion on it. During each testing session, participants were given a visually specified target force and were asked to match the target force magnitude by pinching the force transducer between the right thumb and index finger. The magnitude of the target force was presented as a column in a bar graph on the flat panel display placed at a comfortable distance in front of the participant. A second column adjacent to the target bar represented the current

force output produced by the participant. Force levels produced were indicated by changing amplitudes with each press on the load cell. To produce the ascending and descending target force ramps, the amplitude of the target column changed 100 ms before each subsequent pinch. Participants were instructed to continually match their force output with the magnitude specified by the target column by modulating their grip force with each press.

All test participants were given five practice trials with both ramp directions (ramp up and ramp down) and full visual feedback of their force output. Following this, experimental conditions were presented in a blocked manner. For a given ramp direction, participants were tested with full visual feedback prior to being tested with trials where it was removed. Movement rate was specified by a metronome with a frequency of 2 Hz, corresponding to time intervals of 500 ms between peak forces. Each trial lasted 30 s. In certain experimental conditions, visual feedback of both the current force output and target force amplitude was removed 10 s into the trial. Participants were instructed to make continued responses for the remaining 20 s by increasing or decreasing their force output on each press to match the rate of change of the target force ramp presented in the first 10 s of the trial. Thus there were two visual feedback conditions (visual feedback and no visual feedback). There were five repetitions of each condition.

Force data were stored for offline analysis using a customized PC workstation. A custom written script in MATLABTM extracted the peak force (PF) magnitude from each pinch on the force transducer, as well as the iteration and time at which it occurred. PFs were extracted to quantify the magnitude of force produced to be compared against the target force level. Mean PF time series were then computed for each participant and group means were compiled for each ramp condition. Variability in performance was quantified through calculation of constant and variable error. Only the continuation phase ($t = 10\text{--}30$ s) from each trial was used for analysis. Means were calculated across 5 repetitions per condition as well as across participants. SPSSTM software was used to conduct separate analysis of variance (ANOVA) with repeated measures for constant and variable error values in the two target force ramp conditions as well as independent samples t -tests comparing slope and intercept values between PF series produced by participants to those of the target PF series.

The PF time series produced in the increasing and decreasing ramp conditions can be seen in Fig. 1. Bi-directional errors in force magnitude were observed for the two ramp directions once visual feedback of force output was removed. In the ramp up direction, this resulted in the development of positive errors in force magnitude. In the ramp down direction, however, the opposite trend was noted. Once visual feedback was removed, participants' force output was continually lower than target magnitudes. Except for one subject who constantly overproduced the force levels, there were very few inter-individual differences in performance. We recognized the presence of this outlier in our subject data (see Fig. 1B and D). However, analysis of the data after removing data from this subject revealed no major differences in the results obtained. Considering this, we included all the data from all eight subjects in our analyses.

This effect is further illustrated in Fig. 2. A set of 2 (ramp conditions: ramp up and ramp down) \times 2 (visual feedback conditions: full and no) ANOVAs with repeated measures revealed an interaction between ramp direction and visual feedback condition for mean constant error in the continuous ramp condition (Fig. 2A; $F(1,7) = 42.55$, $p < .001$, $\eta^2 = 0.86$). Constant error values were low and did not differ between ramp directions when visual feedback of force output was present throughout the trial. In trials where visual feedback was removed, however, the direction of errors was dependent on the ramp direction. In ramp up trials, mean constant error was positive, demonstrating that participants consistently

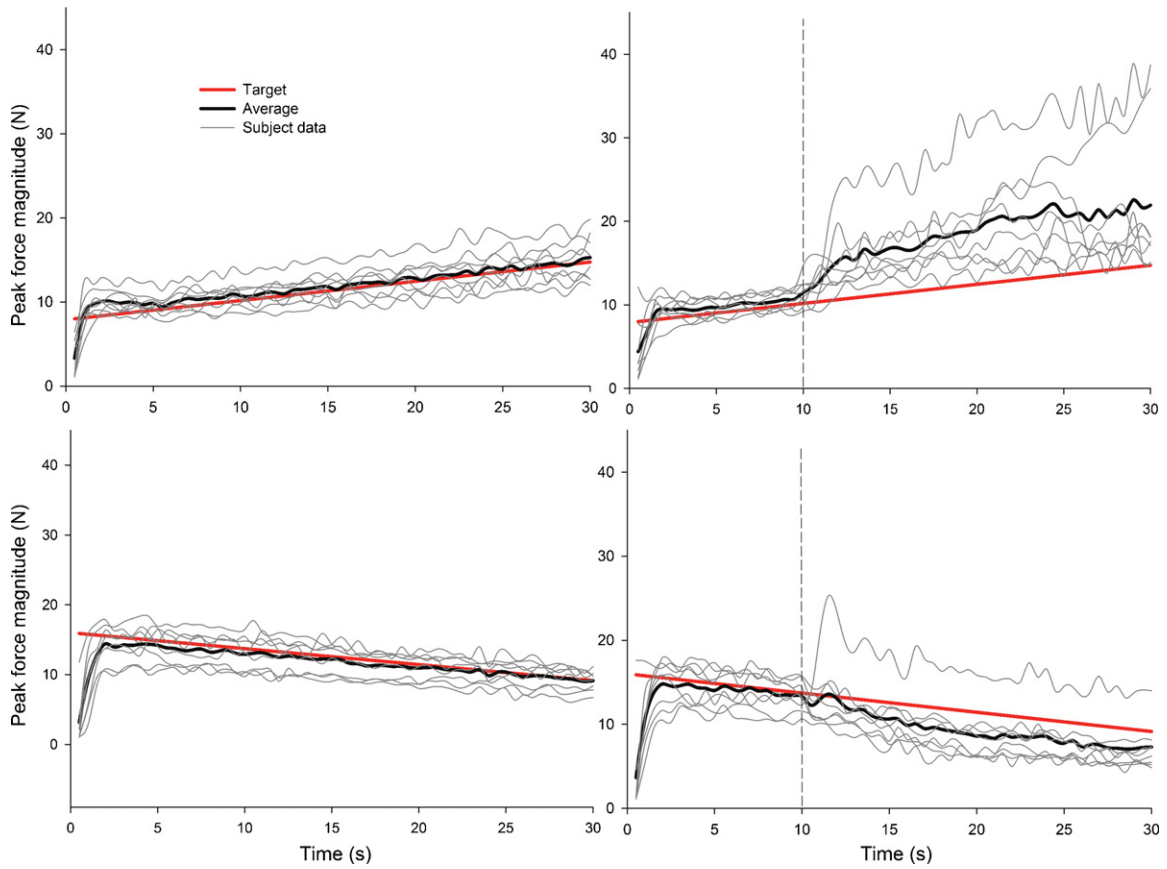


Fig. 1. The peak force series are plotted for both ramp directions and visual feedback conditions. Top panel: peak force series produced in the ramp up direction. Bottom panel: peak force series produces in the ramp down direction. (A and C) Visual feedback remained present throughout the trial. (B and D) Visual feedback of force output was removed after 10 s. Vertical dotted lines indicate the time at which visual feedback was removed.

over produced force in these trials. In ramp down trials, mean constant error was negative, indicating a continual undershooting of target force magnitudes. Despite this trend, it should be noted that the difference in constant error values between the two visual feedback conditions in the ramp down condition was not statistically significant. 2×2 ANOVAs with repeated measures were also performed for both target force ramp conditions on mean variable error. Fig. 2 illustrates the interactions obtained for both conditions ($F(1,7) = 28.00, p < .01, \eta^2 = 0.80$). In both cases, regardless of

ramp direction, mean variable error remained low and constant in the presence of visual feedback of force output. When visual feedback was removed, an overall increase in variable error was observed. We also noted that this error was smaller in the ramp down direction.

To further assess these dependencies on ramp direction, independent samples t -tests were performed comparing participants' mean slope and intercept values with those of the target peak force series. Analysis of mean slope revealed a significant difference

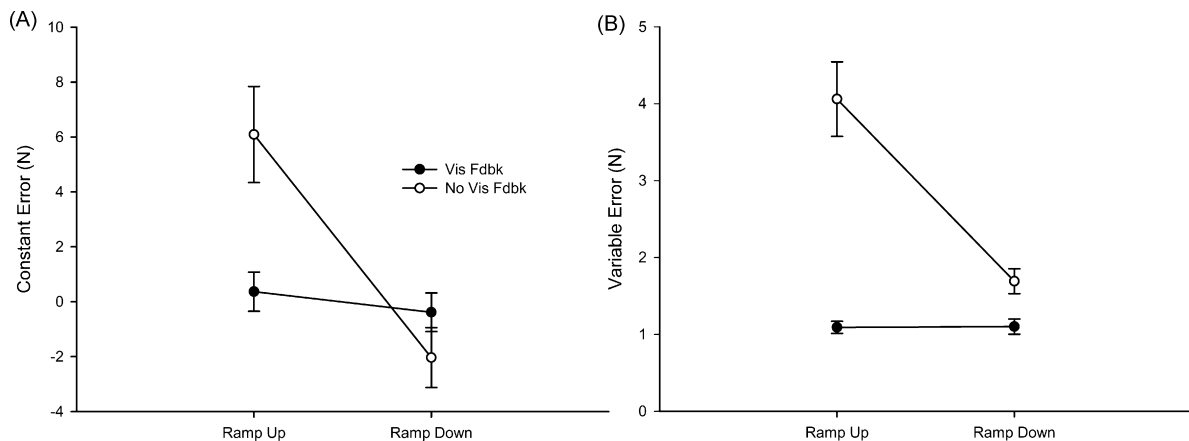


Fig. 2. (A) Constant error values are plotted for both ramp directions as well as both visual feedback conditions. Removal of visual feedback resulted in a positive mean error in the ramp up direction, whereas it resulted in a negative mean error in the ramp down direction. (B) Variable error values are plotted for both ramp directions as well as both visual feedback conditions. In the absence of visual feedback, mean variable error decreased in the ramp down direction. Error bars indicate standard error of the mean.

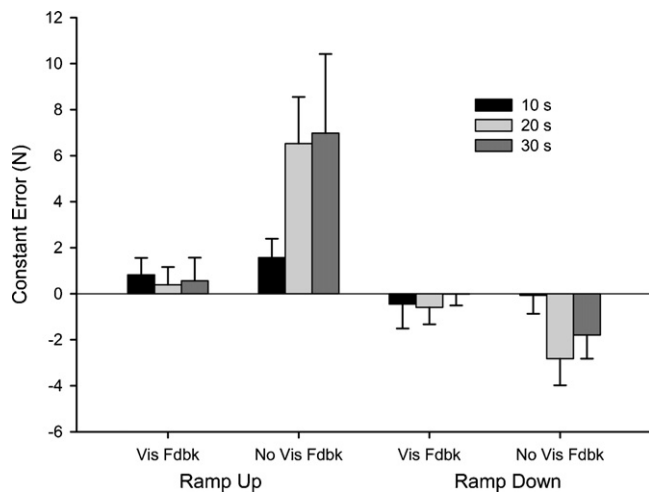


Fig. 3. Constant error values at three time points ($t = 10, 20$ and 30 s) are plotted for both ramp directions as well as both visual feedback conditions. Bi-directional errors in force magnitude are visible for the two ramp directions in the absence of visual feedback. Error values were also dependent on the time at which they were measured. There is an initial increase in errors between 10 and 20 s followed by stabilization of errors, although the force magnitudes keep increasing and decreasing in the two conditions, respectively.

between participant and target series only in the ramp down direction, when visual feedback was removed ($t(14) = 2.41, p < .05$). Mean slope values were less steep than for the target peak force series. This was likely due to floor effects in participants' ability to decrease their force output any further.

Analysis of the mean intercept did not reveal any differences between participant data and the target force, suggesting that at point of removal of visual feedback, participants produced target forces in the range of the required force level. We chose to do the simpler analyses of slope rather than use time-series methods such as ARMA/ARIMA to look for trends for two reasons. First, our analysis adequately served to demonstrate that the (de)escalation effect resulted in increase or decrease in error accrual. Secondly, with only forty peak force observations after the visual feedback is removed, complex time series analyses (such as rescaled range analyses) are likely to be less reliable and informative [7].

To test the time dependency in error development following removal of visual feedback of force output, we did the following analyses. Constant error values were calculated for three time points: 10, 20 and 30 s. A repeated measures ANOVA was performed with the factors 3 (time points: 10, 20 and 30 s) \times 2 (ramp conditions: ramp up and ramp down) \times 2 (visual feedback conditions: full and no). The interaction obtained is shown in Fig. 3. A significant interaction was obtained between ramp direction, visual feedback condition and time point ($F(2,14) = 41.74, p < .01, \eta^2 = 0.53$). The bi-directional errors in force magnitude were again observed for the two ramp conditions in the absence of visual feedback of force output. While error values for the three time points did not differ when visual feedback was present, error values were dependent on the time at which they were measured after visual feedback was removed. For both ramp conditions a large increase in force magnitude error is noted between the 10 and 20 s time points. After the 20 s point the error stabilized, confirming what was already noted in the slope analyses.

We predicted that reafference mechanisms reducing the salience of self-generated forces would result in errors in force magnitude in a sequential force production task. We expected to see evidence of this in consistently increasing positive errors in force magnitude following removal of visual feedback of force output in the ramp up condition. Almost immediately following

removal of visual feedback, positive errors in force magnitude were made by the participants (please see Fig. 1B). This supports the notion of a predictive mechanism causing self-generated forces to be perceived as weaker. Participants produced more force than was required in order to compensate for the forces perceived to be weaker. In the ramp down direction the predicted trend was observed, but in the opposite direction. When target forces decreased in a predictable manner the trend was to under produce force following removal of visual feedback. In the context of the decreasing ramp, when subjects perceive that the force output in an earlier iteration was lower than it actually was, they compensated by producing even less on the subsequent iteration. Despite consistent errors in magnitude, the mean slope in both target force ramp direction conditions did not differ significantly from the slope of the target force series. This suggests that participants were able to accurately scale the relation between sequential forces. Taken together, these results suggest that the escalation effect noted in the sequential force production tasks is not the result of accumulation of errors in the force production mechanisms themselves.

Similar preservation of accurate scaling relations but inaccurate force magnitude production in healthy individuals has been found in previous rhythmic force production tasks (c.f. [11,12]). This finding falls in line with evidence from functional imaging studies that the brain areas involved with controlling the magnitude of force output and scaling the relative magnitudes in a series of forces may be different. Control of force magnitude is associated with activation of primary motor and sensory areas, supplementary motor area, premotor and prefrontal areas, parietal and cingulate cortices and cerebellum [4,6]. However circuits involving the basal ganglia, specifically the subthalamic nucleus and internal segment of the globus pallidus, are activated when the accurate scaling of forces relative to one another is required [11,12,15].

Blakemore et al. [2] have found neural correlates for the mechanism of reafference in self-produced stimuli using functional imaging. Stimuli from self-produced movements are associated with reduced activity in both the somatosensory cortex (S1) and cerebellum when compared with externally generated stimuli. The decrease in S1 activation correlates with neurophysiological data showing reductions in neuron activity following voluntary touch, compared to external touch of the same area [5]. The changes in S1 activity are thought to be mediated by the cerebellum, whose activity decreased when self-produced movements resulted in a tactile stimulus. Interestingly, cerebellar activation was not mediated by movement alone and showed increased activation when externally produced tactile stimuli were applied. Blakemore et al. [3] took these results to suggest that the cerebellum distinguishes movements based on their specific sensory consequences. Voss et al. [16] have shown that theta-burst stimulation of the primary motor cortex during a force matching task results in decreases in the sensory attenuation known to occur with self-generated movements. Taken together, these findings further support the proposed distinction between the perception of force magnitudes and relative scaling between them in the brain.

Our results showing bi-directional changes in force magnitudes may also be explained in the context of central predictive mechanisms. It is well known that sensory input is highly variable due to noise present in the motor system and the differential manner in which self-produced and externally sourced stimuli are processed [1–3,8,13,16–18]. It has been proposed that in addition to incoming sensory information, the CNS also makes use of knowledge from prior experience [9,17,18]. A possible mechanism for this has been proposed using Bayesian integration, where it is hypothesized that the CNS optimally combines this prior knowledge with sensory inputs to generate a state estimate [9,17,18]. Due to central modulation of incoming proprioceptive information, the self-generated feedback from each press on the load cell gave an

unreliable estimate of the force produced when visual feedback of force output was absent [13]. This sensory input was then combined with the prior knowledge that the target force series was increasing or decreasing in a predictable manner. Combination of the present state estimate of the motor output with prior knowledge of the target force series could also create an over-production effect in the ramp up condition and a de-escalation in the ramp down condition. Thus our results provide an interesting problem to model using Bayesian methods. Körding et al. [9] have found evidence for Bayesian integration in force estimation in a task that required the production of an experienced force. The possibility of a similar mechanism working in a sequential task warrants further study. In all of these studies, an issue that remains unclear is whether the escalation of forces has an upper bound. This issue has not been looked at in Shergill et al.'s paper [13] and the present study.

Voss et al. [16] have shown that stimulation of the motor cortex improves production of self-generated stimuli. It would be interesting to see if this improvement in the production of self-generated stimuli would extend to a reduction of the force (de)escalation effect in constant and predictable environments. We are currently pursuing this idea in our laboratory with theta-burst stimulation over the primary motor area (M1) in human subjects.

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