

Timing and visual feedback constraints on repetitive finger force production

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Abstract While much is known about sequential effects in motor timing, less is understood about whether movement parameters such as force show sequential dependencies. In this study, we examined the effect of timing constraints on repetitive unimanual force production sequences. Ten healthy participants produced a series of pinch grip forces in time to a metronome and to visually specified force amplitudes. Either visual feedback of force produced or the auditory metronome removed 10 s into the experimental trial, with participants performing continued responses for the remaining 20 s. In the continuation trials, a negative lag-1 autocorrelation in the inter-response intervals (IRIs) was observed as is commonly seen in motor timing tasks. However, removal of visual feedback resulted in a systematic increase in mean force output through the course of the trial, resulting in positive lag-1 autocorrelation values. An interaction was found between mean IRI and peak force (PF) magnitude, with greater force variability seen for the larger intervals. However, the imposition of dual force and timing constraints had no effect either on the underlying variability of the PF or on the IRIs. The results are discussed in the context of force and time being independently specified components of a generalized motor program.

Keywords Timing · Force production · Visual feedback · Repetitive movements

Introduction

A common observation in rhythmic finger tapping is that inter-response intervals (IRIs) vary—longer-than-average intervals typically alternate with intervals that are shorter-than-average and vice versa. The seminal work by Wing and Kristofferson (1973) explained the variability of rhythmic sequence timing using a two-level timing model. The model proposed the idea of an internal clock that provides a stochastic timekeeping signal specifying each internally formulated interval, which is prone to statistical variation. Before an observable movement can be recorded, however, the output of the clock is subject to delays in motor execution. Due to the theorized independence between clock and motor components, a series of consecutive IRIs shows variance that has been influenced by an additive effect of these two noise sources. The production of time intervals has long been studied through examination of serial rhythmic movement tasks across various subject populations, using an array of effectors and pacing conditions (see Wing 2002 for review). With the exception of a few studies, the timing of actions has been the primary focus of this research and there has been little investigation of the simultaneous production of force (Pope et al. 2005), although serial production of force has been studied to some extent (Wing et al. 2004). In this paper, we explore the question of whether such sequential dependencies might be seen in the repetitive production of pinch grip force.

A fundamental question we ask in this study is whether the control processes for force and time are autonomous or, conversely, if they are contingent upon one another. A prevailing view in the neuropsychological literature is that the control of timing is independent of force control. This view stems from evidence that participants consistently show diminished accuracy and greater variability in

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producing a series of peak forces (PFs), contrasting with the ease with which they are able to maintain relatively accurate series of IRIs (Pope et al. 2005; Sternad et al. 2000). Patient studies also support the argument that force and time are separately controlled entities in the brain. Pope et al. (2006) observed that the performance of patients with Parkinson's disease in a rhythmic force production task showed marked impairments in force production, but the ability to accurately produce IRIs remained relatively spared. Neuroimaging evidence from a similar experiment suggests a special role for the basal ganglia in force production (Pope et al. 2005). Patients with focal basal ganglia lesions seem to have minor problems with force control, but timing functions are intact (Aparicio et al. 2005). On the other hand, individuals with cerebellar disorders often exhibit impaired control in discrete timing tasks, but are spared in the ability to produce accurate force magnitudes (Schlerf et al. 2007; Spencer et al. 2003, 2007; Spencer and Ivry 2005).

The conjecture that time and force are independently controlled, however, is in strong contrast to the anecdotal observation that in order to execute any movement correctly the relative timing of force generation and relaxation must be appropriately scaled. Billon et al. (1996) examined participants performing one accentuated tap in a series of five taps. It was noted that the interval prior to the accentuated tap was consistently shortened, while the one following it was lengthened, suggesting that preparing for a specific impact force affects timing variability. Sternad et al. (2000) examined timing, force and concomitant force and time constraints on performance of a sequential finger tapping task. In conditions with the dual task constraints, the variability in the PFs increased for larger movement periods. Taken together, these results indicate that the presence of an explicit temporal goal can also influence force production and variability patterns.

While subjects are relatively good at producing target force levels with visual feedback (external specification of required force), there are some well-identified phenomena seen when visual feedback is removed. Recent studies have noted that isometric force output shows a sharp decay in the absence of feedback. This decay began between 620 ms (Vaillancourt and Russell 2002) and 1,600 ms (Davis 2007) after the withdrawal of feedback, indicating the presence of "memory" processes for the required force level. While the role of feedback withdrawal has been shown for both uni- and bimanual force production, the question of how repetitive sequential force production is affected when visual feedback of the target force level is removed has not been addressed. Here, we ask: what are the effects of timing and/or sequential constraints on force production in the presence and absence of visual feedback? How different is repetitive force production compared to isometric

production after withdrawal of visual feedback of the target force level?

The goals of the present study were twofold. First, we sought to determine whether repetitive, unimanual force production is different when the force target and timing sequence are internally or externally specified. Secondly, the aim was to further investigate whether the imposition of both force and timing constraints to the task produced systematic dependencies between these two movement facets. We predicted that the imposition of force constraints on rhythmic timing would not influence the underlying timing variability, i.e. the time series of IRIs would show the characteristic negative lag-1 autocorrelation as predicted by Wing–Kristofferson (WK) model. We also hypothesized that in the absence of visual feedback, force levels produced in adjacent timing intervals would alternate between large and small resulting in a negative lag-1 autocorrelation structure for the sequence of PFs. We predicted that removal of visual feedback of force output would result in an overall decline in mean force output, as seen in isometric force production tasks.

Methods

Participants

Ten participants (6 male, 4 female; mean age 24.5 years) volunteered for this experiment. All participants were students from McMaster University. Participants were right handed according to both self-report as well as the Edinburgh Handedness Inventory (Oldfield 1971). Participants were free of any known neurological impairment or musculoskeletal impairment to the upper extremities and had normal or corrected normal vision at collection. In keeping with the Declaration of Helsinki, prior to participation, volunteers gave their informed consent in accordance with McMaster Research Ethics Board regulations.

Apparatus

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 1,000 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 which indicates no significant drift or offset in the force data due to ongoing use of the apparatus.

Task

Subjects were seated in a comfortable non-rotating chair with their right forearm resting on a table. They were positioned so they could reach the force transducer without strain to the forearm and successfully perform a pinch grip (between the right thumb and index finger) motion on it. During the experiment, subjects were presented with a target force and asked to match a visually specified target force by pinching the force transducer between the right thumb and index finger. The target force was presented as a column in a bar graph on a 19 in. 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 of the subject. The force levels of the subject were indicated by changing amplitudes with each press on the load cell. The system gain was set so that 5 N of force produced by the subject corresponded to a 1 cm increase in amplitude. Subjects were instructed to match the second column level to meet the target force level by modulating the pinch grip force. The goal of the task was to consistently match force output to the target amplitude. Subjects were given up to five practice trials to familiarize themselves with the experimental apparatus. Two target forces were used in the experiment: 8 and 16 N. Each trial lasted 30 s. The movement rate was specified by a metronome (1 or 2 Hz), which corresponded to time intervals of 1,000 or 500 ms. In certain experimental conditions, subjects were instructed to continue the repetitive force production after either the visual feedback of the target force or the metronome (or both) was removed after the first 10 s of the trial. Thus, there were two timing conditions (synchronization and continuation) and two visual feedback conditions (feedback vs. no feedback). All the trials were presented in a randomized manner. There were six repetitions of each trial that yielded a total of 96 trials per subject.

Data analysis

Force data were stored for offline analysis on a customized PC workstation. A custom-written program in MATLAB™ extracted the PF for each pinch on the transducer as well as

the iteration and time at which they occurred in the continuous force–time series. The program was also used to quantify the IRIs: the time between the measured PF responses. Trial means were then computed from the series of PF and IRI values. Variability in performance was determined through calculation of standard deviation and coefficients of variation. As subjects were not informed of the experimental condition prior to the beginning of the trial, the first 2 s of data was not used in order to avoid contamination from transient behavior as subjects adjusted their performance to the visual display and metronome frequency. Only the continuation phase data from each trial were used for analysis. Means were calculated across six repetitions per condition as well as across participants. Autocorrelations at lag-1 for all trials were performed using methods specified in Wing (2002).

Statistical analysis

SPSS statistical software (SPSS 16.0, Chicago, IL) was used to conduct separate analysis of variance (ANOVA) with repeated measures for all dependent variables (2 metronome frequency conditions: 1, 2 Hz; 2 timing conditions: synchronization, continuation; 2 force target levels: 8, 16 N; 2 visual feedback conditions: full visual feedback, no visual feedback) to assess statistical differences between conditions.

Results

IRIs and their variability

A main effect of metronome frequency confirmed that participants successfully produced two different movement frequencies corresponding to the two frequency manipulations ($F(1, 9) = 3583, p < 0.001, \eta^2 = 0.10$). There was also a frequency \times timing interaction found for mean IRI ($F(1, 9) = 14.79, p < 0.01, \eta^2 = 0.62$). Mean IRI in continuation timing condition was shorter than that in synchronization timing (0.94 and 0.48 s in continuation vs. 0.99 and 0.5 s in synchronization), which indicates that participants had a tendency to increase their movement frequency in the absence of a pacing metronome.

The influence of force constraints was seen in the significant interactions obtained for mean IRI between visual feedback condition, timing condition and metronome frequency. Figure 1a illustrates the interaction found for mean IRI between visual feedback and timing conditions ($F(1, 9) = 10.22, p < 0.05, \eta^2 = 0.53$). Figure 1b shows the interaction found for mean IRI between visual feedback condition and metronome frequency ($F(1, 9) = 7.24, p < 0.05, \eta^2 = 0.45$). The aforementioned influences of timing condition and

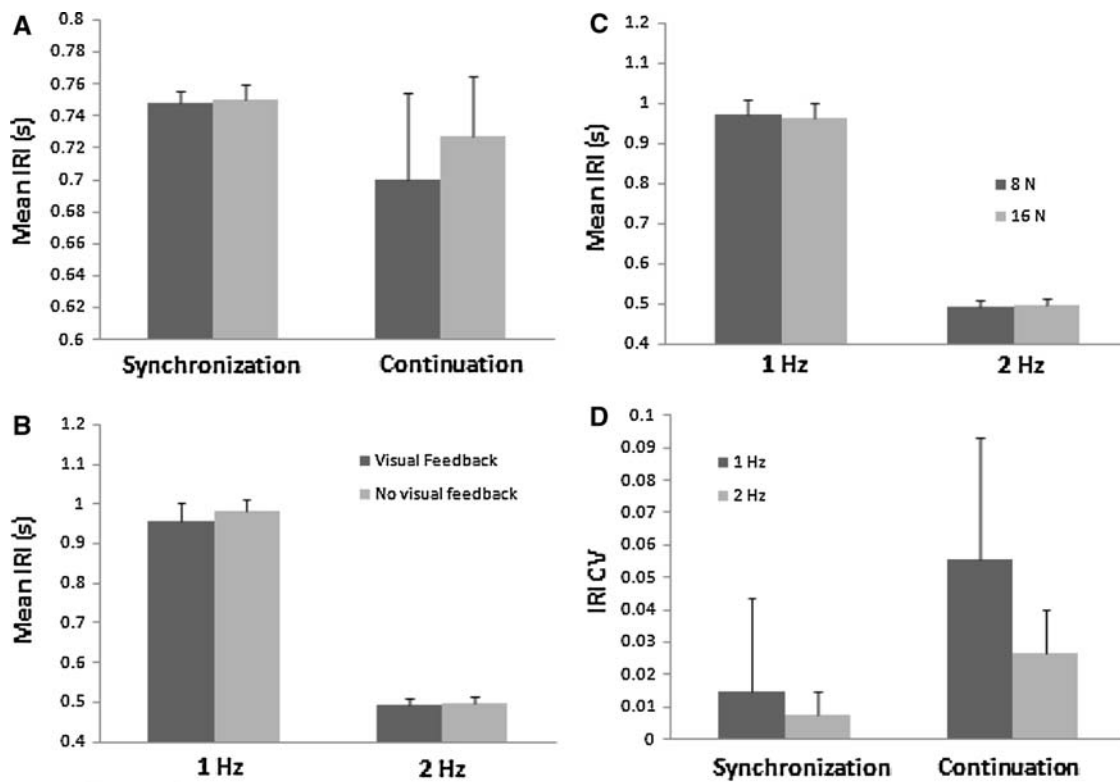


Fig. 1 **a** Mean IRIs for synchronization and continuation timing conditions are plotted for both visual feedback conditions. **b** Mean IRIs for both movement frequencies (1 and 2 Hz) for the two visual feedback conditions. IRI decreased with continuation timing as well as with the faster movement frequency. However, mean IRI increased in the absence of visual feedback of force output only in continuation timing and 1 Hz movement frequency conditions. **c** Mean IRIs for both

movement frequencies for the 8 and 12 N force targets. Timing ability was influenced idiosyncratically depending on force and movement frequency. **d** IRI CVs for synchronization and continuation timing conditions of the slow and fast movement frequencies. IRI variability was larger in the 1 Hz condition and increased for both movement frequencies in the continuation timing condition. In all plots, error bars stand for 1SD

metronome frequency were again reflected here. IRI decreased with continuation timing as well as with the faster movement frequency. However, mean IRI increased in the absence of visual feedback of force output in the continuation timing and 1 Hz movement frequency conditions. Further evidence for the influence of force constraints on timing ability is shown in Fig. 1c. A significant interaction was found for mean IRI between movement frequency and force target ($F(1, 9) = 5.79, p < 0.05, \eta^2 = 0.39$). Once again, the drop in mean IRI with the faster movement frequency reflected the difference between the two prescribed rates. However, it can be seen that timing ability was influenced idiosyncratically depending on force and movement frequency. In the 1 Hz condition, mean IRI was greater with the lower, 8 N, force target. Though in the 2 Hz condition, mean IRI increased with the larger, 16 N, force target.

Significant interactions were obtained for both IRI SD ($F(1, 9) = 56.48, p < 0.001, \eta^2 = 0.86$) and IRI CV ($F(1, 9) = 69.12, p < 0.001, \eta^2 = 0.89$; Fig. 1d) between movement frequency and timing condition. Across both factors, IRI variability was larger in the 1 Hz condition and increased

for both movement frequencies in the continuation timing condition. More importantly, we observed that timing variability was not dependent on either force target magnitude or visual feedback condition.

As another assessment of the variation in the IRI series, autocorrelations were performed at lag-1. A significant main effect of timing condition was observed ($F(1, 9) = 9.27, p < 0.05, \eta^2 = 0.51$). For both timing conditions, negative mean lag-1 r values were obtained. The mean lag-1 r for synchronization timing was very close to zero (-0.00029) indicating almost complete synchronization with the pacing metronome. The mean lag-1 r value for continuation timing was significantly more negative ($-0.07, p < 0.05$), falling between zero and negative one half (the boundaries specified by the WK model).

PFs and their variability

A main effect of force target indicated that participants successfully produced two different force levels corresponding to the 8 and 16 N force target conditions ($F(1, 9) = 810.37,$

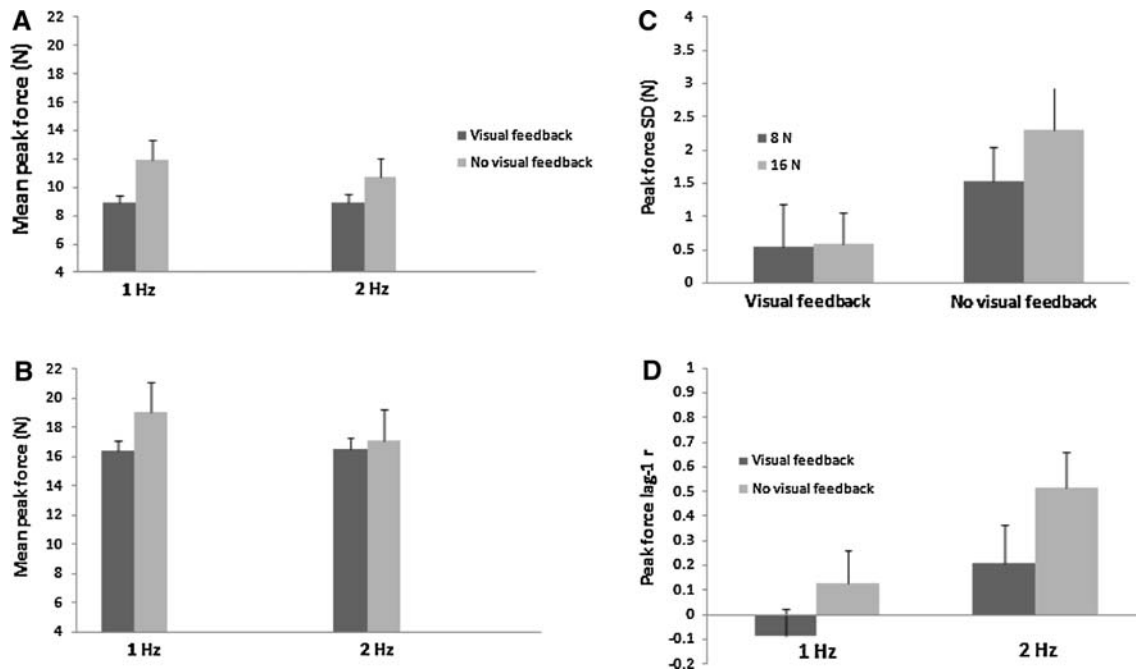


Fig. 2 Mean force output for the 8 N (a) and 16 N (b) target forces in the 1 and 2 Hz movement frequencies is plotted for both visual feedback conditions. For both force targets and movement frequencies, mean PF increased in the absence of visual feedback of force output. In the absence of visual feedback, however, mean PF decreased with the higher 2 Hz movement frequency. c PF SDs for both visual feedback conditions for the 8 and 16 N target forces. Irrespective of target force magnitude, PF variability increased in the absence of

$p < 0.001$, $\eta^2 = 0.99$). Mean PF was larger in the absence of visual feedback (8.93 and 16.47 N when feedback was present, 11.33 and 18.05 N when feedback was removed). A significant interaction was also obtained for mean PF between visual feedback condition and movement frequency ($F(1, 9) = 10.15$, $p < 0.05$, $\eta^2 = 0.53$; Fig. 2a, b). For both movement frequencies, mean PF increased in the absence of visual feedback of force output. In the absence of visual feedback, however, mean PF decreased with the higher 2 Hz movement frequency. Subjects did not report any differences in the level of difficulty with the manipulation of force or timing constraints.

Figure 2c illustrates the significant interaction observed for PF SD between force target and visual feedback condition ($F(1, 9) = 13.87$, $p < 0.01$, $\eta^2 = 0.61$). Inspections of Fig. 2c reveals that irrespective of target force magnitude, PF variability increased in the absence of visual feedback. Examination of PF CV revealed a main effect for visual feedback condition ($F(1, 9) = 70.42$, $p < 0.001$, $\eta^2 = 0.89$), showing an increasing CV in the absence of visual feedback. Unlike the SD results, however, no significant effects of target force magnitude were seen in the CV values.

Lastly, to examine the effects of simultaneous time interval constraints on the variability of the force production sequence, the PF series were analyzed using an

visual feedback. Without visual feedback, however, PF variability increased with target force magnitude. d Peak force lag-1 r values for both the 1 and 2 Hz movement frequencies are plotted for the two visual feedback conditions. For both movement frequencies, PF lag-1 r becomes more positive in the absence of visual feedback. For both visual feedback conditions, mean PF lag-1 r also becomes more positive for the faster movement frequency. In all plots, error bars stand for 1SD

autocorrelation at lag-1. Figure 2d illustrates the significant interaction for mean PF lag-1 r between visual feedback condition and movement frequency ($F(1, 9) = 5.14$, $p < 0.05$, $\eta^2 = 0.36$). For both movement frequencies, contrary to our predictions, PF lag-1 r becomes more positive in the absence of visual feedback, suggesting a systematic increase in force magnitude over the course of the trial once the visual feedback is removed, as illustrated in the sample time series in Fig. 3. For both visual feedback conditions, mean PF lag-1 r also becomes more positive for the faster, 2 Hz, movement frequency. Taken together, these results suggest that error accumulated to a greater extent in the absence of force feedback and as movement frequency increased.

Discussion

There were two principal objectives in conducting the present experiment. Firstly, we examined whether repetitive unimanual force production differed from isometric/brief impulse tasks when the force target and timing sequence were internally or externally specified. Secondly, we investigated whether the imposition of dual force and timing constraints to a rhythmic task produced

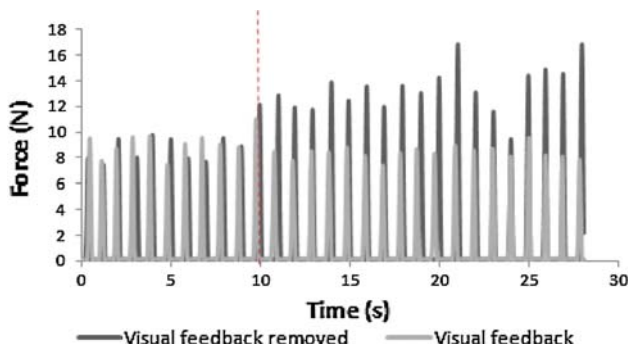


Fig. 3 Visualizing the data: Sample force time series from one participant from the 1 Hz continuation condition with a target force of 8 N. The vertical dotted line indicates the time at which visual feedback of force output and the pacing metronome were removed. Note the systematic increase in the peak force levels after the removal of visual feedback

any systematic dependencies between these two movement parameters.

Participants were highly successful in producing the two desired movement frequencies, although movement frequency increased in the absence of a pacing metronome. More importantly, interactions between force and timing were found in the mean IRI data. Intervals produced systematically increased in the absence of visual feedback. In previous work by Sternad et al. (2000), it was not until both force output and time interval constraints were simultaneously imposed in a task that a significant interaction was found between target period and target force. The interaction obtained for mean IRI between PF and movement frequency in the present study is in general agreement with the postulation by Sternad et al. (2000) that something unique occurs when both force and time constraints are present in a task, something which does not occur in the presence of only one.

Our data also revealed that variability was greater for the slower, 1 Hz, movement frequency. The autocorrelation at lag-1 revealed only a main effect for timing condition, with a negative lag-1 value for all continuation trials. This result is in broad agreement with several studies on continuation timing, such as those for finger, eye and speech movements (Wing 2002). It is important to note that we did not find any systematic dependencies between IRI variability on either the force target or feedback condition, which is also consistent with the results of Sternad et al. (2000). Given that we did not find any large differences in IRI variability as a function of the force and feedback manipulation, we did not partition the variance into clock and motor components. Taken together, these findings attest to the robustness of central timing mechanisms and suggest that the imposition of force constraints to a rhythmic task does not differentially affect timing variability.

As was the case for movement frequency, participants were found to be successful in producing the two target force magnitudes prescribed by the task. PF variability also increased with increasing PF magnitude fell in agreement with other work on sequential force production (Inui et al. 1998). Previous research on isometric force production has noted one consistent finding—without visual feedback, force output declines exponentially (Baweja et al. 2009; Davis 2007; Vaillancourt and Russell 2002). In the present experiment, we observed a systematic increase in force output in the absence of visual feedback. Our results show that when visual feedback is not present to regulate the force levels, the errors tend to be positive and accumulate in the course of the trial (as seen in Fig. 3).

There are important differences between continuous force production which is under the realm of intermittent control mechanisms (Slifkin et al. 2000) and the task presented here. Visual feedback stabilizes the intermittent fluctuations, but removal of this information results in a decline in mean force output, which has been attributed to a “memory” process (Davis 2007). The present results show that a different mechanism might be at work in repetitive force production akin to the force escalation effect reported by Shergill et al. (2003). When participants were asked to press on a force transducer in an attempt to reproduce a magnitude of force applied to them, Shergill and colleagues discovered that participants continuously underestimated their produced force levels, thus leading to an escalation effect. This was attributed to central predictive mechanisms involving reafference (Blakemore et al. 2000) that reduce the salience of self-generated forces by causing them to be perceived as weaker (in the absence of feedback from any other modality). The perception of self-generated forces is especially attenuated during self-generated movement. Our present results suggest that a similar mechanism might be involved when visual feedback is removed during repetitive force production. The force levels produced in the previous interval may be perceived to be weaker, resulting in an accrual of positive errors (more force) over the course of the trial. Perceptual judgment studies or a between-person force production tasks may be used to test this experimentally.

In order to discern the effects of the simultaneous force and time constraints on the correlational structure of the force production sequence, the PF series was analyzed using an autocorrelation at lag-1. The mean lag-1 r became more positive in the absence of visual feedback as well as with the shorter target period suggesting that in these conditions there was a greater accumulation of errors. These results suggest that the presence or absence of the visual target information may have a larger effect than the absence of a metronomic timing stimulus on the accumulation of errors in the force series.

As seen in the results of timing variability, no systematic relationships were found between PF variability and the timing goals of the task in contrast to those of Sternad et al. (2000), who reported increasing PF variability with longer IRIs when the dual task constraints were in place. However, in the study by Sternad et al. (2000), participants received continuous visual feedback of their force output relative to the prescribed target magnitude. Thus, a direct comparison of our results is not possible.

In summary, there were two main findings from this experiment. First, the nature of visual feedback in the regulation of force production is different for isometric and repetitive tasks. While withdrawal of visual feedback results in a decline of force output in isometric production tasks, in a sequential task the same condition results in a gradual increase in force output. This was seen in the positive lag-1 autocorrelation values seen in the force values suggesting an accumulation of positive error over the course of the trial. Secondly, while an interaction was found between mean interval and PF magnitude, no other relationships were found between target period and force in the task presently examined. More importantly, the imposition of force level constraints to the rhythmic timing task did not alter the underlying structure of timing variability. Taken together with the lack of interaction between variability in the forces produced and the temporal demands of the task, the results speak to the robustness of central timing processes and suggest that the imposition of dual force and time constraints did not differentially affect performance.

The idea of the independent modulation of force and time has been suggested in the concept of a Generalized Motor Program (Ivry 1986). The first level of this model involves program construction with separate subcomponents outlining force activation and deactivation as well as timing instructions. These components remain separate from one another until the second stage when the motor program is actually implemented. The lack of interaction seen between the force and time constraints on the variability of either is in general agreement with the idea that these two components of movement are specified separately in the motor program. This is not to say that they do not interact with each other at a lower level of movement organization. It is also not clear if the dependence between the two components might change as a function of movement rate. Further research might be needed to investigate the neurophysiological basis of this distinction, using patients with known deficits in either discrete timing tasks or force production. The positive lag-1 effect and the escalation in force levels in the absence of visual feedback also need considerable attention in future studies, especially in the context of long-term correlations in sequential data (Wing et al. 2004). The question of what the upper bound is for the

force escalation effect is also likely to be an important topic of research in the future.

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References

- Aparicio P, Diedrichsen J, Ivry RB (2005) Effects of focal basal ganglia lesions on timing and force control. *Brain Cogn* 58:62–74
- Baweja HS, Patel BK, Martinkewiz JD, Vu J, Christou EA (2009) Removal of visual feedback alters muscle activity and reduces force variability during constant isometric contractions. *Exp Brain Res* 197:35–47
- Billon M, Semjen A, Stelmach GE (1996) The timing effects of accent production in periodic finger-tapping sequences. *J Mot Behav* 28:198–210
- Blakemore SJ, Wolpert D, Frith C (2000) Why can't you tickle yourself. *NeuroReport* 11:11–16
- Davis N (2007) Memory and coordination in bimanual isometric finger force production. *Exp Brain Res* 182:137–142
- Inui N, Ichihara T, Minami T, Matsui A (1998) Interactions: timing and force control of finger tapping sequences. *Percept Mot Skills* 86:1395–1401
- Ivry RB (1986) Force and timing components of the motor program. *J Mot Behav* 18:449–474
- Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9:97–113
- Pope P, Wing A, Praamstra P, Miall C (2005) Force related activations in rhythmic sequence production. *NeuroImage* 27:909–918
- Pope P, Praamstra P, Wing A (2006) Force and time control in the production of rhythmic movement sequences in Parkinson's disease. *Eur J Neurosci* 23:1643–1650
- Schlerf JE, Spencer RMC, Zelaznik HN, Ivry RB (2007) Timing of rhythmic movements in patients with cerebellar degeneration. *Cerebellum* 6:221–231
- Shergill SS, Bays PM, Frith CD, Wolpert DM (2003) Two eyes for an eye: the neuroscience of force escalation. *Science* 301:187
- Slifkin A, Vaillancourt D, Newell K (2000) Intermittency in the control of continuous force production. *J Neurophysiol* 84:1708–1718
- Spencer RMC, Ivry RB (2005) Comparison of patients with Parkinson's disease or cerebellar lesions in the production of periodic movements involving event-based or emergent timing. *Brain Cogn* 58:84–93
- Spencer RMC, Zelaznik HN, Diedrichsen J, Ivry RB (2003) Disrupted timing of discontinuous movements by cerebellar lesions. *Science* 300:1437–1439
- Spencer RMC, Verstynen T, Brett M, Ivry R (2007) Cerebellar activation during discrete and not continuous timed movements. *NeuroImage* 36:378–387
- Sternad D, Dean WJ, Newell KM (2000) Force and timing variability in rhythmic unimanual tapping. *J Mot Behav* 32:249–267
- Vaillancourt D, Russell D (2002) Temporal capacity for short-term visuomotor memory in continuous force production. *Exp Brain Res* 145:275–285
- Wing AM (2002) Voluntary timing and brain function: an information processing approach. *Brain Cogn* 48:7–30
- Wing AM, Kristofferson AB (1973) Response delays and the timing of discrete motor responses. *Percept Psychophys* 14:5–12
- Wing AM, Daffertshofer A, Pressing J (2004) Multiple time scales in the serial production of force. *Hum Mov Sci* 23:569–590